

Benthic metabolism and sulfur cycling along an inundation gradient in a tidal *Spartina anglica* salt marsh

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Abstract

Central aspects of carbon and sulfur biogeochemistry were studied along a transect extending from an unvegetated mudflat into a *Spartina anglica* salt marsh. Conditions along the transect differed with respect to tidal elevation, sediment characteristics, vegetation coverage, and benthic macrofauna abundance. Dark sediment O₂ uptake and CO₂ emission at the highly bioturbated mudflat were low and relatively unaffected by tidal coverage. Sulfate reduction accounted for 30–60% of the daily CO₂ emission from the open mudflat sediment. Sediment O₂ uptake within the nonbioturbated and vegetated marsh was up to seven times higher during air exposure than during inundation, whereas the difference in CO₂ emissions always was less than a factor of 2. The contribution of sulfate reduction to CO₂ production was low (<21%) and decreased progressively with tidal elevation as a result of the oxidizing capacity of *S. anglica* roots in the vegetated marsh. The boundary between the mudflat and the retreating marsh is a unique environment. High near-surface pore-water concentrations of dissolved organic carbon (DOC) above the marsh cliff and highly elevated total carbon dioxide (TCO₂) pore-water concentrations at both sides of the cliff during air exposure coincided with extremely high TCO₂ emissions and apparent respiratory quotients (up to 14) only below the marsh cliff during inundation. We propose that substantial seepage of DOC-poor and HCO₃⁻-rich pore water may have occurred from the elevated marsh to the unvegetated sediment below during low tide followed by massive release of HCO₃⁻ during high tide. Accordingly, sulfate reduction accounted for more than the TCO₂ release above the marsh cliff, but only for about 40% below the cliff. Mineralization rates and pathways in salt-marsh sediments vary considerably on small spatial and temporal scales and are dependent on inundation frequency as well as the composition and distribution of flora and fauna.

Salt marshes form a transitional zone between the marine and terrestrial environment in sheltered and estuarine areas. They are defined by the presence of distinct vascular plant assemblages, commonly dominated by species of *Spartina*, with tolerance for periodic seawater inundation. Temperate salt marshes are among the most productive ecosystems in the world and are recognized for their important ecological function and societal values (Boorman 1999). They form a buffer zone that protects coastal areas from flooding during catastrophic storm events and act as a sink for both natural and anthropogenic nutrients and organic matter derived from both land and sea.

An understanding of microbial transfer between the organic and inorganic reservoirs is vital for determining the role of salt marshes for the dynamics of organic matter in estuaries and coastal waters. Most of the materials entering salt marshes are converted, assimilated, dissipated, and buried within the marsh system (Alongi 1998). As a consequence of efficient particle trapping, salt-marsh sediments

are usually comprised of organic-rich and relatively impermeable clay. O₂ rarely penetrates deeper than a few millimeters into the surface of these sediments (Holmer et al. 2002), and most organic matter mineralization must occur under anoxic conditions. The high abundance of sulfate in seawater has led to the conclusion that terminal microbial oxidation of organic matter in salt-marsh sediments is dominated by sulfate reduction (Hines et al. 1989; Howarth 1993). However, recent studies have suggested that microbial Fe(III) reduction may contribute significantly to carbon cycling in salt-marsh sediments affected by dense root masses and bioturbation (Lowe et al. 2000; Kostka et al. 2002; Gribsholt et al. 2003).

It has been documented that there is considerable temporal and spatial variability in the carbon (e.g., Smith et al. 1983; Howes et al. 1985) and sulfur (e.g., Howarth and Giblin 1983; King 1988) biogeochemistry of salt-marsh sediments. The ability of dense root and rhizome systems of marsh plants to translocate organic matter and oxidants into the sediment creates a dynamic subsurface redox biogeochemistry capable of generating steep chemical gradients and an associated diverse microflora (Hines et al. 1999). The biogeochemical conditions are even more complex when burrowing infauna form a mosaic of intermittently irrigated burrows intertwined between roots and rhizomes (Kostka et al. 2002; Gribsholt et al. 2003). Biogenic structures therefore appear to be a key factor for the temporal and spatial distribution and partitioning of electron acceptors (e.g., O₂, Fe(III), and SO₄²⁻) in the terminal oxidation of organic carbon.

Salt marshes are one of the most vulnerable ecosystems to the sea level rise caused by anthropogenic emissions of

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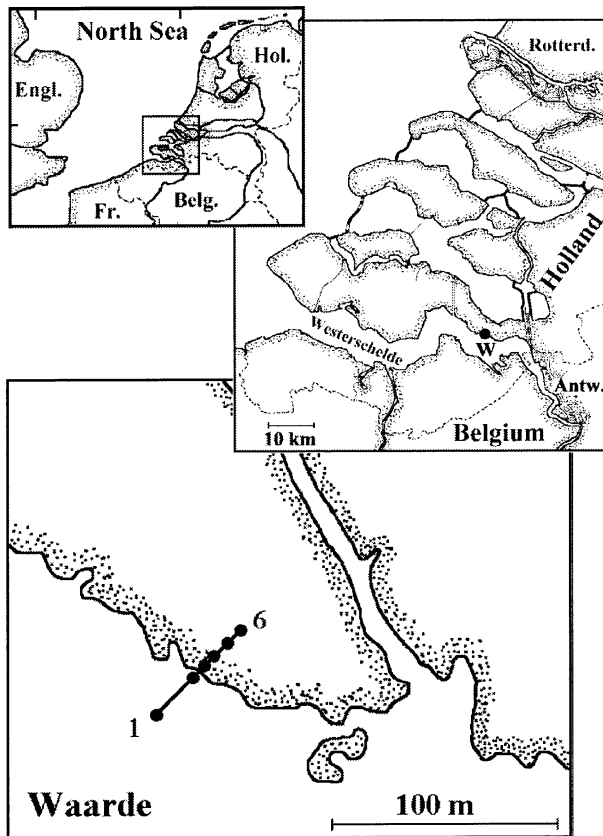


Fig. 1. Map of the Westerschelde Estuary with the Waarde salt marsh (W) ($51^{\circ}24'N$, $4^{\circ}07'E$) and sampling transect indicated.

greenhouse gasses (Boorman 1999). A rise in sea level without a concomitant augmented marsh accretion will increase the frequency and duration of tidal flooding in low marsh areas. The associated increased erosion of the outer marsh edge and deleterious effects on the marsh biota may cause a collapse in the essential functioning of salt marshes as a protective buffer zone between sea and land. Increased inundation may cause a decline in *Spartina* growth and an associated expansion of anoxic and sulfidic sediment, which in turn may lead to a further deterioration of the biological community. However, it is unknown how other physical and biological factors, such as hydrology, sediment transport, plant community structure, and bioturbation, may affect the above scenario.

Most published salt-marsh studies are from North America, and they have primarily focused on sediments vegetated by the short form versus the tall form of *Spartina alterniflora*. Much less is known of the carbon and sulfur dynamics associated with other marsh plant species (Hines et al. 1989), and the general tidal dependence of gas exchanges and redox-sensitive microbial processes in marsh sediments have not been fully elucidated. To our knowledge, no integrated studies of carbon and sulfur cycling have yet been conducted in Northern European salt marshes. The purpose of the present study was to evaluate changes in rates and pathways of carbon and sulfur biogeochemistry across the boundary between an unvegetated mudflat and a *Spartina anglica* salt

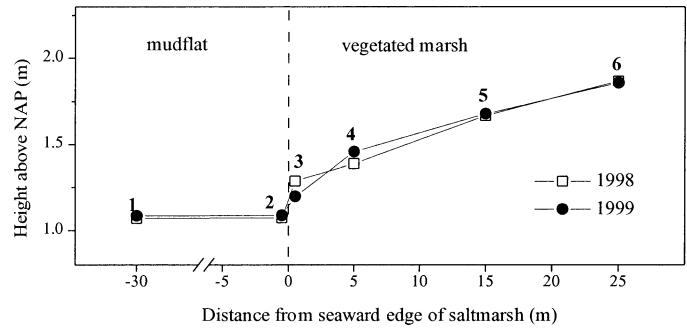


Fig. 2. Topography of transect in meters relative to NAP (Dutch Ordnance Level, corresponding approximately with mean sea level). Bold numbers are station numbers. Station 1 represents the open mudflat, Sta. 2 the mudflat next to the vegetated marsh boundary, and Sta. 3 the vegetated marsh boundary. Sta. 4, 5, and 6 are within the vegetated salt marsh.

marsh in the Westerschelde Estuary, The Netherlands. Total benthic metabolism was measured as sediment O_2 uptake and CO_2 release under inundated and air-exposed conditions, whereas quantification of sulfate reduction represented anaerobic organic matter degradation within the sediment. The obtained rates were related to the distribution of flora and fauna as well as carbon and sulfur chemistry in the sediment and are discussed in relation to possible effects of hydrology.

Methods

Study area—The sampling area was located in the tidally dominated Waarde salt marsh ($51^{\circ}24'N$, $4^{\circ}07'E$) in the Westerschelde Estuary, southwest Netherlands (Fig. 1). The brackish Waarde marsh is situated 35 km from the mouth of the estuary near the port of Antwerp. The vegetation in the low intertidal marsh is dominated by the halophyte *Spartina anglica*, while the high intertidal zones are dominated by less marine-adapted species (*Scirpus maritimus* and *Phragmites australis*). The marsh is covered by a semidiurnal tide with a range of 4 m and has an erosion cliff of 10–100 cm at the front of the marsh.

Six sampling stations were placed along a transect perpendicular to the coast (Fig. 1). Stations 1 and 2 were situated on the open mudflat 30 m outside the marsh edge and at the mudflat immediately outside the marsh boundary, respectively, whereas Sta. 3 was located on top of the marsh cliff immediately inside the vegetated marsh. Stations 4–6 were situated at 5, 15, and 25 m within the vegetated salt marsh, respectively. Profiles of the marsh surface elevation relative to NAP (Dutch Ordnance Level, corresponding approximately with mean sea level) of the transects are shown in Fig. 2. Sampling was carried out at low tide during two 10-d campaigns from 15 September to 24 September 1998 and from 25 August to 4 September 1999. As a result of the destructive nature of the sampling procedures, different transects stationed 50 m apart were sampled over the 2 yr. The temperature and salinity in the tidal water were $\sim 15^{\circ}C$ and ~ 20 ‰, respectively, during both campaigns.

Sediment sampling and handling—Intact sediment cores were taken by Plexiglas core tubes (8.0 cm in diameter). The core tubes were pushed into the sediment, sealed with rubber stoppers, and dug out of the sediment. Fifteen cores were collected at each station and sampling occasion for determination of fluxes, sulfate reduction rates, redox, pore-water solutes, sediment characteristics, root biomass, and macrofaunal biomass.

Cores for determination of sulfate reduction rates were transported to Denmark for processing within 24 h. Those used for determination of fluxes and redox were stored at in situ temperature (15°C) until further handling within 2–3 h. All other cores were sectioned into 1-cm intervals in the upper 4 cm and 2-cm intervals down to 18-cm depth immediately after return to the laboratory. From 4 cm downward, only every other section was used for analysis. Rooted sediment cores were cut in sections with a pair of scissors, and care was taken to avoid dragging roots and sediment from one section to another.

O₂ and CO₂ exchange—Total benthic metabolism was determined at 15°C as dark O₂ and CO₂ exchange across the sediment–water interface of inundated sediment cores (w+) and across the sediment–air interface of air-exposed sediment (w–), as described in Gribsholt and Kristensen (2002b). Inundated flux determinations were done as 4-h closed-core incubations. The air-exposed cores were gently supplied with a 6–10 cm continuously stirred water column about 1 h prior to flux measurements, using seawater collected from the Westerschelde Estuary the same day. Start and end samples for O₂ were analyzed according to the standard Winkler technique (Parson et al. 1984), and samples for total carbon dioxide (TCO₂) were analyzed within 24 h using the flow injection/diffusion cell technique of Hall and Aller (1992). Air-exposed flux measurements were conducted on the same cores and were initiated about 0.5 h after careful removal of the overlying water. O₂ consumption was calculated using the concentration change determined with a polarographic O₂ electrode (Radiometer) in a 1–2-cm closed air space (50–100 ml) after a 5–10-h incubation period. CO₂ production was calculated as the steady-state concentration difference between excurrent gas and atmospheric air determined in a flow-through system maintained for 5–10 h. Moistened atmospheric air was pulled into the headspace at a constant rate, and the exiting gas passed through was monitored by a Li-COR infrared gas analyzer (model LI-6251). As both inundated and air-exposed incubations were conducted over time spans equivalent to an average flood and ebb period, the obtained fluxes are representative of the mean gas exchange over the entire duration of each of the two tidal phases. Any change in fluxes that may have occurred during each tidal phase is therefore included in the reported mean rates.

Sulfate reduction assay—Sulfate reduction rates (SRRs) were determined by the core-injection technique (Jørgensen 1978). All sediment cores (8 cm in diameter) used for the sulfate reduction assay were stored at 15°C for about 24 h before being subsampled with smaller core tubes (2.6 cm in diameter) equipped with a sharpened cutting adapter at the

lower end. Subsampling was done carefully and with simultaneous cutting of any roots and rhizomes to avoid compaction. The 24-h time lag between sampling and incubation has proven to be optimal for SRR determinations in salt-marsh sediments, as labile DOC leaching from roots and animals damaged during coring, causing temporary enhancement of SRR, is exhausted within 24 h (Gribsholt and Kristensen 2002a). Subsequently, volumes of 2 μl radiolabeled sulfate (³⁵S-SO₄²⁻) (70 kBq) were injected through silicone ports positioned at 1-cm intervals along the depth axis of the core tubes. The cores were incubated in the dark for 1 h at 15°C. Incubation time was kept short to avoid reoxidation of sulfides and hence an underestimation of sulfate reduction rates (Fossing 1995), but the incubation time was sufficiently long to obtain reliable sulfate reduction data. The incubations were terminated and sulfide preserved by slicing 1- or 2-cm sediment sections directly into 50-ml plastic centrifuge tubes containing 5 or 10 ml of 20% (w/w) zinc acetate solution. Tubes were then capped, vigorously shaken, and stored frozen until analysis.

Sulfide was extracted from the sediment by the two-step distillation procedure of Fossing and Jørgensen (1989). Approximately 2 g of homogenized and centrifuged sediment (10 min, 3,000 × g) was distilled at room temperature with 8 ml of 12 mol L⁻¹ HCl for 30 min to release acid-volatile sulfide (AVS) as H₂S, which was trapped as ZnS in 10 ml of 5% zinc acetate. The chromium reducible sulfur (CRS) was obtained by reduction with 16 ml of 1 mol L⁻¹ Cr²⁺ in 0.5 mol L⁻¹ HCl followed by boiling and distillation for 30 min into separate zinc acetate (10 ml of 5%) traps. Radioactivity was counted on subsamples from supernatant (³⁵S-SO₄²⁻) and traps (³⁵S-ΣH₂S) with Ultima Gold scintillation cocktail in a Packard TriCarb 2000 scintillation counter. The total sulfate reduction rate (SRR_t) was calculated as the sum of the AVS (SRR_{avs}) and CRS (SRR_{crs}) fractions. Total reduced inorganic sulfur pools (TRS_{avs} and TRS_{crs}) in the traps were analyzed spectrophotometrically according to Cline (1969).

Redox profiles—Vertical profiles of redox (E_h) were determined in duplicate on separate air-exposed cores with a platinum electrode connected to a standard calomel reference electrode. Measurements were performed in steps of 0.5 cm (0–2-cm depth), 1 cm (2–7-cm depth), and 2 cm (7–19-cm depth). The E_h signal was allowed to stabilize for 2 min at each depth before the reading was noted. This parameter was only determined during the 1998 campaign.

Sediment and pore-water analysis—Sediment density was obtained from wet weight of a known sediment volume. Porosity was calculated from water loss of a known sediment volume after drying at 105°C for 6 h. Organic content was measured as loss-on-ignition (LOI) at 520°C for 6 h and as particulate organic carbon (POC) and nitrogen (PON), determined with a Carlo Erba Elemental Analyzer EA 1100A after the method of Kristensen and Andersen (1987).

Pore water was extracted by centrifugation (10 min, 3,000 × g) of 1- to 2-cm sediment sections in double centrifuge tubes equipped with precombusted Whatman GF/F filters for analysis of SO₄²⁻, Cl⁻, H₂S, TCO₂, and DOC. Visible roots

Table 1. Below ground biomass in 1998 and 1999 and above ground standing biomass (mean \pm SD) along the Waarde transect in 1998. The distance is given in meters from the seaward edge of the saltmarsh. The below ground biomass is the depth integrated root biomass in the upper 18 cm of the sediment. Values in brackets are percent living above ground biomass ($n = 3$).

Station	Distance (m)	Below ground biomass		Above ground biomass 1998		<i>Spartina anglica</i> 1998		
		1998	1999	Total	Living	% of living biomass	Shoot density	Shoot weight
		(kg dw m ⁻²)	(kg dw m ⁻²)	(kg dw m ⁻²)	(kg dw m ⁻²)	(%)	(m ⁻²)	(g)
1	-30	0	0	0	0	—	—	—
2	-0.5	4.6 \pm 2.0	1.1 \pm 0.1	0	0	—	—	—
3	0.5	6.7 \pm 0.9	3.4 \pm 0.4	1.11 \pm 0.05	0.78 \pm 0.07 (70)	91 \pm 16	1927 \pm 479	0.4 \pm 0.1
4	5	6.6 \pm 1.3	3.5 \pm 0.4	0.99 \pm 0.02	0.52 \pm 0.06 (52)	95 \pm 6	613 \pm 309	0.9 \pm 0.4
5	15	5.5 \pm 1.0	3.5 \pm 0.4	1.52 \pm 0.14	0.89 \pm 0.31 (57)	86 \pm 10	747 \pm 145	1.0 \pm 0.0
6	25	4.3 \pm 0.4	5.5 \pm 1.1	1.33 \pm 0.24	0.93 \pm 0.28 (69)	65 \pm 20	610 \pm 52	0.9 \pm 0.1

and rhizomes were removed from the sediment prior to centrifugation. Analysis for SO_4^{2-} and Cl^- were performed on acidified ($\text{pH} < 3$) samples by ion chromatography with a Dionex autosuppressed anion system (IonPac AS4A-SC column and ASRS suppressor). Samples for dissolved sulfide H_2S were fixed in 20% ZnAc and analyzed as described above. TCO_2 was analyzed within 24 h as described above. Dissolved organic carbon (DOC) was measured with high-temperature catalytic combustion on a Shimadzu TCO-5000 Total Organic Carbon Analyzer after acidification with 2 mol L^{-1} HCl ($\text{pH} < 3$) to remove dissolved inorganic carbon.

Flora and fauna—Above-ground plant density and biomass were determined in 1998 only by harvesting all standing plant material (stems and leaves) within three randomly chosen 0.1-m² plots at each station. The plant material was divided into live (green color) and dead (yellowish or brownish coloration). The live material was separated into species, counted, and dried separately. Root biomass was determined by washing sediment on a 1-mm mesh. The below-ground component was not divided into roots and rhizomes, and no distinction was made between live and dead material. Dry weight (DW) was determined by drying at 65°C for 24 h.

Benthic macrofaunal density and species composition was determined by sieving sediment samples through a 1-mm mesh. All visible fauna were collected and preserved in 4% formalin for 1–2 weeks and were subsequently stored in 70% alcohol. Animals were identified to the species level under a dissecting microscope, and the individual length and DW were determined for *Nereis diversicolor* and *Macoma balthica*, whereas only the average weight of *Corophium volutator* and the total weight of tubificid oligochaetes were recorded. All other fauna were noted only for their presence.

Results

Flora and fauna—The vegetation in the low marsh zone (Sta. 3 and 4) was dominated by the halophyte *S. anglica* (91–95% of the total biomass) (Table 1), but species diversity increased with tidal elevation. In addition to *S. anglica*, the flora at Sta. 5 and 6 contained a large fraction of *Aster tripolium*, *Triglochin maritime*, and various grasses. Thus, at Sta. 6 these three groups accounted for 23%, 1%, and 11%

of the living biomass, respectively. The biomass of individual *S. anglica* shoots near the seaward edge was only 40% of that noted in the higher marsh zones, but the density was 2.5 times higher. In 1998 the total above-ground biomass generally increased with elevation, whereas the below-ground biomass decreased. The below-ground biomass remained constant with elevation in 1999, until a large increase was observed at Sta. 6. At the edge of the marsh, the below-ground biomass (1998) was six times larger than the biomass of the total standing canopy, but this difference decreased with elevation to a factor 3 at Sta. 6. The below-ground biomass was significantly higher in 1998 than 1999, except at the highest elevation (Sta. 6). There was a large quantity of dead roots and rhizomes at the unvegetated Sta. 2 below the marsh cliff, indicating that the marsh is on retreat.

The mudflat macrofauna was dominated by the polychaete *Nereis diversicolor*, the bivalve *Macoma balthica*, and the amphipod *Corophium volutator*. These species were found in high densities at Sta. 1 and 2 (Table 2). Recovered tubificid oligochaetes contributed significantly to the total biomass, but since these animals tended to pass through the mesh during sieving, the biomass of this group is probably underestimated. The highest faunal numbers and biomass were generally found at the open mudflat (Sta. 1), whereas benthic infauna was very scarce within the vegetated salt marsh. Only a few specimens of *N. diversicolor* and *C. volutator* were observed at Sta. 3, 4, and 5, and no benthic macrofauna was observed at Sta. 6.

Sediment characteristics and redox—Sediment properties varied between stations and from year to year (Table 3). The porosity, organic matter content (LOI), and depth-integrated POC and PON, which generally decreased with depth in the sediment (data not shown), were high in the vegetated marsh compared to the unvegetated mudflat. POC and PON at Sta. 5 were 76% and 245% higher than that at the other vegetated stations in 1999. The molar C:N ratio, on the other hand, generally decreased with distance from the marsh edge. The organic matter content was higher (15–185%) at all depths investigated in 1999 compared to the previous year. The same pattern was evident for depth-integrated POC (2–134%), whereas the PON data was less consistent. Accordingly, the C:N ratio was highest in 1999, especially at the

Table 2. Mean (\pm SD) biomass and density of the most dominant macrofauna in 1998 and 1999 at the open mudflat (Sta. 1) and in the mudflat immediately outside the marsh boundary (Sta. 2) ($n = 3$).

Species	Station	Biomass (g m ⁻²)		Density (m ⁻²)	
		1998	1999	1998	1999
<i>N. diversicolor</i>	1	1.6 \pm 0.4	11.7 \pm 5.6	568 \pm 260	5267 \pm 2003
	2	7.2 \pm 3.8	4.0 \pm 0.5	1326 \pm 399	867 \pm 306
<i>M. baltica</i>	1	2.0 \pm 0.3	6.8 \pm 2.2	1117 \pm 256	2067 \pm 945
	2	5.8 \pm 7.3	0	360 \pm 87	0
<i>C. volutator</i>	1	2.7 \pm 1.1	4.1 \pm 0.6	11098 \pm 3959	20800 \pm 1600
	2	0.2 \pm 0.2	0.1 \pm 0.1	492 \pm 370	333 \pm 306
Oligochaetes	1	8.8 \pm 1.7	28.8 \pm 2.9	—	—
	2	1.7 \pm 1.1	0.1 \pm 0.2	—	—

open mudflat. Redox measurements indicated that the sediments were more reduced in the low intertidal zone than higher in the salt marsh (Fig. 3). In particular, the area around the marsh edge at Sta. 2 and 3 showed a clear redox discontinuity and negative subsurface redox values, but just 5 m further into the vegetation (Sta. 4), the deeper sediment (>4 cm) was distinctly more oxidized.

O₂ and CO₂ exchange—Sediment O₂ uptake at the open mudflat (Sta. 1) was slightly higher (1.1–1.9 times) during inundated (w+) (34–54 mmol m⁻² d⁻¹) than during air-exposed (w-) (29–30 mmol m⁻² d⁻¹) conditions (Fig. 4a). The rates increased 44–72% below the marsh cliff (Sta. 2), except during inundation in 1999, where rates were 50% lower than at the open mudflat. Within the vegetated marsh the O₂ uptake was slightly lower (1–40%) than on the open mudflat during inundation (24–34 mmol m⁻² d⁻¹), whereas it was three to seven times higher during air exposure (93–218 mmol m⁻² d⁻¹) and decreasing with tidal elevation along the transect.

CO₂ release by the sediment at the open mudflat was 2.5 times higher during inundation (85 mmol m⁻² d⁻¹) than during air exposure (34 mmol m⁻² d⁻¹) in 1999 (Fig. 4b). Below the marsh cliff (Sta. 2), the CO₂ release increased dramatically (up to 824 mmol m⁻² d⁻¹), compared to the open mudflat. The inundated CO₂ release was 15 and 4 times higher in 1998 and 1999, respectively, whereas rates were up to three times higher (1999) during air exposure. Within the vegetated marsh, on the other hand, the CO₂ release was generally highest (0.9–2.3 times) during air exposure (158–247 mmol m⁻² d⁻¹), compared to inundated conditions (109–172 mmol m⁻² d⁻¹). Rates were here up to two times higher during inundation than at the open mudflat, whereas the rate was five to seven times higher during air exposure.

The community respiratory quotient (RQ = CO₂ production/O₂ uptake) was 1.6 and 1.1 at the mudflat when the sediment was inundated and air exposed, respectively (Fig. 4c). RQ was twice as high below the marsh cliff (Sta. 2) during air exposure, and because of the excessive CO₂ release, it was extremely high (14.1 and 11.3) during inundation. RQ increased from 0.9 to 2.0 with elevation in the vegetated marsh during air exposure and varied between 2 and 6 during inundation. The respiratory quotient was al-

ways higher (1.5–6.4 times) during inundation than during air exposure.

Sulfate reduction rates and total reduced sulfur pools—Volume-specific sulfate reduction (SRR_v) varied by more than two orders of magnitude at the six stations (Fig. 5). Rates were low (8–120 nmol cm⁻³ d⁻¹) on the open mudflat, intermediate just below the cliff (45–540 nmol cm⁻³ d⁻¹), and highest (up to 1,590 nmol cm⁻³ d⁻¹) at the marsh edge. Rates in the vegetated marsh were generally high, but variable with subsurface maxima, except at the highest station, where low rates comparable to those at the mudflat predominated. The 0–18-cm depth-integrated sulfate reduction was 13–16 times higher (106–167 mmol m⁻² d⁻¹) just above the marsh edge than at the open mudflat (7–12 mmol m⁻² d⁻¹) and the high marsh site (10–19 mmol m⁻² d⁻¹) (Fig. 6a).

The depth distribution of total reduced sulfur (TRS) varied considerably between stations (Figs. 6b, 7). The three metabolically active stations nearest to the marsh edge were richer in TRS (>160 μ mol cm⁻³) than the open mudflat and high marsh stations (< 40 μ mol cm⁻³). The linkage between TRS and SRR was evident as a significant correlation between depth-integrated values along the transect: ITRS = 0.071 ISRR + 2.88, $r^2 = 0.37$, $P < 0.05$. The AVS fraction of TRS was positively related with ITRS (%AVS = 1.32 ITRS + 6.92, $r^2 = 0.59$, $P < 0.01$) and ISRR (%AVS = 0.15 ISRR + 7.61, $r^2 = 0.53$, $P < 0.01$) and accounted for less than 10% of TRS at the open mudflat and up to 30% at the marsh boundary, but decreased with elevation to <10% at the highest station (Fig. 6c).

The 0–18-cm depth-integrated turnover time ($T_{ii} = \text{ITRS}/\text{ISRR}$) of reduced sulfur compounds in late summer was 2–13 times faster within the vegetated marsh than on the open mudflat (Fig. 6d). The volume-specific turnover time ($T_{iv} = \text{TRS}/\text{SRR}$) was generally slow in surface layers and increased with depth in the top 3–6 cm, below which it was constant (data not shown). The slow estimated T_{ii} at the open mudflat is emphasized by an extremely slow T_{iv} in the top 3 cm of the sediment (9–13 yr). At Sta. 2, on the other hand, the slowest T_{iv} was observed in the 4–10-cm depth interval. SRR pools, TRS pools, and T_i values were generally higher in 1998 than in 1999 throughout the transect.

Table 3. Sediment characteristics along the Waarde transect in 1998 and 1999. Values of porosity and organic content (LOI) are presented as the range over the 0–18 cm depth interval. Values for particulate organic carbon (POC), particulate organic nitrogen (PON) and C:N ratio of the organic matter are depth integrated values (0–18 cm).

Station	Distance (m)	Porosity (vol/vol)		LOI (%)		POC (mmol cm ⁻²)		PON (mmol cm ⁻²)		C:N (mol:mol)	
		1998	1999	1998	1999	1998	1999	1998	1999	1998	1999
1	-30	0.22–0.50	0.36–0.56	1.4–3.2	1.4–5.5	5.9	6.4	0.4	0.2	14.5	27.2
2	-0.5	0.41–0.52	0.42–0.55	1.3–3.2	2.4–5.5	6.3	11.4	0.3	0.4	21.0	26.1
3	0.5	0.50–0.51	0.51–0.59	3.3–6.0	4.0–7.9	22.7	23.2	1.4	0.9	16.5	25.3
4	5	0.41–0.56	0.56–0.66	2.4–5.5	4.8–11.3	17.2	29.4	1.0	1.6	17.8	17.9
5	15	0.41–0.68	0.55–0.76	1.3–5.2	5.7–14.1	22.1	51.7	1.5	3.1	14.5	16.7
6	25	0.35–0.63	0.45–0.68	0.9–7.7	3.5–9.9	13.3	22.1	1.0	1.4	13.8	15.4

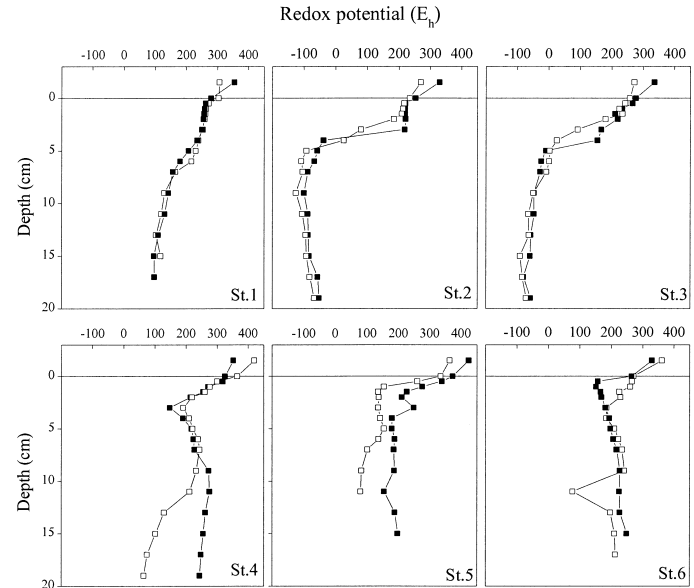


Fig. 3. Depth redox profiles (E_h) in the top 18 cm of sediment along the Waarde transect in 1998. Two replicate profiles are shown for each station.

Pore-water chemistry—Pore-water SO_4^{2-} varied considerably between years, particularly in the upper 10 cm. Concentrations were generally highest in 1999 (Fig. 8). Cl^- concentrations increased with depth at all stations but behaved similarly to SO_4^{2-} in both years, as indicated by the similarity in the $\text{SO}_4^{2-}:\text{Cl}^-$ ratio (Fig. 8) between years. The $\text{SO}_4^{2-}:\text{Cl}^-$ ratio was relatively constant ($\sim 5\text{--}6 \times 10^{-2}$) with depth within the marsh and at the open mudflat but decreased with depth to 3×10^{-2} in the top 6 cm around the marsh edge, indicating SO_4^{2-} depletion. In accordance with the redox profiles, dissolved sulfide (H_2S) was only detected around the marsh edge, where levels of $20\text{--}30 \mu\text{mol L}^{-1}$ were reached below 2- and 4-cm depth at Sta. 2 and 3, respectively (data not shown). The concentration of H_2S was four times higher in 1999 than in 1998.

Pore-water DOC was low ($<2 \text{ mmol L}^{-1}$) at all depths at the mudflat but increased in the vegetated marsh (Fig. 9), with subsurface maxima of up to 20 mmol L^{-1} within the top 5 cm. The depth-integrated DOC concentrations were up to 12.3 and 5.4 times higher in the vegetated marsh compared with the mudflat in 1998 and 1999, respectively (Fig. 10). However, the DOC concentrations within the vegetation may be overestimated, because roots and rhizomes were not completely removed from the sediment prior to centrifugation, resulting in leaching of DOC. Thus, DOC concentrations in pore water obtained from the low Waarde marsh using the method applied here may be up to seven times higher than in pore water sampled nondestructively with sippers (Gribsholt and Kristensen 2002a). The 0–18-cm depth-integrated DOC pool (IDOC) showed a significant positive relationship with the depth-integrated root biomass (IRoot) ($\text{IDOC} = 0.11 \text{ IRoot} + 0.11$, $r^2 = 0.58$, $P < 0.01$). However, the spatial distribution obtained for DOC may reflect the true pattern, since depth-integrated DOC concentrations within the vegetated marsh also correlated significantly with the

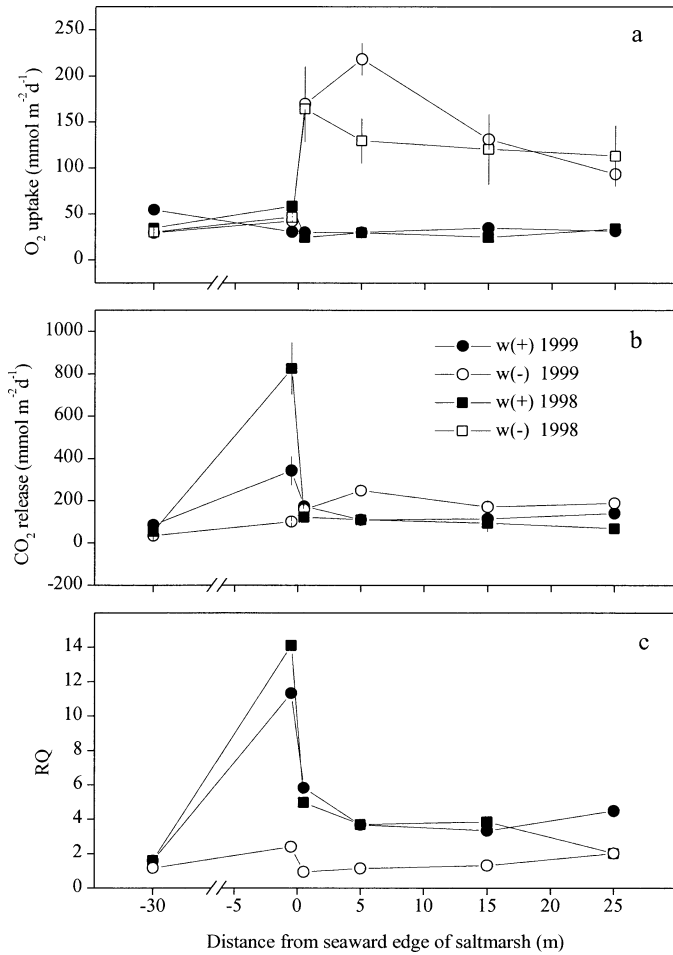


Fig. 4. (a) O₂ uptake, (b) CO₂ emission, and (c) respiratory quotient (RQ) in water covered (w+) and air-exposed (w-) sediment along the Waarde transect in 1998 and 1999 (mean ± SD; n = 3).

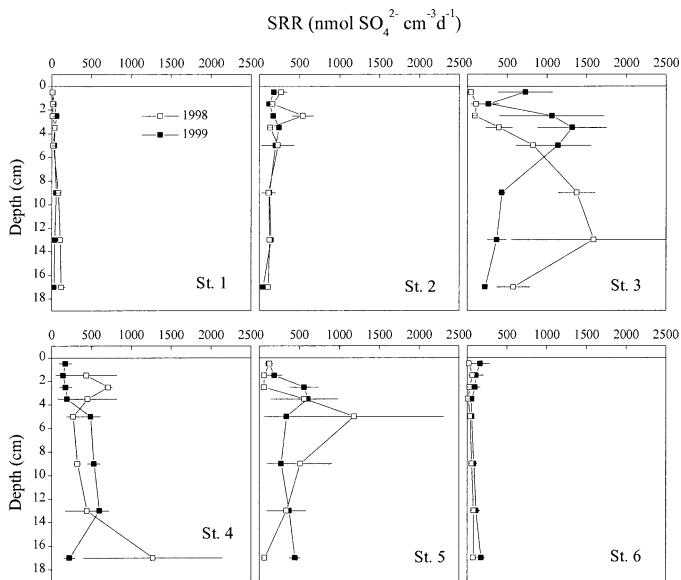


Fig. 5. Vertical distribution of sulfate reduction rates (SRR) at the six stations along the Waarde transect in 1998 and 1999 (mean ± SD; n = 3).

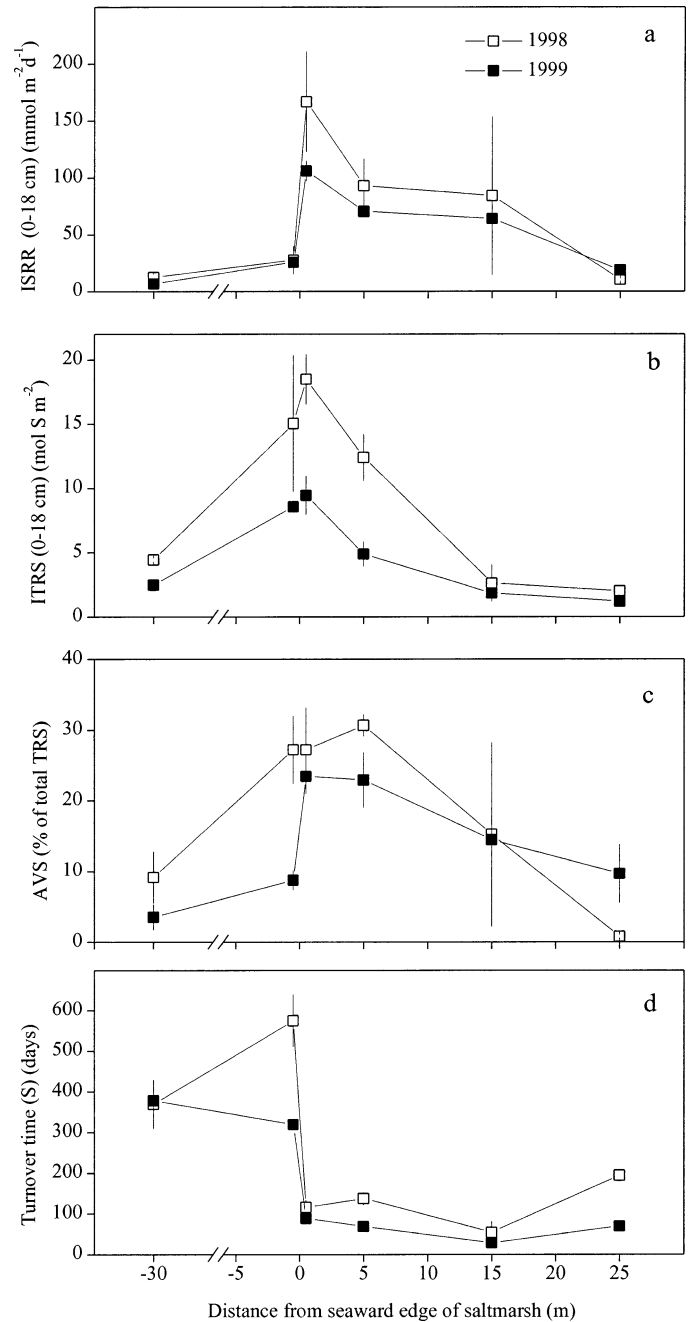


Fig. 6. (a) Depth-integrated (0–18-cm) sulfate reduction rate (ISRR), (b) depth-integrated (0–18-cm) total reducible inorganic sulfur pools (ITRS), (c) acid volatile sulfur (AVS) as % of the total pool of reduced inorganic sulfur (TRS), and (d) depth-averaged turnover time of S along the Waarde transect estimated in late summer 1998 and 1999 (mean ± SD; n = 3).

depth-integrated SRR (ISRR = 163.3 IDOC - 39.1, $r^2 = 0.53$, $P < 0.01$).

Pore-water TCO₂ generally increased with depth at all stations (Fig. 9). The highest concentrations were observed around the marsh cliff (Sta. 2 and 3), where TCO₂ increased from 7 mmol L⁻¹ in the surface layer to 28–30 mmol L⁻¹ at 8–10-cm depth. The 0–18-cm depth-integrated TCO₂ pool

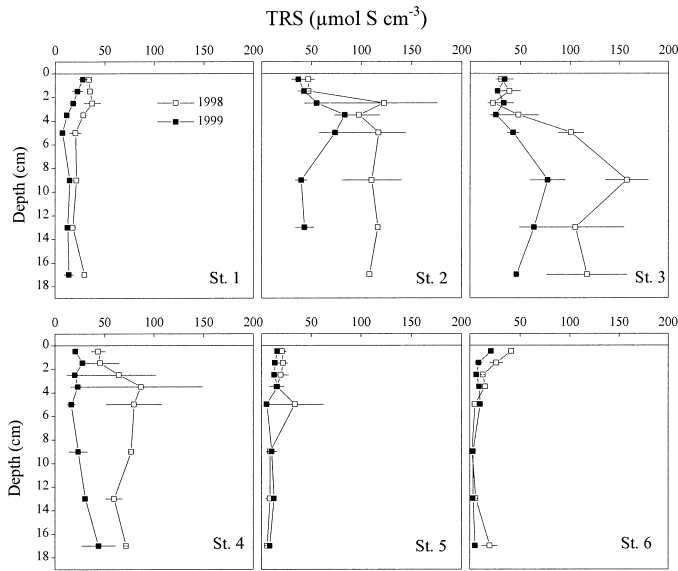


Fig. 7. Vertical distribution of total reducible inorganic sulfur pools (TRS) at the six stations along the Waarde transect in 1998 and 1999 (mean ± SD; n = 3).

was 6.0 and 7.5 times higher below and above the marsh edge, respectively, than at the open mudflat (Fig. 10). The TCO₂ level in the vegetated marsh remained high (10–20 mmol L⁻¹) but decreased gradually with distance from the edge.

Discussion

Distribution of flora and fauna—The Waarde salt marsh is retreating, as indicated by a seaward erosion cliff and the presence of old degrading root material below the cliff (Fig.

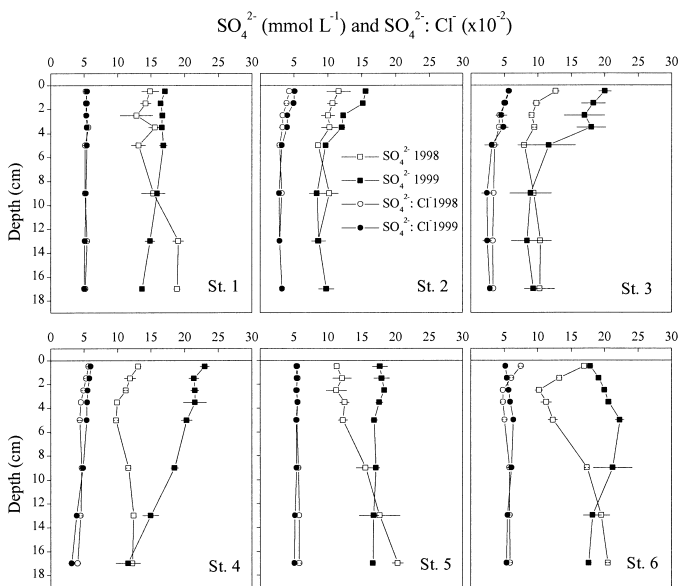


Fig. 8. Vertical distribution of SO₄²⁻ and SO₄²⁻:Cl⁻ ratios (× 10⁻²) at the six stations along the Waarde transect in 1998 and 1999 (mean ± SD; n = 3).

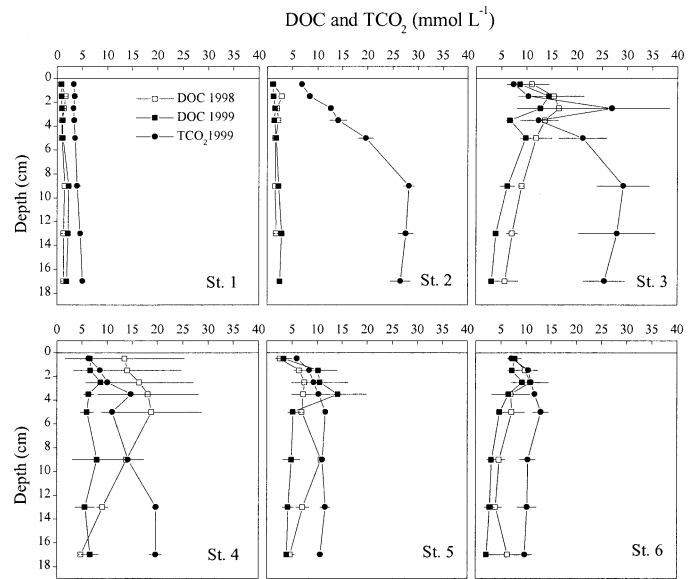


Fig. 9. Vertical profiles of dissolved organic carbon (DOC) and total carbon dioxide (TCO₂) at the six stations along the Waarde transect (mean ± SD; n = 3).

2, Table 1). However, markers placed at the marsh edge did not show any noticeable retreat of the marsh during our 1-yr study period. There is no pioneering zone and the vegetation in the lower marsh is formed almost exclusively by monospecific stands of *S. anglica*, which is typical of low intertidal and clay-rich marshes in northwestern Europe. Above- and below-ground biomass is similar to those observed for other Dutch and Danish *S. anglica* salt marshes (Hemminga et al. 1996; Morris and Jensen 1998; Gribsholt 2001). The decreasing root:shoot ratios with tidal elevation indicate that plants translocate more energy into root production under waterlogged and thus unfavorable sediment conditions.

The marine macrofauna at Waarde is typical of European *Spartina* salt marshes with dominance of small infaunal deposit feeders (the polychaete *Nereis diversicolor*, the amphipod *Corophium volutator*, and tubificid oligochaetes) and surface deposit-feeding gastropods (*Hydrobia ulvae*), as opposed to most North American salt marshes, where fiddler

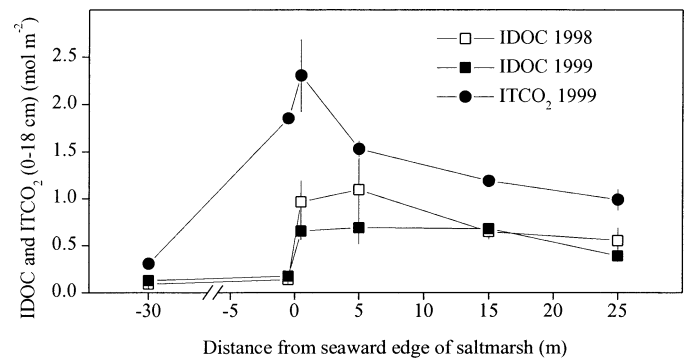


Fig. 10. Depth-integrated (0–18-cm) dissolved organic carbon (IDOC) and total carbon dioxide (ITCO₂) pools along the Waarde transect (mean ± SD; n = 3).

crabs dominate completely. Unfortunately, detailed surveys of the marine invertebrate fauna of European salt marshes are few (Jackson et al. 1985; Frid and James 1989; Mason et al. 1991) and concentrate on mudflat, creek bank, and marsh pool environments. The species composition generally differs between vegetated and mudflat habitats (Jackson et al. 1985), with species diversity significantly lower in vegetated than unvegetated marsh areas and adjacent mudflats (Frid and James 1989). A profound and almost complete absence of burrowing infauna in densely vegetated marsh areas, as found at the Waarde marsh, has not been reported previously in Europe. However, Gribsholt and Kristensen (2002b) observed a similar antagonistic effect of *S. anglica* on *N. diversicolor* in mesocosms. We hypothesize that this pattern is a result of food limitation, as shading of the substrate by the dense vegetation reduces benthic microalgal production and/or roots impose a physical barrier to burrowing activities of animals.

Large differences in sediment characteristics between the 1998 and 1999 transects, which were 50 m apart, indicate that the significant variations in both faunal abundance and below-ground biomass between years may largely be attributable to spatial rather than interannual differences.

Exchange of O₂ and CO₂ across interfaces—Studies of benthic metabolism in intertidal areas using simultaneous measurements of O₂ and CO₂ flux in sediments covered by tidal water as well as those exposed to the atmosphere are rare. Our results clearly show that gas fluxes in the Waarde salt marsh are very dependent on temporal scales imposed by tides and to spatial scales controlled primarily by topography and vegetation (Fig. 4). Benthic O₂ uptake and CO₂ production are widely used measures of total microbial metabolism in sediments (Kristensen et al. 1995). O₂ uptake not only represents microbenthic sediment respiration by bacteria, microalgae, and micro-, meio-, and macrofauna but also chemical and chemoautotrophic oxidation of microbial metabolites. The release of CO₂ from sediments, on the other hand, is equivalent to total benthic carbon mineralization when carbonate precipitation and dissolution is assumed negligible (Kristensen et al. 1995). However, care should be taken when CO₂ exchange in salt-marsh sediments is interpreted, because diagenetic reactions involving iron and sulfur may drive some carbonate precipitation and dissolution (Coleman 1993). CO₂ fluxes in vegetated environments may also be biased by respiration of roots and rhizomes (Howarth 1984). Nevertheless, our rates of sediment O₂ uptake and CO₂ release in the Waarde marsh are comparable to those obtained in North American salt marshes (Alongi 1998) and other intertidal areas (Kristensen et al. 1995). The tidal dependence of gas exchange by sediments in the vegetated Waarde marsh is also similar to the O₂ uptake pattern found for vegetated intertidal sediments in mangrove forests—the ecological equivalent of salt marshes in many tropical areas (Holmer et al. 1999).

The much higher respiration rates we observed when measuring fluxes when sediments are air exposed, as opposed to submerged, emphasize the importance of including both submerged and air-exposed periods when calculating carbon and oxygen budgets. The strong dependence of gas exchange on

water coverage may be due to physical as well as biological effects. The primary cause may be differences in the diffusive boundary layer and the area of gas exchange due to differences in surface roughness and drainage. The diffusive boundary layer generally constitutes a 0.2- to 1.2-mm-thick barrier to mass transfer across the sediment–water interface in inundated sediments, whereas no or only a very narrow boundary layer is present in air-exposed sediments (Boudreau and Jørgensen 2001). As a consequence, gas fluxes increase as a result of the steeper gradients at the sediment–water interface during air exposure. Secondly, drainage of water from large sediment interstices, such as cracks around roots, through evapotranspiration by plants or simple seepage, may contribute significantly to the gas exchange during low tide. These interstices act as anoxic macropores during water cover, with limited effect on gas fluxes (Boudreau and Jørgensen 2001). Air-filled interstices, on the other hand, increase the area of oxic–anoxic interfaces and provide sites with steep gradients and rapid gas exchange. Morris and Whiting (1985) found significant gas advection into the sediment associated with falling water table during low tide in a South Carolina *S. alterniflora* salt marsh, even though only a small fraction of the water in the sediment had drained. Although the enhanced flux driven by transiently steeper gradients in air-exposed sediment are likely to diminish after some time, the higher availability, aerial distribution, and deeper penetration of O₂ may cause a more persistent replacement of slow anaerobic respiration with much faster aerobic respiration (Kristensen and Holmer 2001). Air exposure showed only minor effects on gas fluxes on the open and smooth mudflat at Waarde (Sta. 1). Any enhanced gas exchange caused by physical or biological effects of air exposure at bioturbated mudflats may be counteracted and even exceeded during inundation when the abundant infauna turns active and enhances gas exchange by vigorous irrigation (Furukawa 2001). Unfortunately, it is impossible here to discriminate between the physical and biological impact on gas fluxes. However, as steady state rarely is achieved during inundated or air-exposed conditions, the measured gas exchange can only represent the total sediment metabolism when rates are weighed according to tidal coverage.

The impact of plants and animals on sulfate reduction—The role of plants on SRR in the Waarde marsh is unquestionable, as the highest rates were found in the zones with highest root biomass and pore-water DOC concentrations (Figs. 6, 10). Higher SRR in 1998 compared to 1999 is most likely due to spatial variation in plant biomass between transects. Similar high rates of sulfate reduction associated with roots have been reported from North American *S. alterniflora* marshes and tropical mangrove forests (e.g., Hines et al. 1989, 1999; Holmer et al. 1994). However, interactions between salt-marsh plants and sediment biogeochemistry are complex, with several interrelated mechanisms and processes. Through downward translocation of O₂ and associated root leakage, marsh grasses create a heterogeneous environment with a mosaic of oxic and oxidized rhizospheres in the otherwise reduced sediment (Holmer et al. 2002), as evident from elevated redox values deep in the vegetated sediments. Sulfate reduction is potentially inhibited in the oxic/oxidized

microniches created by the roots, as sulfate-reducing bacteria are strictly anaerobic organisms. The gradually decreasing rates of sulfate reduction (Fig. 6) and increasing redox conditions (Fig. 3) observed with tidal elevation in the Waarde marsh indicate that the oxidizing capacity of roots and inhibitory effect on sulfate reduction is inversely related to the degree of inundation. Conversely, leakage of labile DOC from roots, as well as reoxidation of reduced sulfide, may alleviate the O_2 effect and enhance sulfate reduction in the rhizosphere. Thus, Hines et al. (1989) found that sulfate reduction in a *S. alterniflora* marsh increases greatly in spring, when plant growth is rapid (high delivery of DOC via roots), and decreases when plants are in a late-summer senescent stage (low delivery of DOC via roots). In general, however, rhizosphere sulfate reduction rates must be controlled by a balance between the oxidizing capacity and DOC delivery of roots and not by only one of these parameters.

Benthic macrofauna increase the O_2 penetration depths and redox conditions in sediments and stimulate microbial metabolism through feeding, burrowing, and burrow irrigation (Furukawa 2001). Bioturbation has in certain cases been shown to stimulate and in other cases to inhibit sulfate reduction. Hansen et al. (1996) found an enhanced rate of sulfate reduction near burrow walls of the soft-shelled clam *Mya arenaria* in an intertidal mudflat. In a *S. alterniflora* salt marsh, on the other hand, Gribsholt et al. (2003) found that sulfate reduction was suppressed near burrow walls of the fiddler crab *Uca pugnax* and that rates generally were highest in nonbioturbated sediment. Opposing effects of bioturbation on SRR by different species can be ascribed to differences in burrowing and ventilation behavior among macrofauna. Substrate enrichment resulting from organic excretion from the clam rather than ventilation determines the microbial activity around *M. arenaria* burrows, whereas the increase in sediment surface area (controlling the oxygen flux) is the driving force behind the specific geochemistry around *Uca* burrows. The low sulfate reduction at the open mudflat in Waarde may be caused by the oxidizing effect of the abundant macrofauna present with *N. diversicolor* as a dominating feature. Banta et al. (1999), for example, found that irrigated burrows of *N. diversicolor* increased the oxidation level and significantly lowered the sulfate reduction rates in sandy sediment. However, the exact role of macrofauna on sediment processes is difficult to evaluate from the Waarde data, because all areas within the vegetated marsh were heavily affected by plant roots and were useless as nonbioturbated reference locations.

Only a fraction of the sulfide produced by sulfate reduction is preserved as FeS (i.e., AVS) or FeS_2 (i.e., CRS) in coastal sediments. The remainder is oxidized or lost to the atmosphere (Jørgensen 1987). The balance between the sulfide sinks not only depends on sediment properties, such as organic content, iron content, bioturbation, and vegetation type, but also on seasonal variations in temperature. Most of the reduced sulfur storage at the Waarde marsh is in the CRS form, which is typical for marine environments in general (Swider and Madureira 1989) and for salt marsh (Howarth and Giblin 1983; Howarth 1984) and mangrove sediments (Kristensen et al. 1995) in particular. The elevated redox conditions created by roots and bioturbation may favor a

rapid formation of FeS_2 , either through direct precipitation of Fe^{2+} with polysulfides or via FeS oxidation with S^0 and polysulfides. The positive relationship observed between %AVS and SRR (Fig. 6) indicates that conversion of FeS to FeS_2 for unknown reasons is hampered in our highly active salt-marsh sediments and that sulfide apparently is stored as FeS in proportion to the rate of sulfate reduction.

The cycling of sulfur compounds is rapid in the Waarde marsh, with concomitant formation and oxidation of reduced inorganic sulfur pools. The present study shows that particularly vegetated low marsh sediments, where sulfate reduction is the dominant anaerobic respiration process (see below), accumulate reduced inorganic sulfur in late summer, as indicated by RQ values that are consistently higher than 1 (Fig. 4). In the high marsh, however, the high RQ values may partly be due to other dominant anaerobic respiration processes (e.g., iron reduction). The higher RQ values observed in inundated compared to air-exposed sediments indicates a significant sulfide build-up during inundation and a higher degree of oxidation during air exposure. However, net accumulation of reduced sulfide may not persist during cold winter months, when low rates of sulfate reduction and high availability of O_2 results in a net oxidation of reduced sulfur (Kristensen et al. 2000). The estimated turnover time of reduced inorganic sulfur in the Waarde marsh must for the same reason be considered a late-summer snapshot and by no means provides the true all-season turnover time. Nevertheless, the obtained turnover estimates indicate that the *Spartina* roots have sufficient capacity to increase sulfide oxidation and maintain a fast turnover in the vegetated lower marsh, where sulfate reduction rates are high. Conversely, the very high oxidation capacity in the bioturbated mudflat and the vegetated high marsh appears to hamper sulfate reduction rates and thus lower the turnover rates.

Partitioning of sediment carbon oxidation—Sulfate reduction typically contributes about 50% of the C oxidation in subtidal coastal sediments overlaid by oxic bottom water, but it may be even more important in salt-marsh and sheltered subtidal sediments (Thamdrup and Canfield 2000). The role of sulfate reduction for total benthic carbon oxidation along the Waarde transect can only be assessed when the CO_2 release is weighed according to the average time of inundation at each station. Accordingly, the depth-integrated sulfate reduction (0–18 cm) accounted for 32–63% of the total carbon oxidation on the open mudflat (Sta. 1) and for at least 100% in the vegetated sediment up to 15 m from the marsh edge (assuming a C:S ratio of 2) but was of limited significance (13–21%) 25 m inside the marsh (Fig. 11). The low contribution of sulfate reduction on the open mudflat and particularly in the high marsh makes aerobic respiration and iron reduction the most important microbial respiration pathways. Unfortunately, it is not possible to separate these two processes from the present data. However, large pools of particulate Fe(III) ($22\text{--}63 \mu\text{mol cm}^{-3}$ w/w) are present in the top 20 cm of the vegetated Waarde sediment, and anoxic incubations have revealed that microbial iron reduction may potentially account for up to 77% of the CO_2 production in the high marsh (Gribsholt unpubl. data). This is similar to the partitioning of carbon oxidation re-

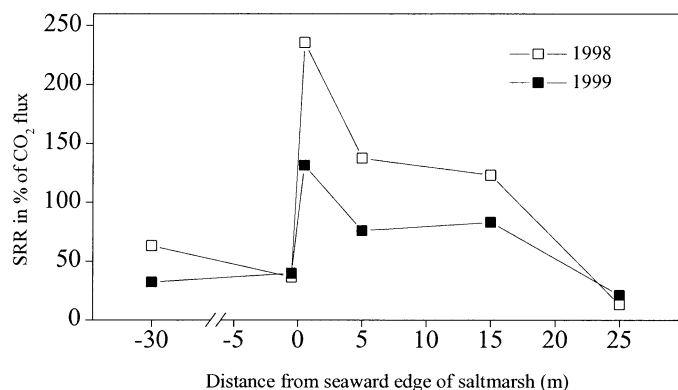


Fig. 11. Depth-integrated (0–18-cm) sulfate reduction rate (Σ SRR) as % of dark CO_2 release by the sediment [$2 \times \Sigma$ SRR/ CO_2 -flux) $\times 100$]. Average submergence time used to calculate the diel CO_2 release at the temporarily inundated marsh is estimated from the topographic levels and predicted tidal coverage at Hansweert (The Netherlands) in 1999. CO_2 release during air exposure in 1998 was estimated from measured O_2 uptake and the RQ values obtained in 1999.

ported by Kostka et al. (2002) for densely vegetated *S. alterniflora* sediments in the United States and by Kristensen et al. (2000) for vegetated mangrove sediments in Thailand.

Mudflat/marsh boundary—a unique interface—The boundary between the tidal mudflat and the vegetated salt marsh constitutes a unique environment. Sulfate reduction rates were high near the marsh edge at Waarde and exceeded the reoxidation capacity of the plants, resulting in strongly reduced sediments. The measured sulfate reduction rates converted to C units were higher than the total CO_2 release on top of the marsh cliff in both 1998 and 1999, whereas only 40% of the daily CO_2 loss below the cliff can be ascribed to sulfate reduction. Thus, the CO_2 release and the respiratory quotient below the cliff were very high (2.4–14.1). This indicates that sources other than sulfate reduction must have supplied CO_2 below the cliff. One obvious source is seepage of HCO_3^- -rich and relatively DOC-poor pore water from deeper parts of the elevated marsh just inside the cliff.

Salt-marsh sediment geochemistry is greatly influenced by hydrology, but little is known of the drainage patterns in the Waarde salt marsh. Movement of water by lateral drainage is a major component of the creek bank water balance in the *S. alterniflora*-dominated Great Sippiwissett Marsh (New England) and is an important pathway of carbon and nitrogen transfer of pore-water pools to tidal waters (Howes and Goehring 1994). Movement of water by drainage is known to be particularly significant within the narrow band of tall *Spartina* bordering creeks in North American *S. alterniflora* marshes (e.g., Morris and Whiting 1985; Yelverton and Hackney 1986), while evapotranspiration is the primary process controlling water movement in the stagnant inner marsh. Carbon can therefore be exported from the marsh sediment via plant uptake, through diffusive loss to water or air, and through lateral drainage of pore water.

We propose, therefore, that the steeply elevated marsh cliff at the Waarde salt marsh creates a hydraulic gradient

Table 4. Average depth integrated sulfate reduction rate Σ SRR (0–18 cm) at the marsh boundary (below and above the cliff) as % of average dark CO_2 release in inundated (W+) and air-exposed (W-) sediment as well as the calculated diel mean in 1998 and 1999. Average submergence time is estimated from the topographic coverage and predicted tidal level at Hansweert, The Netherlands.

Year	W+	W-	Diel mean
1998	41.1	148.2	115.5
1999	51.4	102.2	87.0

during each subsiding tide, resulting in lateral seepage of deep HCO_3^- -rich pore water. This explains the high pore-water TCO_2 and low DOC concentrations just below the cliff. The surprisingly low CO_2 release that occurs below the cliff during air exposure is probably caused by restraints on the conversion of dissolved HCO_3^- to free CO_2 as a result of elevated pH (around 8) in the near-surface pore water. The extremely high TCO_2 release at high tide, on the other hand, must be driven by the steep gradients and high concentrations of pore-water HCO_3^- . Beside lateral seepage, the release of TCO_2 below the cliff may also be enhanced by irrigation of the dense *N. diversicolor* population (Banta et al. 1999). The loss of TCO_2 by pore-water seepage reduces TCO_2 release and causes the discrepancy with the depth-integrated SRR at the top of the cliff. When the data from the two stations around the cliff are joined, SRR accounts for more than the CO_2 release during air exposure but only half of the TCO_2 release during inundation (Table 4). The estimated diel fraction of carbon oxidation due to sulfate reduction around the marsh cliff is 87–116%, which is similar to the contribution found at the marsh sites some distance from the cliff. However, more information on the hydrography and hydrology is needed to fully elucidate the dynamics of biogeochemical processes and transport conditions at the mudflat/marsh boundary.

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