
*Biogeochemistry* **49:** 103–121, 2000.


# Methane emission from tidal freshwater marshes

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Received 21 December 1998; accepted 18 August 1999

**Key words:** tidal freshwater marsh, methane dynamics, methane emission, rhizosphere, *Phragmites*, *Scirpus*

**Abstract.** In two tidal freshwater marshes, methane emission, production and accumulation in the pore-water have been studied. The two sites differ in their dominant vegetation, i.e. reed and bulrush, and in their heights above sea level. The reed site was elevated in relation to the bulrush site and had higher rates of methane emission and production. It is argued that this difference in methane emission between sites was primarily due to a different effect of reed and bulrush plants on methane dynamics rather than methane oxidation related to tidal elevation. Methane emission showed strong seasonality related primarily to plant physiology and only secondarily to temperature. Two control sites at which vegetation was removed systematically had lower emission rates indicating an overall stimulating effect of plants on methane emission from tidal marshes. Flooding reduced methane emission, probably by blocking the primary sites of methane release in the lower part of the plant stems.

## Introduction

Natural wetlands are thought to be a major source of atmospheric methane (Cicerone & Oremland 1988). Quantification of this source is difficult, because individual wetlands often show great spatial and temporal variations in methane emission. This variability in time and space is related to environmental factors that affect methane production, oxidation or transport. These factors include the type and amount of organic matter (Kelly & Chynoweth 1981), the dominant organic matter decomposition pathway (DeLaune et al. 1983; Bartlett et al. 1987; Middelburg et al. 1996), temperature (King & Wiebe 1978; Bartlett et al. 1987), hydrological conditions (Roulet et. al. 1992; Fechner & Hemond 1992; Kelley et al. 1995) and vegetation (Dacey & Klug 1979; Sebacher et al. 1985; Wilson et al. 1989; Schütz et al. 1991; Whiting et al. 1991; Chanton et al. 1992).

In tidal freshwater marshes plants and daily fluctuations in water level may affect methane emission by controlling its production, oxidation and

transport. Plants may support methanogenesis directly through root exudation (Raimbault et al. 1977; Whiting & Chanton 1992) and indirectly through enhancing carbon input by (1) litter accumulation (Whiting & Chanton 1993) or (2) canopy-friction induced trapping of suspended organic matter (Middelburg et al. 1997). Oxygen may enter intertidal vegetated sediments directly by diffusion at low tide and indirectly via the aerenchyma of the plants, at low and high tide (King 1994). Oxygen in the rhizosphere attenuates methane emission directly through methane oxidation (King 1994; Van der Nat & Middelburg 1998a) and indirectly through suppression of methanogenesis (Roden & Wetzel 1996; Van der Nat & Middelburg 1998b). Moreover, wetland plants serve as direct conduits to the atmosphere facilitating vertical methane transport into the atmosphere (Sebacher et al. 1985; Chanton & Dacey 1991; Whiting & Chanton 1992; Van der Nat et al. 1998). Finally, lateral transport of dissolved methane through drainage, driven by tidal flushing, may transport a significant portion of dissolved methane horizontally before release into the atmosphere (Kelley et al. 1995).

This paper reports the spatial and temporal variability in methane emission and pore water methane concentrations from a tidal marsh in the Scheldt estuary. Two sites, differing in plant community structure and flooding frequency and duration, were monitored regularly over a period of two years and the processes involved in methane cycling are discussed. An experimental container subject to water level fluctuations was constructed to determine the effect of tide on methane emission.

## Material and methods

### *Study area*

Station Burcht is an oligohaline tidal marsh located near Antwerp in the Scheldt Estuary. The salinity of the river Scheldt water off Burcht averaged ~2.5‰, with limited seasonal variability. Vegetation at Burcht shows a clear zonation pattern with a 10 m broad dense *Scirpus lacustris* (bulrush) stand closest to the river and a 20 m broad dense *Phragmites australis* (reed) stand. The two sites have been designated SCR (*Scirpus* Close to River) and PFR (*Phragmites* Far from River). SCR and PFR have tidal elevations of ~2.5 m and ~3.2 m above sea level, respectively. This 0.7 m difference in tidal elevation results in large differences with respect to flooding frequencies, duration of submergence and flood height. Total period of submergence in 1995 of PFR and SCR was 210 and 1027 hours, respectively, whereas the averaged period of submergence per flooding was 0.7 and 1.6 hours, respectively. Averaged height of the flood water above the sediment surface during

high tide was 16.6 cm (PFR) and 43.4 cm (SCR). In two 2×2 m plots (SCR-P and PFR-P) the newly emergent vegetation was cut weekly directly above the sediment. Plots were shrouded for darkness to mimic plant shading and limit microphytobenthos growth by installation of a 40% light transparent cloth ~20 cm above the sediment. Cloth could be easily removed before sampling.

*Methane emission*

The enclosed chamber technique used to measure methane emission has been described previously (Van der Nat et al. 1998). Methane emission was calculated by linear regression analysis from the change of methane concentration in the mixed chamber with time over a 30 to 45 minute period ($n$ = 20–30). The methane accumulating in the chamber is transported by three mechanisms: molecular diffusion, gas bubble ebullition and by transport through plants. The amount of methane transported through ebullition was calculated using a partitioning approach (Middelburg et al. 1996; Van der Nat & Middelburg 1998b). Measurements with an initial chamber methane concentration exceeding ambient levels > two times and emissions with a regression coefficient <0.90 ($n \geq 20$) were discarded. Molecular diffusion rates were calculated according to Fick's first law modified for sediments (Berner 1980), using the methane concentration gradient at the sediment surface. The diffusion and bubble fluxes were subtracted from total emission values to obtain the plant transport rates. Emission measurements were always conducted during spring tide and air exposure. Flux measurements could only be performed at low tide because of logistic constraints (i.e. >4 m tidal range). Fluxes were determined under light and dark conditions as well as after clipping the plants close to the sediment surface. $CO_2$ levels within the chamber were maintained at or above ambient levels during periods of $CO_2$ uptake by injecting small amounts of $CO_2$ into the chamber. The chamber was shrouded for dark measurements with a black-out cloth.

*Pore water sampling*

Pore water was sampled by *in situ* dialysis (Hesslein 1976), using a sampling device known as a 'peeper' (height×width = 60×10 cm) which contained 25 membrane cells that were in contact with sediments via a 0.2 mm biologically inert acrylic copolymer membrane filter (Versapor-200, Gelman Sciences). At both ends, the cells were connected with Tygon tubes to sampling ports at the sediment surface. The samplers were installed January 1994. Pore water samples were withdrawn with a syringe at one sampling port while nitrogen gas was introduced via the other port. Deoxygenated de-ionised water was used to refill the compartments after sampling. The sample was

transported into 5, 10 or 20 ml glass vial sealed with a septum crimp-cap (Chrompack) and immediately acidified by adding 50 to 200 $\mu$l 20% $H_2SO_4$. The acidified samples were analysed for methane in the headspace using the phase equilibrium technique (McAullife 1971). Methane was analysed with a Carlo-Erba high resolution MEGA 5340 gas chromatograph, equipped with a flame ionisation detector. The headspace gas concentrations were recalculated to pore-water concentrations using equations given by Wiesenburg and Guinasso (1979). Earlier experiments showed that addition of $H_2SO_4$ did not affect methane concentrations significantly. Sedimentary pool sizes (reservoirs) were calculated from the profiles of pore-water methane concentration, after correction for sediment porosity. Porosity was calculated from water content (weight loss on drying at 105 °C) assuming a dry density of 2.55 g $ml^{-1}$. Sediment porosity in the PFR system ranged from 0.66±0.03 at the surface to 0.63±0.03 at depth. Porosity in the SCR system ranged from 0.76±0.04 at the surface to 0.73±0.02 at depth.

*Anaerobic incubations*

Sediment cores were collected in July 1995 using acrylic tubes (55 cm long, 7 cm internal diameter). Sediment of equal depth of three cores was thoroughly mixed, put into glass vials, diluted with sterilised water and sealed with screw caps provided with rubber septa. Amendments were given in the form of acetate (final concentration 2.5 mM) and $H_2$ (7.5% headspace). A detailed description of the method and some control experiments are given elsewhere (Van der Nat et al. 1997). Increase of $CH_4$ and $CO_2$ in the incubation flask headspace was monitored by daily analyses of 50 $\mu$l headspace samples. This procedure for measuring $CH_4$ and $CO_2$ production was chosen mainly by the lack of a reasonable alternative in vegetated systems (Yavitt et al. 1988). Unfortunately, the procedure may not yield accurate *in situ* rates due to the coring technique and incubation circumstances such as shaking and exclusion of atmospheric $O_2$ input (Kelley et al. 1995). Therefore production rates are considered potential rates. Rates are calculated for the period when increases in headspace concentrations were linear ($R^2 > 0.95$), i.e. the first 3 days of the incubation period.

*Biomass*

Above-ground biomass was estimated by averaging the weight of two vegetation samples that had been dried for 3 days at 60 °C. Only green and healthy looking plants were included. The $CO_2$ fixation rates were measured similar to methane emission by linear regression analysis from the change of chamber $CO_2$ concentration with time. An initial $CO_2$ concentration of ∼1000 ppmv

was used. Rates were linear ($R^2 > 0.90$) in the 700 to 400 ppmv range. For estimating below-ground biomass, cores ($n = 5$) were collected in September 1994, using acrylic tubes (55 cm long, 7 cm internal diameter). Cores were sliced and washed and the obtained biomass was separated in live roots and rhizome material.

*Sediment and environmental parameters*

Each month the organic carbon content of the sediment, stripped from foreign material and root biomass, was determined according to Nieuwenhuize et al. (1994). No distinct temporal pattern could be detected and the results were pooled ($n = 21$). Incident light (PAR) was measured with a Macam type SD 101 light sensor. Light intensity inside the chamber was more than 90% of the light intensity measured outside the chamber. Simple mercury glass thermometers measured air and sediment temperature. Sediment temperature was measured ~1 cm below the sediment-air interface. Chamber air temperature followed outside air temperature closely and deviated usually no more than 2 °C. Humidity inside the chamber was also monitored by the multi-gas monitor and was usually within 25% of ambient conditions.

*Experimental intertidal marsh*

A mixture (1:4) of garden soil (Barenburg products) and Burcht sediment was mixed and transferred to a container (l×w×h = 2.0×0.5×0.8 m). The container was placed in a temperature (18±0.5 °C), humidity (70%±7) and $CO_2$ concentration (380±40 ppmv) controlled room. The sediment was allowed to settle for a period of 4 months. After this period sediment height was ~35 cm. *Scirpus* plants were collected in the field and planted carefully in a similar density as found in the field. Two polypropylene collars with a diameter of 24 cm were installed in the centre of the container to ascertain consistent placement of the gas collecting chambers and minimise disturbance during successive emission measurements. A 16 hours day period with a light intensity of ~0.4 mmol photons $m^{-2}$ $s^{-1}$ at the sediment surface (about 1.6 m below lamps) was set, except during the measurements when light was continuously supplied to avoid interference of the light regime with methane emission (Van der Nat et al. 1998). Two times a day the tide changed resulting in 4 hours periods of low and high tide separated by 2 hours of pumping time. Pumping rate was ~0.4 cm $min^{-1}$. The tidal range was ~33 cm. A large basin (~500 l) was used as a reservoir for the overlying water. Experiments were conducted on plants of the second generation. To avoid pressure problems with the changing water level the flux chambers were equipped with a hollow capillair needle sticking through the

chamber's side. Chamber methane concentrations were recalculated to absolute methane content in order to incorporate the change in chamber volume during floodwater pumping.

*Integration and statistical analysis*

Annual flux estimates were calculated by integration of the curves connecting averages of replicate measurements. Pore-water reservoir sizes were obtained by integrating pore-water data to 55 cm and taking into account porosity. For each plant species the difference between light, dark and clipped emission was tested with the *t*-test using pooled variances. Other statistical analysis was done with one- or multi-way ANOVA tests, depending on the number of factors, so possible interactions between factors would be revealed. In all analysis where $p < 0.05$, the factor tested was considered statistically significant.

## Results

*Methane emission*

Methane emission rates, sediment temperature and above-ground biomass values are presented in Figure 1. Emission rates were variable, even when measurements were conducted consecutively on the same day and collar. There are nevertheless consistent trends on a (i) spatial basis, (ii) temporal basis, and, (iii) with respect to the immediate effect of light.

(i) Methane emission was much lower at SCR than PFR (Table 1, and notice the difference of scale in Figure 1). Maximum differences were observed mid-seasonally when plants were mature and sediment temperature had reached its highest levels. In 1994 annual emission rates differed by more than 10 times (0.28 vs. 4.7 mol $CH_4$ $m^{-2}$ $yr^{-1}$ for SCR and PFR, respectively, Table 1). Continual removal of the vegetation at the adjacent corresponding plots reduced emission to 0.13–0.15 and 0.54–0.56 mol $CH_4$ $m^{-2}$ $yr^{-1}$ for SCR-P and PFR-P respectively (Table 1), indicating a net positive effect of *Phragmites* and *Scirpus* plants on methane emission. $CO_2$fixation rates in July 1994 on a clear and sunny day were $2.9 \pm 0.23$ and $2.0 \pm 0.21$ mol $m^{-2}$ $d^{-1}$ for PFR and SCR, respectively.

(ii) Methane emission showed strong seasonality. Emission started during spring and increased until maxima were reached in mid- (SCR) and late-summer (PFR). Emission rates declined again during late summer (SCR) and autumn (PFR). Seasonal patterns were reproducible for at least 2 years. Increment of sediment temperature levels in the plots due to the absence of plant

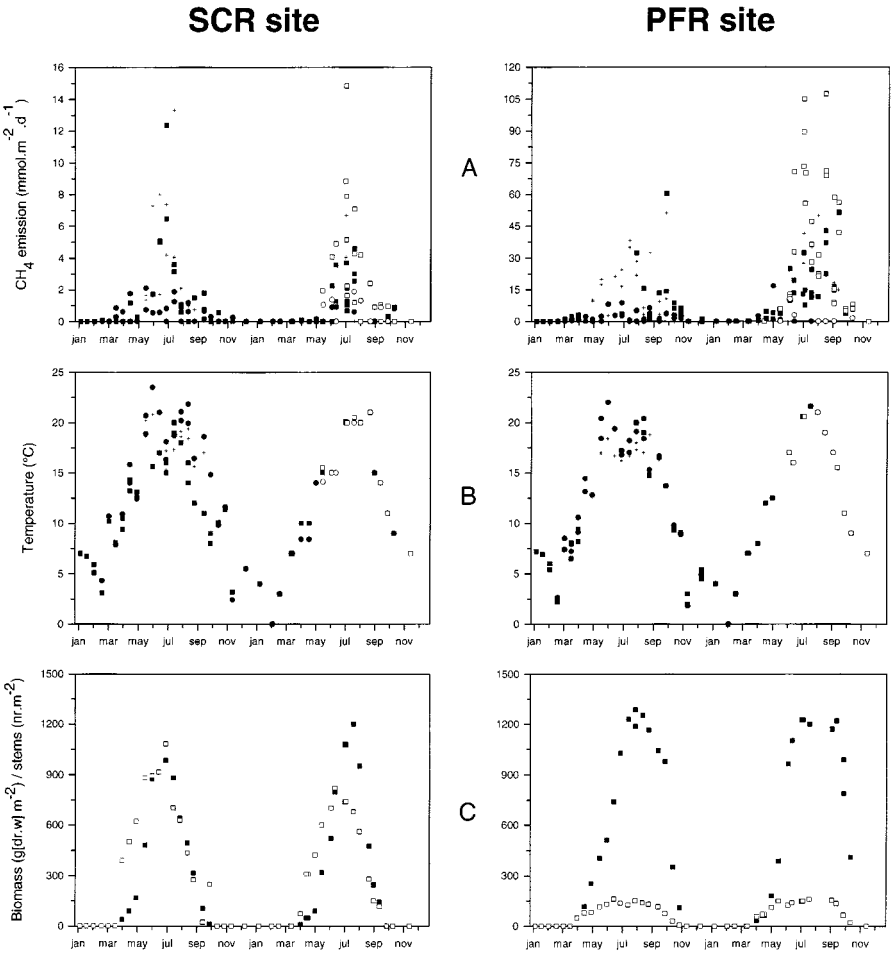


*Figure 1.* Time course of methane emission (A), sediment temperature (B) in clipped (+), intact vegetation (squares) and non-vegetated plots (circles) under light (open symbols) and dark conditions (closed symbols) and (C) above-ground biomass dry weight (closed squares) and number of stems.m$^{-2}$ (open squares) at SCR (left) and PFR (right). Please note the differences in scale in panel A.

shading was not apparent. No difference in sediment temperature between SCR and PFR was observed.

(iii) Methane emission rates under light conditions were usually higher than under dark conditions, especially at PFR (Figure 1; Table 1). Highest light/dark emission ratios were noted when plants were mature and fully green and lowest ratios when plants were small or senescing. In addition, the ratio varied with the amplitude in light intensity. Relative high ratios were measured on clear sunny days with light intensities exceeding 1.3 mmol m$^{-2}$

*Table 1.* Annual methane fluxes (mol $CH_4$ $m^{-2}$ $yr^{-1}$).

| Site | Period | Vegetation | Condition | Flux |
|---|---|---|---|---|
| SCR | 1993 | Clipped | Dark | 0.51 |
| SCR | 1993 | Intact | Dark | 0.38 |
| SCR-P | 1993 | Removed | Dark | 0.13 |
| PFR | 1993 | Clipped | Dark | 3.11 |
| PFR | 1993 | Intact | Dark | 2.3 |
| PFR-P | 1993 | Removed | Dark | 0.56 |
| SCR | 1994 | Intact | Dark | 0.17 |
| SCR | 1994 | Intact | Light | 0.36 |
| SCR-P | 1994 | Removed | Dark/light* | 0.15 |
| SCR | 1994 | Intact | Dark/light* | 0.28 |
| PFR | 1994 | Intact | Dark | 3.02 |
| PFR | 1994 | Intact | Light | 5.91 |
| PFR-P | 1994 | Removed | Dark/light* | 0.54 |
| PFR | 1994 | Intact | Dark/light* | 4.71 |

* Integration based on 14h light and 10h dark periods.
SCR-P and PFR-R represent plots at which emergent vegetation was removed weekly.

$s^{-1}$. The effect of light was comparatively small at the non-vegetated plots. Clipping the reed plants significantly lowered methane emission compared to rates measured with intact plants under light conditions ($p$ = 0.036), but not under dark conditions. Clipping the bulrush plants did not significantly affect the outcome of the measurements.

Episodic increases of chamber methane concentrations, indicating occurrence of ebullition was only observed occasionally at SCR when plants were senescing and contributed less than 10% to total methane emission at that time. The contribution of molecular diffusion in the sediment contributed less than 5% to total emission.

*Dissolved methane*

Dissolved methane pore-water depth profiles are shown in Figure 2. In the surface layer methane concentrations were between 0.1 and 5 $\mu$M, i.e., similar to that in river Scheldt water, but they were above those in equilibrium with the atmosphere ($\sim$0.003 $\mu$M). Methane reservoirs were much larger at PFR than SCR (Table 2). The winter methane reservoir sizes were about double those of spring/early-summer. The seasonal decrease of the methane reservoir started in March/April whereas the subsequent increase started in

*Table 2.* Dissolved methane reservoir (mmol $m^{-2}$).

| Date | PFR | SCR |
|---|---|---|
| 25 Jul 1994 | 77.9 | 49.1 |
| 25 Aug 1994 | 137.6 | 88.3 |
| 21 Sep 1994 | 132.2 | 89.7 |
| 22 Nov 1994 | 142.8 | 79.1 |
| 20 Feb 1995 | 151.1 | 92.6 |
| 18 Apr 1995 | 125.9 | 38.7 |
| 18 May 1995 | 65.8 | 41.1 |
| 18 Jun 1995 | 52.6 | 34.7 |
| Annual average | 111 | 64 |

August. Relatively low dissolved reservoir sizes at PFR during the months May–July were accompanied by a shift towards concave methane versus depth profiles, whereas profiles at SCR were concave over the whole season. Concave profiles indicate that methane losses due to oxidation and venting dominate over methane gains from production or lateral inputs.

*Methane and carbon dioxide production*

Potential rates of methane and carbon dioxide production were measured in July 1995. Methane production without a lag-phase was observed only in the surface layer slurries (0- to 2-cm) and 40- to 45-cm slurries (Table 3). In the 2- to 5-cm and 15- to 20-cm slurries, methane production started after a lag phase of $>3$ days. Methane production was not observed in the slurries treated with BES, a specific inhibitor of methanogenesis. Addition of methanogenic precursors stimulated methane production 2 to 3 times at SCR and 7 to 9 times at PFR. The depth integrated production rate of methane at PFR ($16.4\pm2.2$ mmol $m^{-2}$ $d^{-1}$) was significantly higher than that at SCR ($6.4\pm0.9$ mmol $m^{-2}$ $d^{-1}$), whereas gross mineralisation (depth integrated $CO_2$ + $CH_4$ production) at PFR ($118\pm5$ mmol $m^{-2}$ $d^{-1}$) was lower than that at SCR ($130\pm9$ mmol $m^{-2}$ $d^{-1}$). This difference depended however on depth (interaction term significant at $p < 0.0001$) with mineralisation rates at SCR in the surface layer being higher than those at depth (Table 3). The contribution of methanogenesis to carbon mineralisation at depth was consequently higher at PFR (71%) than SCR (37%).

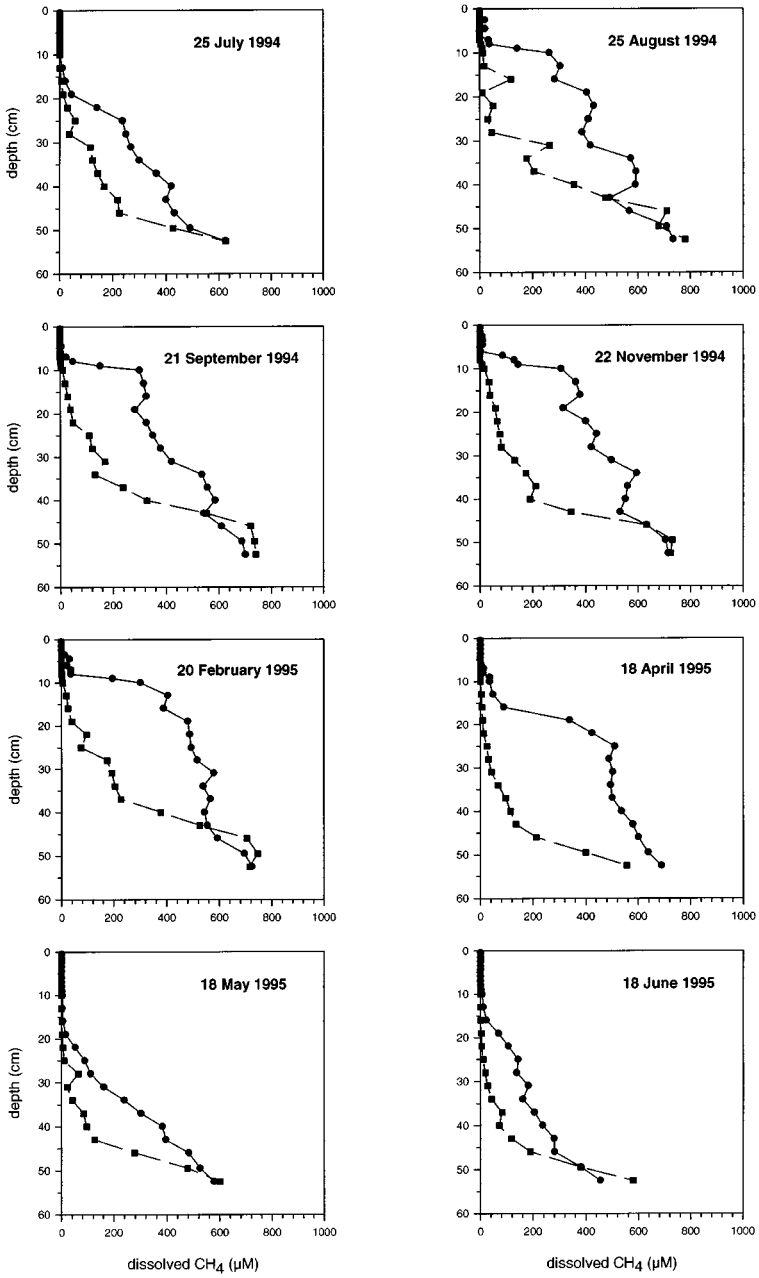


*Figure 2.* Depth distribution of dissolved pore-water methane at SCR (squares) and PFR (circles). The dates refer to the days when pore-water samples were recovered.

*Table 3.* Methane and carbon dioxide production.

| Site | Depth interval (cm) | $CH_4$ production ($\mu$mol $l^{-1}$ $h^{-1}$) | $CO_2$ production ($\mu$mol $l^{-1}$ $h^{-1}$) | $CO_2 + CH_4$ ($\mu$mol $l^{-1}$ $h^{-1}$) | Contribution of methanog. (%) |
|---|---|---|---|---|---|
| PFR | 0–2 | 0.27 ± 0.08 | 11.7 ± 1.2 | 12.0 ± 1.2 | 4.5 ± 1.4 |
| | 2–5 | n.s. | 9.7 ± 1.1 | 9.7 ± 1.1 | |
| | 15–20 | n.s. | 10.0 ± 0.9 | 10.0 ± 0.9 | |
| | 40–45 | 3.38 ± 0.46 | 6.2 ± 0.2 | 9.6 ± 0.5 | 71 ± 10 |
| SCR | 0–2 | 0.73 ± 0.12 | 18.5 ± 1.4 | 19.2 ± 1.4 | 7.6 ± 1.3 |
| | 2–5 | n.s. | 16.2 ± 1.5 | 16.2 ± 1.5 | |
| | 15–20 | n.s. | 10.4 ± 1.9 | 10.4 ± 1.9 | |
| | 40–45 | 1.26 ± 0.18 | 5.6 ± 0.2 | 6.9 ± 0.3 | 37 ± 6 |

n.s. = no significant production during first three days.

### *Organic carbon and below-ground biomass*

The concentration of organic carbon at PFR (4.23±0.22 mmol $cm^{-3}$) was independent of depth, whereas that at SCR depended significantly on depth (2.68±0.18 mmol $cm^{-3}$ in the surface layer to 1.84±0.17 mmol $cm^{-3}$ at depth, data not shown). In general, organic carbon contents tended to be lower in the non-vegetated plots than in the adjacent vegetated sites: PFR-P and SCR-P pool sizes were 3.66±0.40 and 1.86±0.16 mmol $cm^{-3}$, respectively.

*Phragmites* roots penetrated the sediment to greater depth than *Scirpus* roots and the amount of root dry weight was also higher for *Phragmites* (Figure 3). Rhizome material was found only in the *Phragmites* system, especially below a depth of 35 cm. Rhizome material was also found at depths $>$90 cm (data not shown). The total weight of dry rhizome material exceeded the total weight of dry roots by more than 10 times.

### *Tidal experimental container*

Methane emission appeared to be a function of tidal height (Figure 4). The low-tide and high-tide emissions averaged 28.2±2.6 and 17.6±1.7 mmol $m^{-2}$ $d^{-1}$, respectively ($n$ = 3). Especially when the flood water level dropped below about 8 cm height, the accumulation of methane in the chamber increased considerably. Base low-tide emission rates were again present after flood water height levelled the sediment surface. Ebullition was observed occasionally during the shift from high to low tide and contributed less than 20% to total methane emission. The time period selected for presentation in Figure 4 was free of bubble methane release.

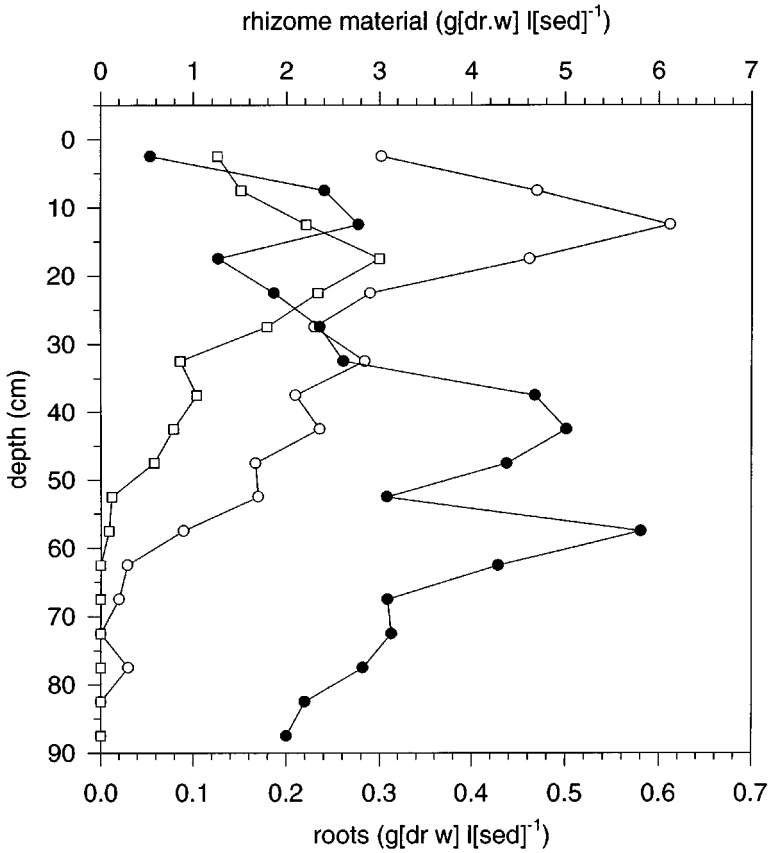


*Figure 3.* Depth distribution of live root and rhizome material at SCR (squares) and PFR (circles). Rhizome material is represented by filled symbols. Standard error bars are not included for reasons of clarity.

## Discussion

Methane emission from the permanently clipped plots (SCR-P and PFR-P) was significantly lower than that from vegetated sites of similar setting (Figure 1, Table 1). Apparently, the processes attenuating emission (stimulation of rhizospheric methane oxidation and suppression of methanogenesis) were outweighed by those enhancing emission (transport and stimulation of methanogenesis).

Methane transport through aerenchymatic plants is usually much greater than diffusion in sediments and ebullitive transport (Sebacher et al. 1985; Chanton & Dacey 1991; Whiting & Chanton 1992; Van der Nat et al. 1998; Van der Nat & Middelburg 1998a, b). It has been suggested that plant trans-

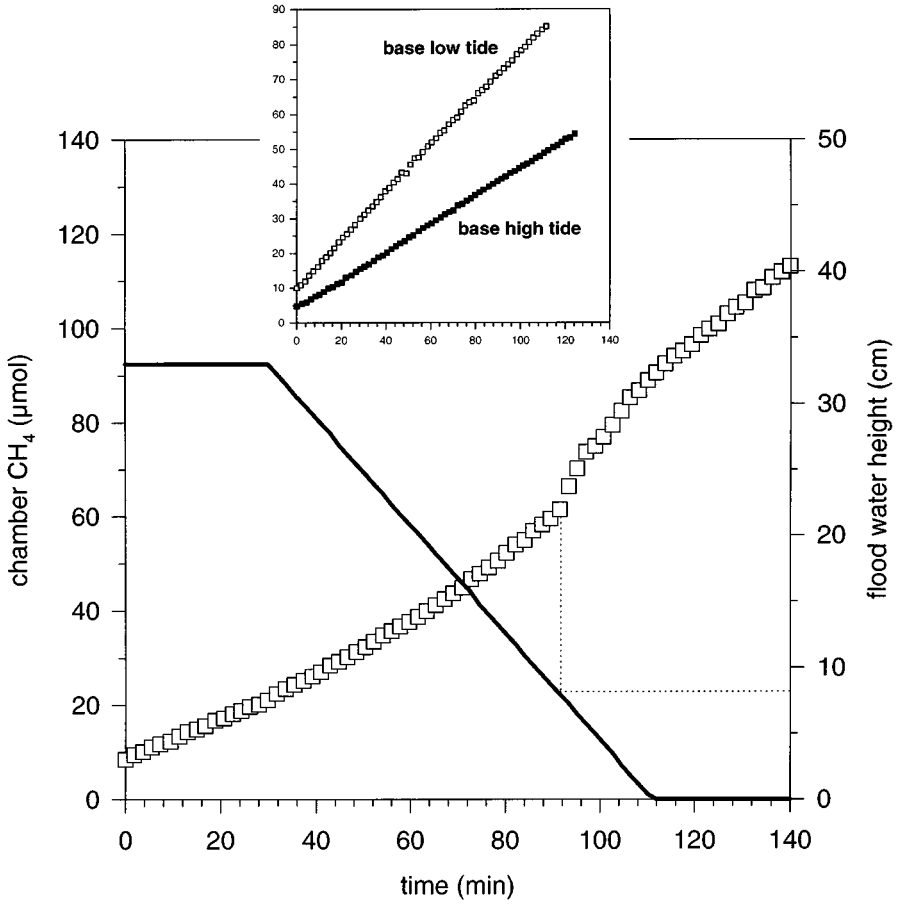


*Figure 4.* The effect of water level on methane accumulation in flux chamber. The inset shows low and high tide measurements conducted when pumps were shut off. The dashed line relates the break in the accumulation of methane with a water level of 8 cm.

port and ebullition may be mutually exclusive processes (Holzapfel-Pschorn & Seiler 1986; Schütz et al. 1989). The presence of methane-transporting plants may enhance methane emission even further by allowing methane to bypass zones of methane oxidation (Shannon & White 1994). In our study more than 85% of net methane emission was a result of methane venting to the atmosphere through the *Scirpus* and *Phragmites* system. This escape route seems especially important at our sites because fluctuating water tables (due to tides and water uptake by plants) and air-exposure support intensive methanotrophy to greater depth (Van der Nat et al. 1997).

The significant light/dark difference in methane emission by *Phragmites* ($p$ = 0.01; Figure 1) is typical for emergent plants exploiting diffusive

transport during periods of low illumination or in the dark and additional convective transport during periods of illumination (Sebacher et al. 1985; Van der Nat et al. 1998). *Scirpus* uses a diffusive mechanism irrespective of light condition (Van der Nat et al. 1998) and there is consequently no significant light-dark variation in methane flux. It is interesting to note that the different effect of clipping *Phragmites* and *Scirpus* plants on methane emission (Figure 1) is in accordance with the usage of the different gas transport mechanisms. Clipping a plant that exploits diffusive and convective transport such as *Phragmites* under light conditions should decrease methane emission because the capacity for pressurised transport is aborted. Clipping does not affect steady-state methane emission from plants employing diffusive transport such as *Scirpus* (Figure 1), rice (Denier van der Gon & Van Breemen 1993) and *Carex* (Kelker & Chanton 1997), and plants with light dependent transport modes such as *Phragmites* under dark conditions.

*Seasonal variability*

An important factor controlling seasonal methane emission is plant growth (Schütz et al. 1989, 1991; Wilson et al. 1989; Sass et al. 1990; Conrad 1989; Van der Nat et al. 1998; Van der Nat & Middelburg 1998a, b). The dissolved methane versus depth profiles reflect the balance of processes governing the production, oxidation and transport of methane. Although profiles alone do not allow one to distinguish between these processes, changes in profiles over time together with changes in emissions can provide clues about how plant growth controls seasonal emissions of methane. The sharp decrease in the dissolved methane reservoir size and simultaneous increase in emissions during springtime indicate the importance of transport. An increase in oxidation or a decrease in methane production might explain the decrease in pore-water methane, but would not have led to the observed increment in methane emission. The residence time of methane in pore-water with respect to ventilation (reservoir size/methane emission) at SCR varied from 42 days in May, 7 to 8 days in June–July, to 53 and 230 days in August and September, respectively. At PFR the residence time was much lower and decreased from 11 days in May to 1–2 days in June–August and rose again to 4 days in September. Other research also showed that methane-transporting plants may deplete the pool of dissolved pore-water methane rapidly (Chanton & Dacey 1991; Chanton et al. 1992; Shannon et al. 1996).

The changes in emission and reservoir size closely followed the emergence of new green plant parts. Consistently, when *Scirpus* plants started to senesce in August methane emissions decreased (Figure 1) and the size of the methane reservoir increased (Table 2). However, at PFR the increase in reservoir size was not accompanied by a decrease in emission and did not

follow the dying of the *Phragmites* plants (October). An explanation might be that methane production is stimulated through addition of methanogenic substrates and their rate of supply is closely linked to the plant's growth cycle. Correlation between the plant growth cycle and methane production has been reported before for *Phragmites* (Van der Nat & Middelburg 1998b) and other plants (Sass et al. 1990; Whiting & Chanton 1992; Kelly et al. 1995; Minoda & Kimura 1996).

The difference in time for emission to decline at PFR and SCR indicate that the effect of sediment temperature was less important than that of plant physiology. The effect of temperature on methane emission is not straightforward. (i) Increasing temperatures will not only enhance methane production rates (Kelley & Chynoweth 1981), but also methane oxidation rates (King & Adamsen 1992). (ii) The effect of temperature on methane production in a substrate limited environment is inherently small (Kelley et al. 1995) and the stimulation of methane production by the addition of methanogenic substrate indicates that methanogenesis was probably substrate limited (in July 1995). (iii) Temperature was not measured in the methanogenic zone (>40 cm depth) of the sediment, but temperature fluctuations are normally dampened with depth.

*Spatial variability*

The observed difference in methane emission between SCR and PFR could be related to a difference in tidal elevation (i.e. flooding frequency and duration) or to a difference in plant communities. Several studies already demonstrated a correlation between the toposequence of a particular site and methane emission (Morrissey & Livingston 1992; Moore et al. 1994; Kelley et al. 1995). In general, higher elevated sites are likely to emit less methane than less elevated sites due to differences in oxidising capacity and lateral transport. Indeed, bulk sediment oxidation rates were significantly higher at PFR than SCR (Van der Nat et al. 1997). Moreover, SCR is flooded more regularly than PFR with the likely result that more labile organic matter is being trapped in the canopy. Mineralisation rates in the surface layer at SCR are indeed significantly higher than at PFR, but most of the deposited labile organic matter does not reach the zone of active methanogenesis at depth (Table 3). Flooding can also affect methane emission directly as evidenced by our observations with the tidal experimental container. Methane is released primarily from the lower 20 to 30 cm of the *Phragmites* and *Scirpus* stems emerging above the sediment (Van der Nat et al. 1998). Hence, at high tide when the lower part of the plant stems are under water, methane emission to the atmosphere should decrease (Figure 4). The extent of a tidal effect would differ between PFR and SCR as a result of flooding differences and so contribute to spatial differences

during high tide. In the long run, this direct effect of flooding on methane emission would only matter when methane is oxidised during high tide and not merely delayed from escaping the sediment until low-tide conditions are again present. Accordingly, on the basis of tidal elevation we would expect higher emission at SCR due to lower bulk sediment oxidation rates (Van der Nat et al. 1997) and higher allochthonous inputs of labile carbon at the surface (Table 3). However, observed methane emissions are higher at PFR suggesting that spatial zonation in methane emission is due to zonation of plant species rather than tidal elevation.

In a parallel study, we have studied the effect of *Phragmites* and *Scirpus* on methane dynamics in constructed wetlands (Van der Nat & Middelburg 1998a, b) so that we could eliminate nonplant effects. We concluded that methane fluxes from freshwater marshes are primarily controlled by methane production with methane oxidation and transport being of secondary importance. Moreover, methane emission and production in *Phragmites* systems were higher than those in *Scirpus* systems due to (1) a higher contribution of methanogenesis to mineralisation, (2) lower rates of rhizospheric methane oxidation and (3) carbon addition by *Phragmites*.

Similar observations have been made in this study. Methane production rates and the contribution of methanogenesis to mineralisation were higher at PFR than SCR (Table 3). Carbon addition by *Phragmites* was likely higher than that by *Scirpus* given higher rates of carbon dioxide fixation (up to 2.9 vs. 2.0 mol $m^{-2}$ $d^{-1}$ at PFR and SCR, respectively), higher sedimentary organic carbon contents at depth (4.26 vs 1.84 mmol $cm^{-3}$ at PFR and SCR, respectively) and higher mineralisation rates at depth (Table 3). Moreover, *Phragmites* has its roots and especially its rhizomes extended too much greater (i.e. methanogenic) depths and in much larger quantity than *Scirpus*. Supportive evidence for a difference in carbon addition also comes from the typical convex pore-water methane profile suggesting net production during spring, autumn and winter at PFR (Figure 2). The variation in residence time of methane in pore-water with respect to production ($\sim$8 for PFR and $\sim$15 for SCR, = reservoir size/methane production) further indicates the difference in production at both sites.

Observed higher rates of rhizospheric oxidation and methane production suppression by *Scirpus* compared to *Phragmites* (Van der Nat et al. 1998a, b) possibly also contributed to the observed spatial variability. Rhizospheric methane oxidation can effectively limit methane emission even when potential bulk sediment oxidation rates are already relatively high (due to tidal elevation) because oxygen transported by plants is injected deep in the sediment, where methanotrophs around the root constitute an efficient sink for methane before it can enter the roots (King 1994; Van der Nat et al. 1997).

Moreover, methane consumption rates associated with root material from *Scirpus* are higher those associated with *Phragmites* roots (Van der Nat et al. 1997). In conclusion, spatial variability in methane emission at our tidal marsh was more controlled by the dominant plant species than flooding of the sediment.

## Acknowledgements

We thank Joop Nieuwenhuize and Yvonne Maas for analytical assistance, Riks Laanbroek, Matthieu Starink and Marten Hemminga for reading an earlier version of this manuscript. This is publication no. 2569 of the Netherlands Institute of Ecology, Yerseke and contribution no. 115 to the EU programme ELOISE, project BIOGEST (ENV4-CT96-0213).

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