Methanogenesis and methane emissions: effects of water table, substrate type and presence of *Phragmites australis*

Simon Grünfeld, Hans Brix

Department of Plant Ecology, Institute of Biological Sciences, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark

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Abstract

Effects on methanogenesis and CH$_4$ emission of three water table positions, sediment composition and presence or absence of the emergent macrophyte *Phragmites australis* (Cav.) Trin. ex Steud. were studied in outdoor experimental mesocosms. Water table position significantly affected methanogenesis and CH$_4$ emission, the rates being 40% and 60% lower, respectively, in vegetated organic sediments with a water table 22 cm below the surface as compared with vegetated inundated sediments. Due to the high water-holding capacity of organic sediments, rates of methanogenesis and CH$_4$ emission in organic sediments with a water table 8 cm below the sediment surface were only slightly, but not statistically significantly different from rates in inundated sediments. Sandy sediments with water tables 8 cm below the sediment surface had very low methanogenic activity as compared with organic sediments (1 versus 55 mmol m$^{-2}$ per day). The presence of *P. australis* in inundated sediments attenuated the rate of methanogenesis by 27%, enhanced the proportion of CH$_4$ oxidised from 7% to 18%, and as a result attenuated CH$_4$ emission by 34%. In vegetated sediments CH$_4$ emission peaked at midday and was lowest during the night and early morning in concert with the diurnal changes in internal convective flow in the plants. Internal gas transport through the plants accounted for 62% of the CH$_4$ emitted from vegetated sediments while ebullition dominated in unvegetated sediment. ©1999 Elsevier Science B.V. All rights reserved.

Keywords: Gas exchange; Sediment redox potential; CH$_4$ oxidation; Common reed; Global change

1. Introduction

Natural and agricultural wetlands have been estimated to account for about 40% of the current global CH$_4$ emission (Cicerone and Oremland, 1988; Khalil and Shearer, 1993).
For this reason much attention has been paid to the factors controlling methanogenesis and CH₄ emission from various types of wetlands and their contribution to the global warming effect of CH₄. The emission of CH₄ into the atmosphere is the net result of methanogenesis and CH₄ oxidation, the rates of which are affected by a number of factors. The magnitude and/or onset of methanogenesis depends mainly on sediment redox conditions (Wang et al., 1993), the amount of substrate, especially acetate (Boon and Mitchell, 1995), and sediment temperature (Zeikus and Winfrey, 1976), whereas the rate of CH₄ oxidation mainly depends on the prevalence of oxic zones resulting from oxygen entering from the atmosphere into the surface sediment or from roots of plants into their rhizosphere (Epp and Chanton, 1993; Gilbert and Frenzel, 1995). Recent anthropogenically-induced environmental changes, such as increasing global temperature, eutrophication and water table changes affect methanogenesis and CH₄ oxidation (Verville et al., 1998) and may potentially change the role of wetlands in the global CH₄ cycle. It is therefore, important to assess how changes in these parameters may influence the rates of methanogenesis and CH₄ oxidation in wetland sediments and alter the balance between the two processes, in order to be able to forecast future emission from wetland ecosystems.

Emergent macrophytes can both enhance and attenuate wetland CH₄ emission. Enhancement occurs through production and release of organic matter (Holzapfel-Pschorn et al., 1986; Schütz et al., 1991), and by transportation of CH₄ via molecular diffusion or convective flow through the internal gas spaces of the plants, thus bypassing oxidation in the anoxic/oxic interface (Shannon and White, 1994; Sorrell and Boon, 1994; Shannon et al., 1996). Many species of emergent macrophytes possess a convective flow mechanism which is many times more efficient in transporting gases than diffusion alone (Brix et al., 1992), and hence these species may accelerate the emission of CH₄ from wetlands (Brix et al., 1996). On the other hand, emergent macrophytes may attenuate CH₄ emission by providing oxygen to the methanotrophic bacteria associated with the rhizosphere. Between 10% and 90% of CH₄ production has been reported to be oxidised in the rhizospheres of various species of wetland plants (Epp and Chanton, 1993; Denier van der Gon and Neue, 1996), the magnitude depending mainly on the efficiency and capacity of their gas transport system (Conrad, 1989). Furthermore, emergent macrophytes can reduce methanogenesis by increasing sediment redox potential due to their root oxygen release (Schipper and Reddy, 1996) or due to the effect of transpirational water loss. Up to several litres of water per square meter per day can be transpired from a dense stand of wetland plants (Dacey and Howes, 1984), and the transpired water may be replaced by surface water containing electron acceptors, such as oxygen and nitrate, which may reduce methanogenesis and increase CH₄ oxidation.

The Common Reed (Phragmites australis (Cav.) Trin. ex Steud.) is a dominant plant species in much of the land-water ecotone throughout Europe, and is known to have particularly high rates of convective flow (Brix et al., 1992; Armstrong et al., 1996). Phragmites-dominated wetlands therefore provide a significant source of CH₄ emission to the atmosphere (Brix et al., 1996). In this study we examine the effects of water table position, type of sediment and presence of P. australis on methanogenesis and CH₄ emission from freshwater sediments in order to improve the understanding of how future anthropogenically-induced changes in these environmental parameters may affect the global emission of CH₄ from Phragmites-dominated wetlands.
2. Materials and methods

2.1. Experimental set-up

The study was conducted in 15 l buckets (height 30 cm, diameter 27 cm) using three water table positions, organic and sandy sediments, and presence or absence of vegetation, *P. australis*, as set out in Table 1. In order to reduce the size of the set-up to fit the available work capacity, only a subset of the potential combinations of treatments was tested. Five replicates of each treatment were arranged randomly in an outdoor, non-shaded area. The sediments used in the treatments were collected from a natural wetland site and amended with either a commercial organic sphagnum (50% v/v) or fine sand (80% v/v). A drainage layer consisting of 5 cm coarse gravel was placed in the bottom of each bucket. The drainage layer was separated from the overlying sediment by a geotextile to prevent the overlying sediment from blocking the drainage layer and to impede root penetration into the drainage layer. Connecting the drainage layers (via darkened tubing) to constant head tanks controlled the water tables in the buckets. Six-months old potted seedlings of *P. australis* (height about 20 cm) were planted in the buckets in July. The root systems were gently washed free of sediment and the initial plant-weight measured. The plants were fertilised regularly with a commercial nutrient solution (Brøste, Denmark). Initial measurements showed that the methanogenic bacteria in the sediments were substrate limited after 4 weeks. Hence, in order to achieve rates comparable with those found in natural reed vegetations on organic sediments (Sorrell et al., 1997), acetate in the form of sodium and ammonium acetate was added every day thereafter, by a 20 cm needle and syringe to produce a concentration of approximately 8 mM in the interstitial water. Measurements of methanogenesis and CH$_4$ emission were initiated after 9 weeks of growth.

2.2. Plant characteristics

Shoot density and height of the ten tallest shoots from each bucket were measured every two weeks during the 12-week experiment. At the end of the experiment all above and below ground plant tissues were harvested and separated into roots, rhizomes, stems and leaves, and oven-dried for 48 h at 105°C. The specific leaf area was determined on a representative sample of leaves from each bucket.
2.3. Sediment characteristics

Temperature, pH and redox potentials were measured at four depths (2, 8, 16 and 24 cm) prior to harvesting at the end of the experiment. A 60 cm long, 0.5 mm wide platinum electrode, referenced against a standard calomel electrode and calibrated with saturated Quinhydrone solutions (pH 4 and 7), was used to measure depth gradients of redox potential. The electrode was allowed to stabilise for 10 min before each reading. Sediment taken from three cores in each bucket was mixed and oven-dried at 105°C. The total carbon and nitrogen contents of the oven-dried sediment were determined with a CHN-Analyzer (NA 2000, Fisons Instruments, Italy). Loss of ignition was determined by combustion at 550°C for 6 h and the phosphorus content was analysed on an ICP (Perkin-Elmer, USA) after extraction of the ash with 1 M HCl.

2.4. Methanogenesis

At the end of the experiment prior to plant harvesting, three sediment cores were taken from each bucket with a sharpened 5 cm diameter Perspex corer and fractionated into 8 cm sections. The depth-fractions from the three corers were pooled and immediately transferred to an anoxic chamber (COY Laboratory Products INC, MI, USA). Four 30 ml subsamples from each depth-fraction were transferred to gas-tight 100 ml incubation flasks. The flasks were shaken and flushed thoroughly with nitrogen gas in order to remove all pre-existing CH4. Then 5 ml deoxygenated cysteine solution (final concentration = 0.03%) was added in order to ensure anoxic conditions, and the flasks were once again shaken and flushed. To test for substrate limitation, two of the samples were amended with acetate (final concentration 8 mM), and two were incubated without acetate as described by Sorrell et al. (1997). Finally, all flasks were sealed with plastic caps fitted with Teflon lined septa and incubated at in situ temperature (12°C) in a temperature-controlled water bath in the dark. Headspace samples were withdrawn by an injection syringe (Dynatech precision sampling, Louisiana, USA) after 3, 7 and 20 h, and analysed for CH4 on a Shimadzu Model GC-8A Gas Chromatograph using a FID (110°C), nitrogen carrier gas (50 ml min⁻¹) and a Porapak T column (50°C). Before sampling, the flasks were vigorously shaken for 1 min to ensure equilibrium between headspace and sediment CH4 concentrations. Concentrations were corrected for CH4 dissolved in the sediment interstitial water using the Bunsen Solubility Coefficient for CH4 (Yamamoto et al., 1976), and rates calculated from the slope of the methane-time plot and headspace volume. The time courses of CH4 concentration were linear \( r^2 > 0.975 \) during 3–20 h after incubation start. Dry weights of the sediments were measured after drying for 48 h at 105°C, and methanogenesis rates calculated on both volumetric and dry weight bases. The daily addition of acetate to the buckets acetate-saturated the methanogens as addition of acetate to the in vitro incubations had no significant effect on the measured rates of methanogenesis. As a consequence, data for the four sub-samples from each sediment profile, two with and two without added acetate, were pooled in the further data treatment.
2.5. Methane emission

The emission of CH$_4$ from the buckets was measured over a period of 13 days just prior to the termination of the experiment by placing a gas exchange chamber over each bucket and measuring the change in headspace CH$_4$ concentration over time. Each gas exchange chamber consisted of a permanently installed clear Perspex base chamber (40 cm × 40 cm × 100 cm) and a removable clear Perspex top chamber of the same dimensions. The joint between the two chamber sections consisted of a water-filled channel lining the top of the base chamber into which the top chamber was inserted. The water-filled channel acted as a gas-tight seal between the chamber sections. Placing the buckets and the base chambers in ca. 5 cm water sealed the bases of the chambers during incubation. Test experiments showed that less than 6% of injected CH$_4$ gas (chamber concentration 1000 ppmv) leaked out of the chambers during 24 h incubation. The base chambers were equipped with copper cooling coils for temperature and humidity control and fans to secure complete mixing within the chambers. The cooling coils were connected via pumps to a refrigerated water bath (Lauda ETK50, Germany) and the flow of water regulated to ensure ambient temperature levels inside the chamber. Air temperature and humidity were monitored inside and outside the chambers by sheltered sensors (Rotronic MP100TS-000, Switzerland) and irradiance by a PFD sensor (Optisk Laboratorium, Denmark). Signals from all sensors were collected by a data-logger (Delta-T logger, AT Delta-T, UK). An example of the continuous records of ambient temperature, relative air humidity and irradiance during the period of gas-exchange measurements is shown in Fig. 1(a). Irradiance increased rapidly after sunrise, fluctuated between 500 and 1300 μmol m$^{-2}$ s$^{-1}$ during the day, and fell rapidly back to zero around sunset. Ambient temperature was relatively stable during daytime, with an average of 16°C and then decreasing to 4°C by night. Humidity fluctuated between 50% and 65% (RH) during the day and increased to 90–95% at sunset. During 1 h incubations the conditions inside the chambers did not deviate significantly from the ambient conditions, except towards the end of the incubation period where temperature and humidity increased slightly above ambient levels (Fig. 1(b)).

Fig. 1. Examples of (a) continuous records of ambient air temperature, relative air humidity (RH) and photon flux density (PFD) during 4 days from 17.09.1996 to 20.09.1996, and (b) a 1 h sampling series comparing air temperature and humidity inside the chamber with ambient levels. Black bars on the x-axis indicate dark period.
Methane emissions were measured during 1 h incubations every day at noon for 5 days. To elucidate the diurnal variations in emission, additional measurements were carried out in the planted treatments starting at 02:00, 08:00, 12:00 and 18:00 hours. Furthermore, in order to quantify the emission through the plants, emission rates were measured before and after the culms of *P. australis* were cut below the water level in the high water table treatment. Gas samples were taken every 10 min through a rubber-septum sampling port using 2 ml syringes and analysed for CH₄ within 5 min as described above. The last sample in every series was analysed for CO₂ on a Shimadzu Model GC-8A Gas Chromatograph using a TCD (110°C), helium carrier gas (60 ml min⁻¹) and a Porapak T column (50°C). Carbon dioxide concentrations were always close to ambient levels (320–360 ppmv), hence we presume that photosynthesis was not significantly affected.

Rates of CH₄ oxidation were calculated as the difference between the daily rate of emission and the corresponding rate of methanogenesis in the sediments and are expressed as a percentage of methanogenesis.

### 2.6. Statistics

Data were analysed by analysis of variance (ANOVA). Significant differences between means were determined with Tukey HSD tests. All data were tested for normal distribution and for homogeneity of variance by Cochran’s test and, if necessary, log-transformed to stabilise variances. Paired sample for means (two-tailed) were used to test for differences in emission rates before and after the culms of *P. australis* were cut, and for differences in methanogenesis in the absence and presence of acetate. Tests of significance were conducted at the 0.05 probability level unless otherwise stated.

### 3. Results

#### 3.1. Plant and sediment characteristics

The final biomass of *P. australis* was not affected by water table position, but was significantly lower in the sandy sediment than in the organic sediment (Table 2). Final biomass allocation and shoot height was the same in all treatments, but shoots from the sandy sediment reached this height 3 weeks earlier than shoots from the other treatments (data not shown).

The organic and nutrient content of the organic sediment was significantly higher than that of the sandy sediment, but neither water table nor presence or absence of vegetation affected the sediment composition (Table 3). However, the redox potential differed significantly between treatments, especially in the upper layers of the sediments (Fig. 2). Redox potentials at 2 cm depth were ca. 200 mV in sediments with a low water table, while sediments with intermediate and high water table were more reduced (Fig. 2(a)). The capillary rise of water in the organic sediments tended to water-saturate the upper layers in the intermediate water table treatments. Unvegetated sediment was slightly more reduced, although not statistically significant, compared with the corresponding vegetated high water table
Table 2
Final plant biomass (DW), leaf area, shoot density and shoot height for *Phragmites australis* grown for 12 weeks at different water table positions and sediment composition

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Type of sediment</th>
<th>Water table position</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Org</td>
<td>Org</td>
</tr>
<tr>
<td>Leaf (g DW bucket⁻¹)</td>
<td>46.1 ± 9.9 b</td>
<td>34.5 ± 6.2 b</td>
</tr>
<tr>
<td>Stem (g DW bucket⁻¹)</td>
<td>52.6 ± 13.3 b</td>
<td>45.7 ± 10.2 b</td>
</tr>
<tr>
<td>Root (g DW bucket⁻¹)</td>
<td>39.6 ± 10.4 b</td>
<td>41.0 ± 11.3 b</td>
</tr>
<tr>
<td>Rhizome (g DW bucket⁻¹)</td>
<td>122 ± 11 b</td>
<td>121 ± 12 b</td>
</tr>
<tr>
<td>Total biomass (g DW bucket⁻¹)</td>
<td>261 ± 20 b</td>
<td>242 ± 37 b</td>
</tr>
<tr>
<td>Leaf area (cm² bucket⁻¹)</td>
<td>1193 ± 83 b</td>
<td>998 ± 169 b</td>
</tr>
<tr>
<td>Shoot density (No. bucket⁻¹)</td>
<td>118 ± 30 b</td>
<td>122 ± 19 b</td>
</tr>
<tr>
<td>Mean final shoot height (cm)</td>
<td>112 ± 20 a</td>
<td>106 ± 37 a</td>
</tr>
</tbody>
</table>

*a Figures with different letters (within rows) differ significantly *(p < 0.05).* Mean ± SD, *n = 5.*

Table 3
Properties of the sediments in the buckets

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Type of sediment</th>
<th>Water table position</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Org</td>
<td>Org</td>
</tr>
<tr>
<td>Vegetation</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Water table position</td>
<td>Low</td>
<td>Int</td>
</tr>
<tr>
<td>Loss on ignition (% DW)</td>
<td>37.9 ± 2.3 b</td>
<td>38.0 ± 2.3 b</td>
</tr>
<tr>
<td>Organic C (mmol C g⁻¹ DW)</td>
<td>17.4 ± 1.8 b</td>
<td>17.7 ± 1.4 b</td>
</tr>
<tr>
<td>Nitrogen (mmol N g⁻¹ DW)</td>
<td>741 ± 73 b</td>
<td>753 ± 56 b</td>
</tr>
<tr>
<td>Phosphate (mmol P g⁻¹ DW)</td>
<td>33.8 ± 4.3 b</td>
<td>29.7 ± 3.4 b</td>
</tr>
<tr>
<td>pH (depth = 10 cm)</td>
<td>7.4 ± 0.2</td>
<td>7.3 ± 0.2</td>
</tr>
</tbody>
</table>

*a Figures with different letters (within rows) differ significantly *(p < 0.05).* Mean ± SD, *n = 5.*

treatment (Fig. 2(b)). Redox potentials in the sandy sediment (intermediate water table) were significantly higher than in the corresponding organic sediment (Fig. 2(c)).

3.2. Methanogenesis

Methanogenesis rates varied significantly with depth, water table, plant cover and sediment composition. Overall the methanogenesis rates were significantly lower for the low water table treatment compared with the intermediate and high water table treatments, and sandy sediments had significantly lower rates than organic sediments (Table 4). Furthermore, the rates were about 40% higher in sediments without plants compared with the corresponding sediment with plants (Table 4). A two-way ANOVA (Table 5) showed that both sediment depth and water table position affected the rate of methanogenesis in the organic sediments, and furthermore that there was a strong interaction between the two factors. The highest rates were recorded in the bottom horizons (56–82 nmol g⁻¹ DW h⁻¹) while rates in the upper horizons were highest in the high water table treatment (50 nmol g⁻¹ DW h⁻¹) and very low (< 1 nmol g⁻¹ DW h⁻¹) in the low water table treatment (Fig. 3).
Fig. 2. Depth profiles of redox potential in buckets (a) with organic sediments and vegetated by *Phragmites australis* at high (+2 cm, ○), intermediate (−8 cm, □) and low (−22 cm, □) water table positions; (b) with organic sediments and a high water table with (○) or without (■) plants, and (c) with intermediate water tables (−8 cm) and plants on sandy (△) or organic (●) sediment. Measurements were taken prior to harvesting at the termination of the experiment. Mean ± SE, n = 5.

Table 4
Estimated CH$_4$ production rate, diurnal variation in CH$_4$ emission and CH$_4$ oxidation (% of CH$_4$ production) from treatments that differ in sediment composition, plant cover and water table position$^a$

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Type of sediment</th>
<th>Vegetation</th>
<th>Water table position</th>
<th>Methanogenesis (mmol m$^{-2}$ per day)</th>
<th>CH$_4$ emission (mmol m$^{-2}$ per day)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Org</td>
<td>High</td>
<td>Low</td>
<td>41 ± 11 b</td>
<td>17 ± 3</td>
</tr>
<tr>
<td></td>
<td>Org</td>
<td>Int</td>
<td>Low</td>
<td>55 ± 2 c</td>
<td>39 ± 9</td>
</tr>
<tr>
<td></td>
<td>Org</td>
<td>High</td>
<td>Int</td>
<td>68 ± 26 c</td>
<td>70 ± 11 c</td>
</tr>
<tr>
<td></td>
<td>Org</td>
<td>Int</td>
<td>High</td>
<td>92 ± 27 d</td>
<td>72 ± 12 c</td>
</tr>
<tr>
<td></td>
<td>Org</td>
<td>Int</td>
<td>High</td>
<td>1.0 ± 0.5 a</td>
<td>85 ± 22 c</td>
</tr>
<tr>
<td></td>
<td>Sand</td>
<td>Int</td>
<td>Int</td>
<td>46 ± 26 c</td>
<td>6 ± 13 c</td>
</tr>
<tr>
<td></td>
<td>Sand</td>
<td>Int</td>
<td>Int</td>
<td>1.0 ± 0.5 a</td>
<td>7 ± 3 c</td>
</tr>
</tbody>
</table>

CH$_4$ oxidation (% of methanogenesis)

<table>
<thead>
<tr>
<th>Time of day</th>
<th>08:00 hours</th>
<th>12:00 hours</th>
<th>18:00 hours</th>
<th>02:00 hours</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>08:00 hours</td>
<td>22 ± 1 a</td>
<td>46 ± 13 b</td>
<td>55 ± 12 b</td>
<td>n.d.</td>
<td>46 ± 9 c</td>
</tr>
<tr>
<td>12:00 hours</td>
<td>22 ± 1 a</td>
<td>46 ± 13 b</td>
<td>55 ± 12 b</td>
<td>n.d.</td>
<td>46 ± 9 c</td>
</tr>
<tr>
<td>18:00 hours</td>
<td>22 ± 1 a</td>
<td>46 ± 13 b</td>
<td>55 ± 12 b</td>
<td>n.d.</td>
<td>46 ± 9 c</td>
</tr>
<tr>
<td>02:00 hours</td>
<td>22 ± 1 a</td>
<td>46 ± 13 b</td>
<td>55 ± 12 b</td>
<td>n.d.</td>
<td>46 ± 9 c</td>
</tr>
</tbody>
</table>

$^a$Figures with different letters (within rows) differ significantly. Mean ± SD, n = 4 or n = 5.

$^b$n.d.: not determined.

Table 5
Two-way analysis of variance (ANOVA) for sediment methanogenesis rates measured in treatments with three water table positions (low, intermediate and high) and at three depth horizons of the sediment (0–8, 8–16 and 16–24 cm). All treatments were vegetated by *Phragmites australis*

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Df</th>
<th>Sum of squares</th>
<th>F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main effects: water table</td>
<td>2</td>
<td>21535</td>
<td>7.7</td>
<td>0.002</td>
</tr>
<tr>
<td>depth</td>
<td>2</td>
<td>3548</td>
<td>47.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interactions: water table × depth</td>
<td>4</td>
<td>5481</td>
<td>6.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>36</td>
<td>8256</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

...
Fig. 3. Vertical profiles of methanogenesis in organic sediments with: (a) low water table (−22 cm) with plants (*P. australis*), (b) intermediate water table (−8 cm) with plants, (c) high water table (+2 cm) with plants, and (d) high water table (+2 cm) without plants. The rate of methanogenesis in the sandy sediment was <0.2 nmol g\textsuperscript{−1} h\textsuperscript{−1}.

Mean ± SD, *n* = 5.

3.3. Methane emission

During the in situ incubations the CH\textsubscript{4} concentration in the gas exchange chambers generally increased linearly with time (Fig. 4(a)), but in the unvegetated sediment the increase was more step-wise (Fig. 4(b)) indicating that emission largely occurred by ebullition (Chanton and Whiting, 1995). In spite of this, the slopes of the regression lines were always used to calculate the emission rates. In the calculation of the daily rates of emission it was presumed that emission from the unvegetated sediment was constant during a diurnal cycle (Sorrell and Boon, 1992), whereas for the vegetated treatments, the diurnal measurements were used.

Fig. 4. Examples of time course of CH\textsubscript{4} emission from a midday sampling series measured from (a) an organic sediment vegetated with *Phragmites australis*, and (b) an unvegetated sediment.
Methane emission varied with water table, time of the day, plant cover and sediment type (Table 4). The daily rate of CH₄ emission in the low water table treatment was significantly lower than that in the intermediate and high water table treatments, and sandy sediment had significantly lower rates than organic sediments (Table 4). In the vegetated treatments, the CH₄ emission varied diurnally, being highest at midday and in fact sometimes higher than the average rate of methanogenesis in the sediment (Table 4). During the night and early in the morning the emission was reduced to 40–60% of the maximum rates measured during the day. As unvegetated sediments had higher rates of methanogenesis and lower rates of CH₄ oxidation, the daily emissions were about 50% higher than in the vegetated sediments. The effects of presence of *P. australis* on CH₄ emission were further studied by measuring emission before and after the culms had been cut and the internal gas spaces of the culms blocked by water. Emission rates were significantly (*p < 0.01*) reduced by 62% after cutting, indicating that plant-mediated transport was important (data not shown).

### 3.4. Methane oxidation

In the vegetated sandy sediments we only made measurements of CH₄ emission during the day, and CH₄ oxidation could not therefore, calculated. In organic sediments with low water table, the proportion of CH₄ being oxidised constituted 46% of the amount produced, while the percentage was only about 20% in the high and intermediate water table treatments, and only 7% in the unvegetated sediment (Table 4). In absolute terms, the oxidation rates varied between 7.3 mmol m⁻² per day in the unvegetated sediment and 18.8 mmol m⁻² per day in the low water table vegetated sediment.

### 4. Discussion

In this study we have shown a clear correlation between water table location and methanogenesis and CH₄ emission from sediments vegetated by *P. australis*, a general pattern that has also been seen in other wetland studies (e.g. Dise et al., 1993; Shannon and White, 1994; Roslev and King, 1996). This is not surprising as the oxygen availability and hence potential for aerobic degradation of organic matter and CH₄ oxidation increase when the water table is lowered. However, the rates from sediment with a water table position only 8 cm below the surface did not differ significantly from those in inundated sediments, probably because the capillary forces of the organic sediments kept a high moisture content and a low redox potential in the upper sediment layers in spite of the lower water table. This suggests that a slight decrease in water table to a position a few cm below the sediment surface will only affect methanogenesis and CH₄ emission in organic sediments marginally. The water table needs to be dropped to a level at least 10 cm below the sediment surface to have a significant effect on CH₄ emission.

The method of CH₄ transport controls the rate at which CH₄ produced in the sediment reaches the atmosphere and whether or not it bypasses the zone of oxidation. In this study 62% of the CH₄ emission from the vegetated sediments during midday occurred through the internal gas-spaces of the plants, which falls within the range observed in other studies (Chanton et al., 1992; Sorrell and Boon, 1994; Banker et al., 1995; van der Nat et al., 1998).
Rates of CH₄ emission from vegetated sediment peaked at midday and were 50–150% higher than the relatively constant rates observed in the morning and during the night. Methane emission was higher than methanogenesis during the day, showing that CH₄ accumulated in the sediments during the night and was emitted to the atmosphere mainly through the plants during the day. Peaks in emission rates were associated with high solar illumination, high air temperatures and low humidities, factors that are known to stimulate pressurised convective flow in *P. australis* (Armstrong et al., 1996; Brix et al., 1996). We therefore, conclude that the diurnal pattern observed in CH₄ emission was largely due to the diurnal changes in internal convective flow in the plants. This is in line with studies made by others (Chanton et al., 1993; Whiting and Chanton, 1996) who found that species of emergent macrophytes, which only possess diffusive gas exchange in their tissue, do not exhibit these diurnal variations in CH₄ emission. Consequently, it seems that convective flow contributes significantly to the CH₄ emission. This suggestion is supported by Sorrell and Boon (1994), who found that diffusive CH₄ fluxes in the internal gas spaces of *Eleocharis sphacelata* R. Br. were an insignificant mechanism of CH₄ emission compared with convective flow. However, CH₄ oxidation is also higher in vegetated than in unvegetated sediments, leading to lower emission rates probably because of the activity of methanotrophic bacteria in the rhizosphere of the plants (King, 1994; Denier van der Gon and Neue, 1996; van der Nat and Middelburg, 1998). Transpiration-induced transport of alternative electron acceptors into the sediments can also contribute to the higher CH₄ oxidation in vegetated sediments (Dacey and Howes, 1984). However, it was not possible in our experimental set-up to distinguish between the effects of plant-released oxygen and electron acceptors introduced as an effect of plant transpiration. The water supply from the constant head tanks entered the drainage layer of the buckets, and although the redox potentials were not significantly higher in the vegetated inundated sediments, the rates of methanogenesis were significantly lower there compared to the unvegetated sediment. The high oxygen demand of the sediments could mask the effect of oxidants from supply of water and root oxygen release, so that a significant reduction in methanogenesis rates could be observed without any significant increase in measured redox potentials (Jespersen et al., 1998).

It is still unclear whether a changing climate, as forecasted by the global climate models, would result in reduced or increased CH₄ emission from *Phragmites*-dominated wetlands. Changes in temperature and precipitation and the associated effects on water table position will influence methanogenesis and CH₄ emission in a predictable manner (Roulet et al., 1992; Moore, 1994). However, climate changes will also affect plant production and seasonality as well as the area of distribution of *P. australis* (Matthews, 1993). Therefore, these factors need to be evaluated in order to quantify the role of *Phragmites*-dominated wetlands in the global CH₄ cycle. This study has shown that the methanogenesis and CH₄ emission in sediment vegetated with *P. australis* are very dynamic in time and space. The plants themselves, as well as water table position and sediment composition affect methanogenesis, CH₄ oxidation and CH₄ emission. Understanding how these processes are linked to anthropogenically induced changes is fundamental to any reliable prediction of the future contribution of *Phragmites*-dominated wetlands to the global CH₄ emission.
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References


