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Organic sediment formed during inundation of a degraded fen grassland emits large fluxes of CH₄ and CO₂

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Abstract

Peatland restoration by inundation of drained areas can alter local greenhouse gas emissions by altering rates of CO₂ and CH₄ emissions. Factors that can influence these emissions include the quality and amount of substrates available for anaerobic degradation processes and the sources and availability of electron acceptors. In order to learn about possible sources of high CO₂ and CH₄ emissions from a rewetted degraded fen grassland, we performed incubation experiments that tested the effects of fresh plant litter in the flooded peats on pore water chemistry and CO₂ and CH₄ production and emission.

The position in the soil profile of the pre-existing drained peat substrate affected initial rates of anaerobic CO₂ production subsequent to flooding, with the uppermost peat layer producing the greatest specific rates of CO₂ evolution. CH₄ production rates depended on the availability of electron acceptors and was significant only when sulfate concentrations were reduced in the pore waters. Very high specific rates of both CO₂ (maximum of 412 mg C d⁻¹ kg⁻¹ C) and CH₄ production (788 mg C d⁻¹ kg⁻¹ C) were observed in a new sediment layer that accumulated over 2.5 years since the site was flooded. This new sediment layer was characterized by overall low C content, but represented a mixture of sand and relatively easily decomposable plant litter from reed canary grass killed by flooding. Samples that excluded this new sediment layer but included intact roots remaining from flooded grasses had specific rates of CO₂ (max. 28 mg C d⁻¹ kg⁻¹ C) and CH₄ (max. 34 mg C d⁻¹ kg⁻¹ C) production that were 10–20 times lower, and were comparable to those of newly flooded upper peat layer. Lowest rates of anaerobic CO₂ and CH₄ production (range of 4–8 mg C d⁻¹ kg⁻¹ C and <1 mg C d⁻¹ kg⁻¹ C) were observed when all fresh organic matter sources (plant litter and roots) were excluded. In conclusion, the presence of fresh organic substrates such as plant and root litter originating from plants killed by inundation has a high potential for CH₄ production, whereas peat without any fresh plant-derived material is relatively inert. Anaerobic CO₂ and CH₄ production in peat only occurs when some labile organic matter is available, e.g. from remaining roots or root exudates.

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1 Introduction

Peatlands are recognized as a key player in the atmospheric greenhouse gas (GHG) budget. Although only covering ~3% of total land area, the carbon accumulated in peatlands corresponds to almost half of total atmospheric C stock (Houghton et al., 1990; Gorham, 1991). Natural peatlands act as sinks for atmospheric CO₂ and as sources of the methane (CH₄), which is a more efficient GHG. The net climate impact of peatlands is nearly zero (Drösler et al., 2008). Drainage of peatland, e.g. for agricultural use, forestry or for peat extraction, turns peatlands from long-term sinks to significant sources of CO₂, while CH₄ emissions cease. This leads to a dramatic increase in net climate impact (Drösler et al., 2008; Augustin, 2001; Nykänen et al., 1998; Alm et al., 2007). In 2007, drained German peatlands used as cropland and grassland emitted about 24 000 and 13 000 Gg CO₂, respectively, corresponding to approximately 3% and 2% of total anthropogenic CO₂ emissions in Germany (Umweltbundesamt, 2009). Furthermore, drainage causes irreversible chemical and physical changes in peat characteristics and overall peat C loss. However, nutrients (e.g. N, P and K) remain in the drained peat. The resulting strong increase in nutrient concentrations leads to eutrophication of the remaining peat (Zak et al., 2008).

Peatland restoration via rewetting (inundation), i.e. by raising the local groundwater table, is currently being implemented in Germany with the explicit goal of reducing GHG emissions (Höper et al., 2008). Rewetting principally reduces CO₂ emissions but can often lead to a sharp increase in CH₄ release, as confirmed by field studies in fen (Hendriks et al., 2007; Wilson et al., 2008) and bog ecosystems (Tuittila et al., 2000; Drösler, 2005).

Extremely high CH₄ emissions were observed in a flooded fen grassland in NE Germany (up to 205 g C m⁻² y⁻¹) in the years following flooding. Contrary to expectations, in this location the net climate impact after flooding was even higher than under drained conditions as the ecosystem did not immediately return to its long-term CO₂ sink function (Chojnicki et al., 2007; Höper et al., 2008). As yet, the reason for the excessive

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CH₄ release and the weak CO₂ sink function of this flooded fen grassland is not known. However, precise knowledge of these processes is needed to predict if and when a reduction of the expected net climate impact will take place and to propose optimized rewetting measures.

5 A possible source of the high CH₄ production and cause of the weak CO₂ sink function after flooding could be the rapid anaerobic decomposition of organic matter in the nutrient-rich upper part of the peat layer. It has previously been shown that this layer releases large quantities of nutrients and dissolved organic carbon once waterlogged conditions have been re-established in peat (Zak and Gelbrecht, 2007). Furthermore, primary production and the deposition of plant litter in the top layer may increase CH₄ emissions under anoxic conditions (Tuittila et al., 2000; Juutinen et al., 2003; Wilson et al., 2008), as labile organic matter is a prerequisite for anaerobic CO₂ and CH₄ formation (Glatzel et al., 2004; Segers, 1998; Conrad, 1989). Raising the water table not only affects GHG exchange but also the vitality and composition of the vegetation (Drösler, personal communication; Clymo, 1984). On the above-mentioned fen grassland in NE Germany, the vegetation, which was dominated by reed canary grass (*Phalaris arundinacea*), died back during the first year of inundation and mixed with sand to form a new sediment layer with a high content of relatively fresh plant litter.

20 Therefore, we hypothesize that fresh plant litter as a major component of the newly-formed sediment can account for a large proportion of the major CH₄ emissions and reduced CO₂ sink strength as a result of increased CO₂ formation. The aim of this study was to quantify the anaerobic CO₂ and CH₄ production potential of different organic substrates from this highly degraded fen under rewetted conditions. Two incubation experiments were performed to show how GHG emissions differ in pure peat and peat with root litter, compared to the newly-formed sediment layer, while also taking pore water chemistry into account. On the basis of the incubation experiments, the risk of high CO₂ and CH₄ emissions in inundated degraded fen grasslands can be assessed.

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2 Material and methods

2.1 Site description

The sampling site “Polder Zarnekow” is located in the valley of the river Peene, 8 km west of the town Demmin (Mecklenburg-Vorpommern, NE Germany; 53°52.5′ N, 12°52.3′ E). The climate is continentally-influenced temperate with a mean annual air temperature of 8.5 °C and a mean annual precipitation of 544 mm. The mean daily temperature is −0.8 °C in January and 16.7 °C in July (Teterow meteorological station, 24 km south-west of the sampling site). The fen is characterized as a river valley mire system with percolation mires dominated by groundwater flow (Joosten and Succow, 2001).

The site was drained and used in low-intensive agriculture in the 18th century and as intensive grassland in the 20th century (Lenschow et al., 2003). In October 2004, the site was rewetted in the course of an EU-funded conservation project. Since then, field measurements of gas exchange have been performed at this site (see introduction and discussion). Due to substantial peat loss and shrinkage, Zarnekow polder now appears as a shallow lake permanently inundated with a water level of about +0.1 to +0.5 m (Zak and Gelbrecht, 2007). The subjacent peat layer is up to 10 m thick. Due to peat mineralization during decades of drainage, the upper 0.3 m approximately can be classified as highly decomposed peat (H 10) according to the von Post scale (Puustjärvi, 1970), also called “muck-soils” (Okruszko, 1995). Below, slightly to moderately decomposed peat (H 3 to 6) can be found which has either not been affected by the drainage or has been only slightly affected. The former grassland vegetation, dominated by reed canary grass (*Phalaris arundinacea*), died back during the first year of inundation. Since the second year of inundation the water body of the shallow lake has been dominated by water plants like *Ceratophyllum* and *Lemna sp.* adapted to high nutrient concentrations. An organic sediment layer up to 0.3 m thick was formed at the bottom of the shallow lake with a high content of relatively fresh organic matter from the dying off plants. Under the prevailing eutrophic and inundated conditions, the substrate

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pool is assumed to be continuously refilled by litter from submerged macrophytes and helophytes from the nearby littoral zone.

2.2 Incubation experiments

Two different incubation experiments under simulated flooding were performed to elucidate the impact of different organic substrates on GHG emissions. In the first experiment, peat from different soil depths was incubated (hereafter peat profile incubation) (see Table 2). The second experiment (hereafter top soil substrate incubation) focused on three kinds of organic substrates taken from the top layer of the soil. These substrates differed in the amount of fresh plant litter or roots present and in the time elapsed since the flooding of the wetland. In both experiments temperature was kept constant and the anaerobic production potential for CO₂ and CH₄, as well as pore water chemistry, were investigated. An overview of selected characteristics of the incubated soils, including chemical data, is given in Table 1.

2.2.1 Peat profile incubation: experimental set up and chemical analysis

Peat samples were extracted by spade in August 2004 (prior to rewetting on site) from three successive, superimposed soil horizons: upper peat layer (from -0.1 to -0.2 m depth), middle peat layer (from -0.5 to -0.6 m), and lower peat layer (from -1.0 to -1.2 m) (3 replicates each). The groundwater level at the time of sampling was lower than the deepest sampling depth. Consequently, we assume that aerobic conditions were present for all samples taken from different soil depths. Visible fresh roots were removed by hand from the upper peat layer during peat homogenization. However, it was impossible to remove all fresh plant-derived material. As the upper peat layer was the rooting zone of the grassland vegetation, it can be assumed that some fresh organic matter e.g. from rhizodeposition may be present in the peat.

For incubation, water-tight PVC boxes (0.6×0.4×0.4 m; 96 L) were used. The incubation vessels were filled with ~40 kg mixed peat samples from the different horizons (0.2 m high, ~0.05 m³). For experimental rewetting of the peat, 3.4 mM sodium chloride

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solution, equivalent to the average ionic strength of the fen-feeding groundwater was added. To ensure water-saturated conditions throughout the experiment, the water level was kept 5 cm above the peat surface and evaporation loss was replaced with deionized water. Incubation lasted for 363 days in a climate chamber at a constant temperature of 20 ± 1 °C under dark conditions to avoid algae growth. The incubation vessels were kept open to the atmosphere except during the brief intervals when gas fluxes were measured.

The rates of CO₂ and CH₄ emitted from the various substrate surfaces were determined using the closed chamber method, measuring the concentration change in the headspace over time (Schinner, 1993). For this purpose, the incubation vessels were closed for one hour by gas-tight lids equipped with plugs for gas sampling. Gas samples were taken from the headspace using evacuated glass flasks (100 mL) and analyzed by the gas chromatograph (GC 145, Shimadzu) (Lofffield et al., 1997). The linearity of the increase in gas concentration was tested by taking samples at 0, 0.5 and 1 h. Sampling was done every two weeks for the first 8 weeks and monthly thereafter.

Emission rates of CO₂ and CH₄ (mg C d⁻¹ kg⁻¹ C) were calculated by regression with two sampling points (after 0 and 1 h) based on the change in gas concentration and related to carbon content of the peat substrate and time according to Eq. (1):

$$\text{emission rate} = \frac{M \times \rho \times V}{R \times T \times A} \times \frac{dc}{dt} \times \frac{24}{10^3 \times Ct} \times f \quad (1)$$

in which M is the molar mass of carbon dioxide (44 g mol⁻¹) or methane (16 g mol⁻¹), ρ is the air pressure (Pa), V the volume of the head space (m³) in the static measurement method applied in the peat profile incubation or, in case of the dynamic measurement method used in the top soil substrate incubation, the air flow (m³ h⁻¹), R is the gas constant (m³ Pa K⁻¹ mol⁻¹), T the temperature (K), A the area of the incubation vessel (m²), dc the difference of gas concentrations (ppm) during the reference period dt (h), Ct is the carbon content of the peat substrate (kg m⁻²), and f the conversion factor from molecule to element (0.27 for CO₂ to C and 0.75 for CH₄ to C).

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For the analysis of pore water chemistry, rechargeable dialysis samplers were used, as described in detail by Zak and Gelbrecht (2007). Briefly, the one-chamber-sampler (~0.05 L) was adjusted in the peat at 1–11 cm depth at the beginning of the incubation experiment. For sampling, the chamber water was completely removed with a pipette and directly renewed by oxygen-free deionized water in order to avoid oxygen input into the anoxic peat. Sampling was done every two weeks for the first 8 weeks and monthly thereafter over the 363-day incubation period. To prevent oxidation and subsequent precipitation of redox-sensitive substances, pore water samples were taken quickly and stabilized with hydrochloric acid (2 M HCl). Pore water pH was determined using a pH probe (WTW), the redox potential by a Pt electrode with Ag/AgCl reference electrode, and measured values were adjusted to standard hydrogen potential and pH of 7. Soluble reactive phosphorus (SRP) was analyzed photometrically by the molybdenum blue method, NH₄-N was determined photometrically by the indophenol method. Fe and Ca concentrations in the pore water were analyzed by flame atomic absorption spectrometry and sulfate concentrations by ion chromatography. DIC and DOC were measured with a C-Analyzer. Further details on fixation of anoxic pore water samples and chemical analysis can be found in Zak and Gelbrecht (2007).

2.2.2 Top soil substrate incubation: experimental set up and chemical analysis

Three different organic substrates were investigated: (1) organic sediment formed post-flooding (from fragmented fresh roots and leaves, which had accumulated to a thickness of up to 0.3 m above the original fen surface over a period of 2.5 years), (2) a highly decomposed peat with intact *Phalaris arundinacea* roots taken from –0.05 to –0.2 m depth (hereafter “peat with roots”), and (3) a highly decomposed peat without any fresh plant material taken from –0.1 to –0.2 m depth and with roots removed (hereafter “peat only”). Samples were taken from the same location as for the peat profile incubation in April 2007 (2.5 years after rewetting). The soil depths given refer to the soil surface prior to rewetting, so as to be comparable. Organic sediment and “peat only” were sampled by inserting a plexiglass tube ($d=0.13$ m) into the lake bottom, removing the

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supernatant lake water and obtaining the desired organic substrate. “Peat with roots” was extracted by spade from a place with no overlying organic sediment and removal of the upper 0.05 m in order to exclude living above-ground plant material. All three substrates were taken from locations under water-saturated soil conditions. Therefore, we assume equal anaerobic starting conditions for subsequent incubation. Each of the three organic substrates was mixed for several minutes by hand and put into the PVC incubation vessels ($h=0.35$ m, $d=0.15$ m, substrate 0.27 m high, ~ 0.005 m³, 3 replicates each). Sub-samples of the substrates were taken directly after sampling for chemical characterization (see below). Multi-chamber dialysis samplers were inserted into the upper 10 cm of the soil columns to investigate pore water chemistry (for details see Zak et al. (2010)). In addition, silicone probes were inserted at a depth of approximately 0.23 m in the substrate to determine gas concentrations within the substrates (see below). Lake water from the sampling site was added until the substrates were completely covered, in order to maintain anaerobic conditions. The incubation vessels were closed with gas-tight lids equipped with ports for gas measurements and incubated at a constant temperature of 15 ± 1 °C under dark conditions for 53 days.

The carbon dioxide and methane fluxes from the sediment or peat substrates were determined with a steady state flow-through chamber system combined with automated gas analysis equipment. A constant air flow of 6×10^{-3} m³ h⁻¹ was adjusted in the open headspace of the incubation vessels. The measurement of the inflow/outflow (ambient air/headspace air) concentrations was carried out continuously over the entire incubation period. The gas concentrations were analyzed by a photoacoustic infra-red multi-gas monitor (INNOVA 1312, INNOVA AirTech Instruments, Ballerup, Denmark). Since the gas monitor does not compensate fully for cross-interference of CH₄ and water vapour at high concentrations, the air was partially dried at 5 °C by a gas conditioning system (Rosemount) to reduce water vapour concentrations before measurement. The measurement frequency was three times per hour per incubation vessel with three replications each. Gas fluxes (mg C d⁻¹ kg⁻¹ C) were calculated based on the difference in gas concentration and related to carbon content of the sediment or

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peat substrate and time according to Eq. (1) (see previous section).

As a further indicator for the intensity of the gas production processes, CO₂ and CH₄ concentrations in the pore water of the substrates were determined using adapted silicone probes according to Kammann et al. (2001). A silicone probe consisted of a curled-up silicone tube (OD=8 mm, ID=6 mm, L=1.0 m) connected with a stainless steel capillary tube (OD=1.6 mm, ID=0.75 mm, L=0.32 and 0.21 m) and a 3-port-valve at each end as well as an injection port at one end. Gas exchange takes place between the interior space of the probe and the substrate only by diffusion through the walls of the silicone tube until equilibrium is reached. Gases within the silicone tube reached 95% equilibrium with the surrounding atmosphere within several hours (Kammann et al., 2001).

Sampling was done at intervals of 1 to 11 days. The air in the silicone tube was moved to the end with the injection port by inserting water into the silicone probe and taking a gas sample using a gas-tight syringe. Silicone probe samples were diluted with N₂ to concentrations which were in the measurement range of the GC, filled into evacuated 100 ml glass flasks and analyzed with the gas chromatograph (Shimadzu GC-14B, ECD for CO₂, FID for CH₄) (Lofffield et al., 1997). After sampling, the water and air in the silicone probes were removed and the probes flushed with N₂ to ensure anaerobic conditions.

For the analysis of pore water chemistry, the dialysis samplers were removed at the end of incubation, cleaned with deionized water and the water of the soil chambers obtained using pipettes. The pore water was analyzed for pH, redox potential, soluble reactive phosphorus (SRP) and Fe and Ca concentrations as described above.

For solid C and N analysis subsamples of the substrates were taken prior to incubation, sediment/peat substrates and plant material were separated by sieving (2 mm), dried at 40 °C (sediment/peat substrate) or 70 °C (plant material) for 5 days, ground and then analyzed (Elementar CN analyzer vario MAX; combustion at 1100 °C; thermal conductivity detector). Measured values for the sediment/peat substrates were corrected for water content when dried at 105 °C.

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2.3 Statistics

Repeated measures analysis of variance by fitting linear mixed-effects models with Tukey post-hoc comparisons were performed with R 2.10.0 (R, 2009) to compare the time series of gas emissions (significance level of $p < 0.001$). SPSS 17.0 was used for one-way ANOVA and Tukey post-hoc comparisons to compare means of pore water chemistry analysis and cumulative gas fluxes (significance level of $p < 0.05$).

3 Results

3.1 Peat profile incubation

The lowest carbon content and the highest nitrogen and phosphorus contents were found in the uppermost peat layer compared to underlying peat samples (see Table 1). Consequently, lowest C:N and C:P ratios – both indicators for substrate availability – were observed in the upper peat layer (12 and 320), whereas the lower peat layer had the highest values (18 and 1550).

In accordance with the peat characteristics, the three differently decomposed peat samples differed significantly in their CO₂ emissions ($F_{2,6} = 12.6$, $p = 0.0072$). Anaerobic CO₂ production was highest ($p < 0.001$) at the top of the soil profile. A strong increase in CO₂ production in the upper peat layer was found during the first 14 incubation days and, after approximately 150 days, emission rates increased until day 278 (see Fig. 1a). Anaerobic CO₂ production in the middle peat layer was lower than in the upper peat layer but little higher than in the lower peat layer. In the middle peat layer, an increase in anaerobic CO₂ production was detected two weeks later than in upper peat layer. It stayed relatively stable thereafter and decreased at the end of incubation. In the lower peat layer, anaerobic CO₂ production showed some fluctuations over the entire incubation period. The cumulative CO₂ fluxes for the incubation period of 363 days in the upper peat layer were 1.7 times higher than in the middle peat layer and 2.3 times higher than in the lower peat layer (see Table 4).

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CH₄ emissions from the middle and lower peat layer were zero over the entire incubation period. The upper peat layer emitted no CH₄ until day 152. From day 243 onwards, CH₄ emissions increased strongly and reached a plateau at the end of incubation (maximum of 46.9 mg C d⁻¹ kg⁻¹ C) (see Fig. 1b). Cumulative CH₄ fluxes over 363 days were 3.4 g C kg⁻¹ C in the upper peat layer and around zero for the middle and lower peat layer.

During the 363 incubation days, a small fraction of the initial C was respired as CO₂ or CH₄ (Table 4), e.g. from the upper peat layer only 0.55% and 0.4% of the initial C were respired as CO₂ and CH₄.

The experimental rewetting caused a reduction in the redox potential and an increase in pH in all treatments (see Table 3). Sulfate concentrations were generally high at the beginning of the rewetting period. In the upper peat layer, sulfate concentrations decreased rapidly during the first weeks of incubation and stayed around 0.1 mM after day 125 (see Fig. 3). Sulfate concentrations decreased slowly in the middle peat layer but increased in the lower peat layer over the entire incubation period. Fe concentrations increased strongly in the upper peat layer and to a much smaller extent in the middle peat layer. In the lower peat layer, Fe concentrations in the pore water were low overall and showed only a marginal increase over time. The highest concentrations of soluble reactive phosphorus (SRP), ammonium, dissolved inorganic and organic carbon, and calcium were generally found in the pore water of the upper peat layer. These concentrations were 2 to 200 times higher than in underlying peat (Table 3, for single results see Zak and Gelbrecht, 2007).

3.2 Top soil substrate incubation

The C and N content were determined separately for the <2 mm fraction of the sediment/peat and the plant material. The C content of the sediment/peat was surprisingly low in the organic sediment (13%) and in the “peat with roots” (16%), and highest in the “peat only” (40%) (see Table 1). This fact was explained by sand present in the organic sediment and “peat with roots” samples. The C:N ratios were similar in all three soil

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substrates (~11). The C:N ratio of the plant material was 32 for the organic sediment and 38 for the “peat with roots”.

The differences in CO₂ emissions between the three sediment/peat substrates were much more pronounced than for the peat profile incubation ($F_{2,6}=600.5$, $p<0.0001$, see Fig. 1c). Anaerobic CO₂ production was highest in the organic sediment, with a strong increase at the beginning of incubation (maximum of 412 mg C d⁻¹ kg⁻¹ C) and a continuous decline after day 8. CO₂ production in the “peat with roots” was more than 10 times lower than in the organic sediment ($p<0.001$) and increased slowly over the incubation period (range of 17–28 mg C d⁻¹ kg⁻¹ C). In the “peat only”, CO₂ emissions were even lower than in the freshly rewetted upper peat layer of the peat profile incubation and stayed in the range of 4–8 mg C d⁻¹ kg⁻¹ C over the entire incubation period. Cumulative CO₂ fluxes for 53 days were approximately 13 times higher in the organic sediment than in the “peat with roots” and 43 times higher than in the “peat only” (see Table 4).

CO₂ concentrations in the substrate pore water sampled via silicone probes (see Fig. 2) were high in all substrates (1%=10 000 ppm). The release of gas bubbles was observed on several sampling occasions. Analogous to gas emissions from the surface, CO₂ concentrations were significantly higher in the organic sediment ($p<0.001$) and increased strongly over the incubation period until day 46 (up to 29%), with a decrease thereafter. The CO₂ concentrations in “peat with roots” and “peat only” did not differ significantly and increased slowly over time (up to 9.0 and 9.7%, respectively).

With regard to CH₄ production, there were fundamental differences between the three sediment/peat substrates that were incubated (see Fig. 1d). CH₄ emissions from the organic sediment were higher compared to the two other substrates ($p<0.001$) and increased strongly from day 6, reaching a maximum on day 10 (788 mg C d⁻¹ kg⁻¹ C), followed by a continuous decrease until the end of incubation. In contrast, the “peat with roots” showed low CH₄ emissions until day 7 (<1 mg C d⁻¹ kg⁻¹ C) and increased slowly thereafter to a maximum of 34 mg C d⁻¹ kg⁻¹ C at the end of incubation. Thus, the same level was reached as that found for the upper peat layer in the peat profile

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incubation (see Fig. 1b), whereas CH₄ emissions from “peat only” stayed low over the entire incubation period (<1 mg C d⁻¹ kg⁻¹ C). Cumulative CH₄ fluxes (for the incubation period of 53 days) were 31 times higher in the organic sediment than in the “peat with roots” and 675 times higher than in the “peat only” (Table 4).

5 Fundamental and significant differences between the three organic substrates were also observed for CH₄ concentrations in the silicone probes ($F_{2,6}=246.1$, $p<0.0001$, see Fig. 2). CH₄ concentrations were highest in the organic sediment (up to 54%) where they remained relatively constant after day 25. In contrast, in the “peat with roots” CH₄ concentrations started low but increased strongly from day 21 onwards
10 until they reached a maximum of 44% at the end of incubation. CH₄ concentrations in the “peat only” were lower than in the other two organic substrates (maximum of 1.6% at the start of incubation) and even decreased over the incubation period.

Despite the high gas flux rates from the organic sediment, only 3.5% of the initial total carbon was respired as either CO₂ or CH₄ during 53 days of incubation (Table 4). From
15 “peat with roots” and “peat only” the fraction respired was lower (0.2% and 0.04%).

Comparing the gas fluxes of the two incubation experiments, the organic sediment emitted most CO₂ and CH₄ compared to all peat substrates – both peat from different horizons in the peat profile incubation and “peat with roots” and “peat only” in the top soil substrate incubation (Fig. 1 and Table 4). The “peat with roots” showed emissions
20 for both gases that were similar to those of the upper peat layer and emissions from the “peat only” are identical to those of the lower peat layer from the first incubation experiment (see average flux per day in Table 4).

The redox potential (measured at the end of the incubation period) was similar in all three organic substrates (see Table 3). The pH was slightly higher in the “peat with roots”. The concentration of soluble reactive phosphorus (SRP) in the pore water was
25 30 times higher in the organic sediment than in the “peat with roots” and 8 times higher than in the “peat only”. Fe concentrations were highest in the “peat only” (1.5 mM) and the “peat with roots” (1.4 mM) and lowest in the organic sediment (0.4 mM). Ca concentration was highest in “peat only” compared to the other two substrates.

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Despite the fact that the two incubations were performed at different temperatures (20 vs. 15 °C), incubation periods (363 vs. 53 days), and time since flooding (immediately after versus 2.5 years later) their respective findings can be regarded as complementary and some general conclusions can be drawn regarding the effect of different kinds of substrates on the anaerobic production of GHGs. The upper peat layer (from peat profile incubation) and the “peat with roots” (from the top soil substrate incubation) are comparable substrates, since both consist of highly decomposed peat taken from a depth of –0.1 to –0.2 m with some remaining plant-derived material. Both show similar CO₂ and CH₄ production rates (Fig. 1 and Table 4).

4.1 Anaerobic CO₂ production – indication of microbial activity

Anaerobic CO₂ production is an indicator for instantaneously available organic substrates from peat and fresh organic matter over a wide range of substances and energetic quality (Freibauer and Augustin, 2009). The organic sediment consisted mainly of fresh plant litter mixed with sand and microbial degradation emitting CO₂ was, as hypothesized, substantially higher than in the other organic substrates (see Fig. 1c and Table 4). CO₂ emissions from the surface of the organic sediment showed a substrate-limited reaction (hyperbolic function with two parameters; $R^2=0.87$; Paul and Clark, 1996) from day 9 onwards. The gas accumulated in the substrate matrix, as demonstrated by the gas concentrations in silicone probes (up to 29% CO₂ in the organic sediment, see Fig. 2). In all other substrates with peat from both experiments, specific rates of anaerobic CO₂ production were significantly lower. However, significant differences were also recorded between these substrates (Fig. 1). The upper part of the peat profile released significantly more CO₂ than peat from deeper down the profile. This could be due to some residual fresh plant-derived material (e.g. from rhizodeposition) which was presumably present in the uppermost peat layer and which could not be removed entirely before incubation. In the situation in which fresh plant roots

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were present in the peat substrate (“peat with roots”), microbial degradation processes releasing CO₂ were more active compared to peat without fresh organic matter (“peat only”). However, the differences were not statistically significant (see Fig. 1c). The peat in the top soil substrate incubation has had 2.5 years of anaerobic decomposition to deplete “labile” substrates. Despite this fact, CO₂ production in “peat only” (taken 2.5 years after rewetting) was in the same range than those in the lower peat layer and “peat with roots” was comparable to maximum CO₂ emissions from the upper peat layer.

These findings are in accordance with those of another study where rates of CO₂ and CH₄ production were generally greatest in the surface peat, where a strong cover of vegetation had developed and the content of fresh or slightly decomposed plant litter was highest (Glatzel et al., 2004). This suggests that it is the availability of readily degradable plant material that determines CO₂ and CH₄ production rates, whereupon it only accounts for a small fraction of the total C pool. In our study, only 0.9% of the initially existing C from the upper peat layer and 3.5% from the organic sediment were lost as CO₂ or CH₄ (see Table 4).

Anaerobic CO₂ production depends not only on the availability of labile organic substrates but also on the availability of oxidizing substances such as nitrate, ferric iron and sulfate. The concentration of nitrate in the pore water was low throughout the incubation (data not shown). The strong increase in iron concentrations and the depletion of sulfate in the pore water of the upper peat layer indicated that an excess of labile organic substances were available there, in contrast to peat deeper down the profile (Fig. 3). Microbial activity was lower in the middle and lower peat layer as there was a lack of suitable substrate for degradation processes due to the absence of fresh material and the humified nature of the peat. Hence, sulfate concentrations in the pore water decreased only slowly or even increased (see Fig. 3 or Table 3) and favourable conditions for CH₄ production were not established throughout incubation.

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4.2 Onset of methanogenesis and magnitude of CH₄ emissions

The production of CH₄ indicates the instantaneous availability of fresh and energy-rich substrates, and it often decreases with depth, as does the availability of organic matter (Segers, 1998).

CH₄ emissions from the upper peat layer started after a 182-day lag-phase. This retarded onset of methanogenic activity, as well as the zero CH₄ emissions from the middle and lower peat layer, can be explained by competition for organic substrates with iron or sulfate reducers. Thus, it took 125 incubation days before sulfate was almost completely gone (see Fig. 3) and methanogenesis started in the upper peat layer (see Fig. 1b). Therefore, we assume that methanogens were inhibited by competition with iron-reducing or sulfate-reducing bacteria (Smolders et al., 2002). The slow recovery of methanogenesis during the first weeks under waterlogged conditions in the upper peat layer could also be caused by aerobic conditions in the field before sampling. Aerobiosis could damage a methanogenic population either directly by poisoning or indirectly by C-starvation due to competition for substrates with aerobic microorganisms (Segers, 1998). However, Knorr and Blodau (2009) found that methanogenesis recovered locally quite quickly from aeration. Finally, decomposition of organic matter and subsequent production of GHGs can also be inhibited by the presence of organic electron acceptors such as humic substances (Segers, 1998; Blodau, 2002), which might be the case in the humified middle and lower peat layer (Zak and Gelbrecht, 2007).

The substrates used for the top soil substrate incubation were under anaerobic conditions in the field for a longer period (waterlogged conditions for 2.5 years). We assume, therefore, that methanogens were not inhibited by aerobiosis in this experiment. Conditions favourable for methanogenesis were established quickly in the organic sediment with its large amount of labile, fresh plant material. Here, CH₄ emissions started immediately, increased rapidly and were extremely high. From day 10 onwards, CH₄ production showed a substrate-limited reaction (hyperbolic function with two parameters; $R^2=0.89$; Paul and Clark, 1996).

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In accordance with the substantially lower release of GHGs, the microbial degradation of organic matter was significantly lower in the two peat substrates (“peat with roots” and “peat only”). However, differences in decomposition rates could also clearly be seen between these substrates. Microbial activity in the “peat with roots” with its fresh root material was generally higher and methanogenesis started quickly and increased continuously until the end of incubation. The CH₄ formed was not emitted continuously through the surface but accumulated in the substrate up to concentrations of 44%, as shown by the silicone probe results (see Fig. 2). This finding indicates that CH₄ production in the peat was higher than detected in the surface emissions. The “peat only” – consisting of peat substrate without any fresh organic matter – showed, as anticipated, very low microbial decomposition and methanogenesis stayed very low over the entire incubation period (Figs. 1d and 2).

Our findings confirm the results by Tuittila et al. (2000), who observed extremely low CH₄ emissions from highly decomposed bog peat at an abandoned cut-away site and emphasized the importance of fresh plant litter and root exudates as substrates for methanogenesis. A pulse-labeling experiment showed that recently-assimilated carbon was translocated to the roots and available to soil microbial community as root exudates and emitted as CH₄ quickly (King and Reeburgh, 2002). The low availability of appropriate organic substrate for methanogens caused the lack of CH₄ production from a Dutch cut-over bog remnant; peat with relatively low lignin and phenolic content, and with a low C:N, C:P and C:K ratio had a higher potential for CH₄ production (Smolders et al., 2002). The highest rates of anaerobic CH₄ production occurred in samples close to the soil surface with fresh peat accumulation and a high water table (Glatzel et al., 2004). The largest anaerobic CO₂ and CH₄ production were found in peat samples close to the soil surface (Reiche et al., 2009). Our findings show that it is not the quality of the peat substrate itself but the presence of fresh organic matter that determines anaerobic GHG production.

Plants no longer growing on a site can be an important control of CH₄ production rates – the highest CH₄ production occurred at a bog site where sedges had been

growing in the recent past and decomposing sedge residue in the peat below the surface supported CH₄ production (Yavitt et al., 1997). Field measurements on our sampling site revealed extremely high CH₄ emissions (up to 205 g C m⁻² y⁻¹) in the years following rewetting (Chojnicki et al., 2007; Höper et al., 2008). The results of our incubation experiments suggest that the main source of the released CH₄ on-site is the recently formed organic sediment layer. The reed canary grass (*Phalaris arundinacea*) at the Zarnekow site – due to its high productivity even under flooded conditions – produced, prior to its dying off during the first year of inundation, a sufficiently large C pool for CH₄ production (accumulation of 650 g C m⁻² y⁻¹). The main part thereof was presumably transferred to the organic sediment layer. In addition, the substrate pool is assumed to be continuously refilled with labile organic matter by litter from submerged macrophytes and helophytes from the nearby littoral zone under the prevailing eutrophic and inundated conditions.

5 Conclusions

Although laboratory incubations are not considered suitable for assessing the actual relevance of peatlands as a source or sink for CO₂ and CH₄, they can be used as an indicator for the production potential of CO₂ and CH₄ in a certain substrate.

Depending on drainage and land use history after rewetting of fens, highly eutrophic shallow lakes are formed. The bottom of these lakes is typically characterized by highly decomposed peat layers at the top and less decomposed peat layers up to several metres below. The original grassland vegetation is not adapted to inundated conditions and therefore dies back, forming an organic sediment layer. This fresh organic substrate has an extreme potential for CH₄ production. Consequently, the release of CH₄ could be high at least as long as eutrophic and inundated conditions last.

In contrast, pure peat without fresh plant-derived material seems to be relatively inert. Significant methane emissions cannot be expected from pure peat layers under permanently inundated conditions in the field as long as readily degradable substances are lacking.

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To some extent, GHG production may occur when some labile organic matter is available, e.g. from rhizodeposition or fresh litter from plant roots. However, depending on the availability of alternative electron acceptors (e.g. iron and sulfate), CH₄ production will start after an extended lag-phase and the available C pool is more limited than in the newly-formed sediment layer.

The risk of high CO₂ and CH₄ emissions after restoration is limited to waterlogged conditions and the simultaneous presence of readily available and energy-rich substrate for microbial decomposition processes (i.e. eutrophic peat, fresh plant litter, or newly-formed organic sediment, e.g. from plants that are not adapted to flooding). The rapid colonization of flooded areas by adapted plant species such as *Typha sp.*, reeds or sedges might also reduce this potential risk as their litter is slowly decomposed (Brinson et al., 1981). These plants enhance, by means of a shunt-mechanism, the transfer of CH₄ into the atmosphere, but at the same time they transport oxygen into the root zone, which increases methane oxidation (Lai, 2009). In sum, this could lead to a considerable reduction in CH₄ emissions compared to the present situation.

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Table 1. Selected peat characteristics for peat from different horizons, as well as sediment/peat substrates incubated in two experiments sampled from the Zarnekow polder (mean, $n=3$).

	Peat layers (m)	dbd (g cm ⁻³)	H ^c	OM ^d (%)	C ^e (%)	N ^e (%)	C:N ^e	C:P
Peat profile incubation								
Upper peat layer	-0.1 to -0.2	0.30 ^a	10	76	40	3.4	12	320
Middle peat layer	-0.5 to -0.6	0.18 ^a	6	84	44	2.8	16	720
Lower peat layer	-1.0 to -1.2	0.12 ^a	3	89	48	2.7	18	1550
Top soil substrate incubation								
Organic sediment	+0.05 to +0.3	0.2 ^b	-	40	13 (s) 44 (p)	1.1 (s) 1.4 (p)	11 (s) 32 (p)	-
“Peat with roots”	-0.05 to -0.2	0.4 ^b	10	28	16 (s) 44 (p)	1.4 (s) 1.2 (p)	11 (s) 38 (p)	-
“Peat only”	-0.1 to -0.2	0.3 ^b	10	76	39.8	3.5	11	-

^a Dry bulk density from Zak and Gelbrecht (2007).

^b Dry bulk density estimated.

^c Degree of peat decomposition according to von Post-scale (Puustjärvi, 1970; Zak and Gelbrecht, 2007).

^d Organic matter in % of dry weight determined by loss of ignition.

^e Top soil substrate incubation: C- and N-content were determined separately for (s) sediment/peat substrate (<2 mm fraction) and (p) plant material.

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Table 2. Overview of the two incubations performed.

	Peat profile incubation	Top soil substrate incubation
Duration	363 days	53 days
Substrates incubated (3 replicates each)	Peat taken from different depths (upper, middle and lower peat layer)	Top peat layer with differing quality of plant litter (organic sediment, "peat with roots", "peat only")
Incubation conditions	20 ± 1 °C no light, water stagnant conditions	15 ± 1 °C no light, water stagnant conditions
Incubation vessels	Open PVC-boxes (0.6×0.4×0.4 m) with closure lid for gas exchange measurement	Continuously closed PVC-columns (d=0.15 m, h=0.35 m)
Substrate volume	h=0.2 m, V=0.05 m ³	h=0.27 m, V=0.005 m ³
Measurement of gas fluxes	CO ₂ and CH ₄ emission from surface (every two weeks/monthly, closed chamber method)	CO ₂ and CH ₄ emission from surface (continuously, flow-through system)
Determination of gas concentrations in pore water	–	CO ₂ and CH ₄ concentration in silicone probes (every 1–11 days)
Analysis of pore water chemistry	pH, redox potential, soluble reactive phosphorus (SRP), NH ₄ -N, SO ₄ ²⁻ , Fe, Ca, dissolved inorganic and organic carbon (DIC, DOC) concentrations in pore water (at beginning and end of incubation)	pH, redox potential, soluble reactive phosphorus (SRP), Fe and Ca concentrations in pore water (at end of incubation)

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Table 3. Characterization of pore water chemistry for the peat profile incubation and the top soil substrate incubation (letters indicate differences between the treatments, $p < 0.05$).

Incubation ^z	pH		Redox potential E_7 (V)		SRP (μ M)		NH ₄ -N (mM)		Concentrations in the pore water						DIC (mM)		DOC (mM)	
	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End
Peat profile incubation																		
Upper peat layer	6.0 ^a	6.7 ^a	0.51 ^a	0.14 ^a	0.13 ^a	144 ^a	0.02 ^a	1.86 ^a	7.01 ^a	0.00 ^a	0.01	2.37 ^a	3.43 ^a	11.9 ^a	2.80 ^a	29.2 ^a	6.58 ^a	44.4 ^a
Middle peat layer	5.9 ^a	6.8 ^a	0.57 ^{ab}	0.17 ^b	0.13 ^a	0.48 ^b	0.02 ^a	0.35 ^b	8.90 ^a	5.93 ^b	0.00	1.16 ^b	6.93 ^b	12.1 ^a	1.42 ^b	15.1 ^b	4.69 ^b	23.2 ^b
Lower peat layer	5.5 ^b	6.6 ^a	0.59 ^b	0.27 ^c	0.13 ^a	0.68 ^b	0.05 ^b	0.03 ^c	3.42 ^b	7.70 ^c	0.00	0.11 ^c	4.75 ^c	6.45 ^b	0.64 ^c	0.69 ^c	1.49 ^c	1.20 ^c
Top soil substrate incubation																		
Organic sediment		6.7 ^a		0.17 ^a		1085 ^a		–		–		0.35 ^a		9.06 ^a		–		–
"Peat with roots"		7.0 ^b		0.18 ^a		35.7 ^b		–		–		1.38 ^b		9.11 ^a		–		–
"Peat only"		6.9 ^a		0.14 ^a		129 ^c		–		–		1.50 ^c		15.3 ^b		–		–

^z Data given for the peat profile incubation: Start on day 1, End on day 363, further data and details see in Zak and Gelbrecht (2007); in the top soil substrate incubation data are available for the end of the incubation (on day 53). Letters a–c indicate significant differences between substrates, $p < 0.05$.

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Table 4. Cumulative CO₂ and CH₄ fluxes over the incubation period (363 days for peat profile incubation; 53 days for top soil substrate incubation), average per day (mean ± SD, *n*=3), total C in incubation vessels and C respired during incubation (given as total C and in % of total C) (letters indicate differences between the treatments, *p*<0.05).

	Cumulative flux over entire incubation period		Average flux per day		Total C at incubation start (g C)	Total C respired during incubation (g C)	% of total C respired during incubation	
	CO ₂ flux (g C kg ⁻¹ C)	CH ₄ flux (g C kg ⁻¹ C)	CO ₂ flux (g C d ⁻¹ kg ⁻¹ C)	CH ₄ flux (g C d ⁻¹ kg ⁻¹ C)			as CO ₂ (%)	as CH ₄ (%)
Peat profile incubation (363 days)								
Upper peat layer	5.5 (± 0.8) ^a	3.4 (± 0.4) ^a	0.02 (± 0)	0.01 (± 0)	4500	40.2 (± 5)	0.55	0.34
Middle peat layer	3.2 (± 0.4) ^b	0 ^b	0.01 (± 0)	0	3500	11.1 (± 1.3)	0.32	0
Lower peat layer	2.4 (± 1.3) ^b	0 ^b	0.01 (± 0)	0	2500	5.9 (± 3.2)	0.24	0
Top soil substrate incubation (53 days)								
Organic sediment	15.2 (± 1) ^a	20.3 (± 2.3) ^a	0.3 (± 0.02)	0.4 (± 0.04)	126 ^z	4.5 (± 0.4)	1.52	2.03
“Peat with roots”	1.2 (± 0.1) ^b	0.7 (± 0.3) ^b	0.02 (± 0)	0.01 (± 0)	296 ^z	0.6 (± 0.1)	0.12	0.07
“Peat only”	0.4 (± 0.1) ^b	0.03 (± 0) ^b	0.01 (± 0)	0	613 ^z	0.2 (± 0.03)	0.04	0.003

^z Estimated.

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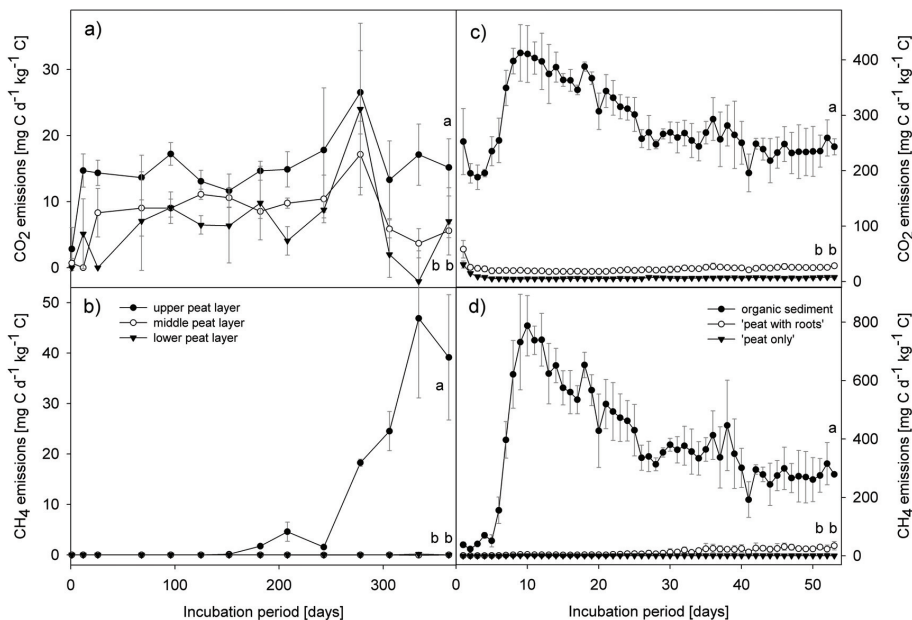


Fig. 1. CO₂ and CH₄ emissions from the surface for peat profile incubation (a, b) and for top soil substrate incubation (c, d) at constant temperature (20°C and 15°C) (mean ± SD, n=3; different letters on the left indicate significant differences, p<0.001).

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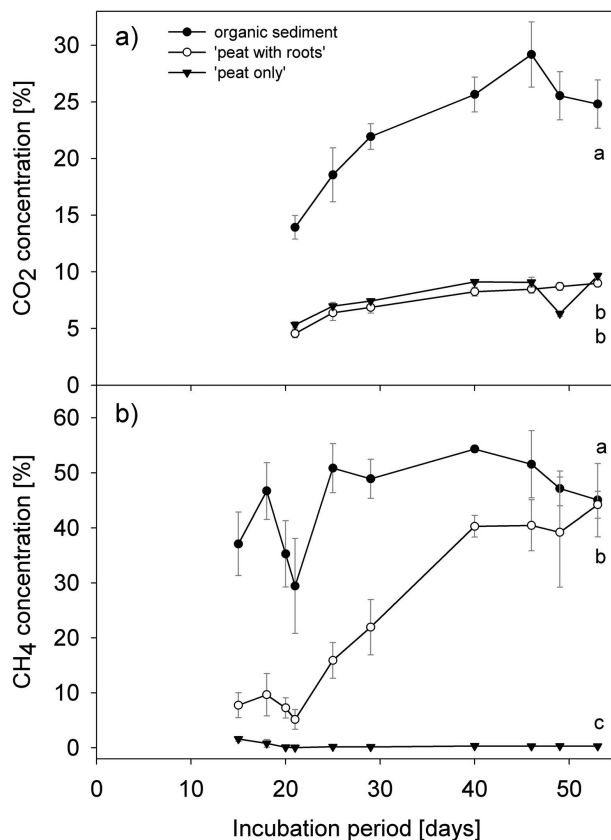


Fig. 2. Top soil substrate incubation: CO₂ (a) and CH₄ (b) concentrations in the silicone probes over a 53-day period at constant temperature of 15 °C (mean ± SD, $n=3$). Three organic substrates (organic sediment, “peat with roots” and “peat only”) taken from the top layer of the peat are compared (different letters indicate significant differences, $p<0.001$).

**CH₄ and CO₂
emissions from
degraded fen**

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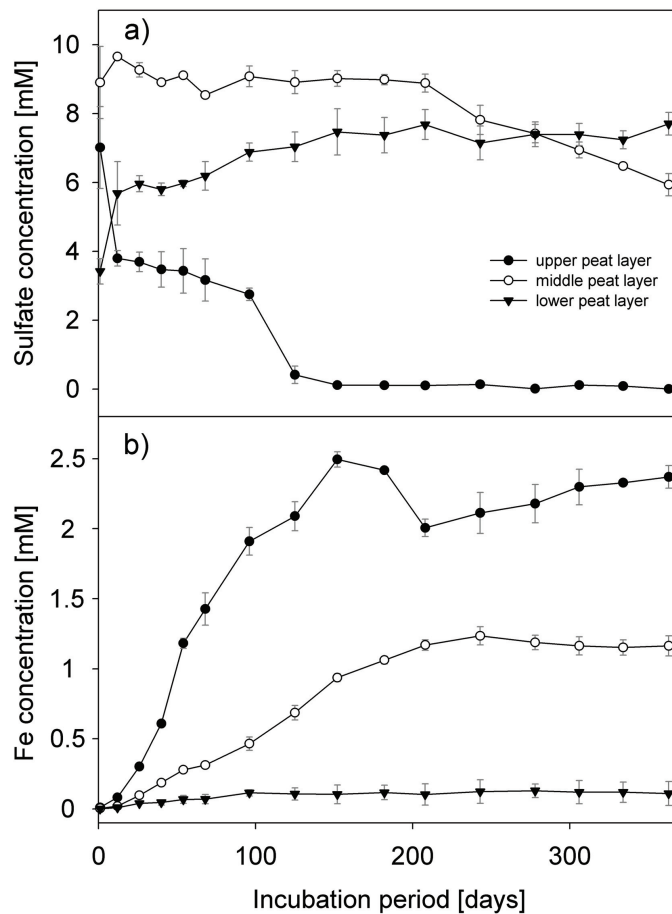


Fig. 3. Peat profile incubation: Sulfate (a) and iron (b) concentrations in the pore water of the upper, middle and lower peat layer over the 363-day incubation period (mean \pm SD, $n=3$).