

# Effects of short-term drying and irrigation on CO<sub>2</sub> and CH<sub>4</sub> production and emission from mesocosms of a northern bog and an alpine fen

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**Abstract** Atmospheric CO<sub>2</sub> and CH<sub>4</sub> exchange in peatlands is controlled by water table levels and soil moisture, but impacts of short periods of dryness and rainfall are poorly known. We conducted drying-rewetting experiments with mesocosms from an ombrotrophic northern bog and an alpine, minerotrophic fen. Efflux of CO<sub>2</sub> and CH<sub>4</sub> was measured using static chambers and turnover and diffusion rates were calculated from depth profiles of gas concentrations. Due to a much lower macroporosity in the fen compared to the bog peat, water table fluctuated more strongly when irrigation was stopped and resumed, about 11 cm in the fen and 5 cm in the bog peat. Small changes in air filled porosity caused CO<sub>2</sub> and CH<sub>4</sub>

concentrations in the fen peat to be insensitive to changes in water table position. CO<sub>2</sub> emission was by a factor of 5 higher in the fen than in the bog mesocosms and changed little with water table position in both peats. This was probably caused by the importance of the uppermost, permanently unsaturated zone for auto- and heterotrophic CO<sub>2</sub> production, and a decoupling of air filled porosity from water table position. CH<sub>4</sub> emission was <0.4 mmol m<sup>-2</sup> day<sup>-1</sup> in the bog peat, and up to >12.6 mmol m<sup>-2</sup> day<sup>-1</sup> in the fen peat, where it was lowered by water table fluctuations. CH<sub>4</sub> production was limited to the saturated zone in the bog peat but proceeded in the capillary fringe of the fen peat. Water table drawdown partly led to inhibition of methanogenesis in the newly unsaturated zone, but CH<sub>4</sub> production appeared to continue after irrigation without time-lag. The identified effects of irrigation on soil moisture and respiration highlight the importance of peat physical properties for respiratory dynamics; but the atmospheric carbon exchange was fairly insensitive to the small-scale fluctuations induced.

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## Introduction

CO<sub>2</sub> and CH<sub>4</sub> are known to act as greenhouse gases and increases in their concentration in the atmosphere

strongly contribute to global climate change (IPCC 2007). Northern wetlands, in particular peatlands, are one of the most important sources of non-anthropogenic methane emitted to the atmosphere and contribute 4–10% to global methane emissions (Fletcher et al. 2004). Peatlands have grown since the end of the last glaciation 8,000–12,000 years ago (Harden et al. 1992) and currently store about 1/3 of the total global carbon (Gorham 1991). It is yet uncertain how C sequestration and methane emissions will respond to climate change; hence, the understanding of the processes leading to C emissions from northern peatlands is required (Laiho 2006).

A number of controls on carbon cycling in peatlands have been identified. Soil moisture and air filled porosity regulate rates of gas and solute transport and microbial respiration. The availability of oxygen is important for heterotrophic and autotrophic respiration, as rates in oxic zones are considerably higher than in anoxic zones (Oquist and Sundh 1998; Updegraff et al. 1995). Methane production is furthermore a strictly anaerobic process (Fetzer et al. 1993) and can only proceed at high water content near or below the water table. Soil temperature has a positive effect on methanogenesis and often appears to be the strongest control on ecosystem respiration (Lafleur et al. 2005). Such relationships are not always straightforward though. Because cool temperature can enhance storage of organic material, the temperature response of heterotrophic respiration can be positively correlated with substrate quality (Updegraff et al. 1995). Organic matter decomposability varies between litter of vascular and non-vascular plants, and between individual species (Belyea 1996; Hogg 1993; Verhoeven and Toth 1995). It is usually lower in *Sphagnum* derived peat with high recalcitrance, low N content and potentially antibiotic properties. In peatlands dominated by aerenchymatic vascular plants, roots are able to bypass the unsaturated zone and allow oxygen to reach the rhizosphere (Brune et al. 2000). Besides, CH<sub>4</sub> efflux to the atmosphere can be mediated by plants. For example, up to 90% of the CH<sub>4</sub> flux can occur as plant mediated diffusion when sedges dominate (Schimel 1995).

Some general patterns of belowground respiration have been identified. Owing to higher temperature, better organic matter degradability and greater oxygen availability, 90% or more of fresh organic matter

decomposition occurs above the water table (Clymo 1984). Thus, water table changes enlarge or reduce the zone of most intensive respiration. Peaks of microbial activity and respiration following changes in soil moisture and aeration have been documented to occur during such changes (Blodau and Moore 2003; Knorr et al. 2008b). Changes in soil moisture and aeration can furthermore lead to a replenishment of non-methanogenic electron acceptors, which may delay the onset of methane production under subsequent saturated conditions (Kettunen et al. 1999; Knorr et al. 2008b; Oquist and Sundh 1998). Drought periods, on a time scale of weeks to months, have lead to an increase in respiration, a decrease of CH<sub>4</sub> production and emission, and potentially lower rates of photosynthesis (Blodau et al. 2004; Shannon and White 1994; Strack et al. 2006). Smaller changes in soil moisture due to intermittent rainfall or hydrologic changes that occur deeper in the soil had on the other hand little impact on C fluxes in bogs (Lafleur et al. 2005) and fens (Chimner and Cooper 2003; Knorr et al. 2008b).

The response of soil respiration to changes in soil moisture and water table position likely differs between bogs and fens due to differences in their physical and biological structure and pool sizes of electron acceptors. Ombrotrophic bogs receive nutrients and electron acceptors only from dry and wet deposition; the vegetation consists mostly of poorly decomposable mosses and shrubs. Fen plant communities have a stronger contribution of more easily decomposable grasses, such as sedges, herbs, and shrubs (Belyea 1996; Bragazza et al. 2007). The water table level in fens is often higher than in bogs, resulting in a thinner aerobic zone. Higher water table levels, transport through plants, along with the higher primary productivity and higher substrate quality, cause higher CH<sub>4</sub> emissions (Chasar et al. 2000).

The impact of seasonal change in water table levels on ecosystem and soil respiration and methane emissions has frequently been investigated in field studies, but the effect of natural precipitation patterns and associated small-scale fluctuations in soil moisture and water table has not. Given typical periods between precipitation events in northern continental wetlands, i.e., days to a couple of weeks, such small scale fluctuations are frequent and may influence soil and plant respiration and methane dynamics. We conducted mesocosm experiments with intact peat

cores from an ombrotrophic bog and an alpine fen to test this hypothesis. We identified the response of CO<sub>2</sub> and CH<sub>4</sub> dynamics to drying and rewetting, and related it to changes in volumetric gas and water content, as well as water table position.

## Materials and methods

### Site description and sampling

Two peat cores each were taken from Mer Bleue (MB), an acidic, ombrotrophic bog in Eastern Ontario, Canada, dominated by mosses and shrubs, and an alpine wetland dominated by grasses and herbs in the Green Lakes Valley, which is part of the Niwot Ridge (NR) LTER (long term ecological research area) in the Colorado Front Range, USA. Surface elevations are 70 m (MB) and 3,590 m asl (NR), mean annual air temperature 5.8°C (MB) and –1°C (NR), and mean annual precipitation 910 mm (MB) and 1,006 mm (NR) (Bubier et al. 2003; Williams et al. 1996). The peat samples were collected in plastic cylinders (30-cm in diameter and depth, “mesocosms”) that held the samples throughout the experiments and were extracted from hollows in MB and grass-covered spots in NR. Water table at the Mer Bleue site generally ranges from 0 to 30 cm below hollow peat surface in summer (Bubier et al. 2003). A water table depth within this range (~19 cm) was adjusted in both peats for comparability. At the day of sampling, water table was lower than 30 cm at both sites. Von Post index of decomposition was 1 in the uppermost cm in both MB and NR peat cores and increased to 3–4 (MB) and 5–6 NR in 30 cm depth, on a scale of 1–10. Values of soil pH were 5–5.5 (NR) and 3.1–5.2 (MB) and lower in the unsaturated zones and during dry periods.

### Treatments

The peat cores were kept under artificial light (2 fluorescent tubes, 24 W each) at 20°C in the laboratory. In two ‘control’ cores water table level was held constant by daily irrigation with fluctuations of ±1 cm (C-MB) and ±2 cm (C-NR). In the other two peat cores (F-MB and F-NR) water table fluctuations were induced after an initial ‘steady state phase’ by omitting irrigation from day 40–45, 46–58 and 59–71, and irrigating at days

46 and 58/59 (‘fluctuation phase’). Water table levels were monitored by means of piezometers. The amount of irrigate used was calculated from the water balance of the controls. The irrigate contained 26 μmol l<sup>-1</sup> SO<sub>4</sub><sup>2-</sup>, 40 μmol l<sup>-1</sup> NO<sub>3</sub><sup>-</sup>, 50 μmol l<sup>-1</sup> NH<sub>4</sub><sup>+</sup>, 30 μmol l<sup>-1</sup> Ca<sup>2+</sup>, 15 μmol l<sup>-1</sup> Mg<sup>2+</sup>, 52 μmol l<sup>-1</sup> Na<sup>+</sup> and 10 μmol l<sup>-1</sup> K<sup>+</sup>; approximating precipitation chemistry at the Mer Bleue site (Blodau and Moore 2003). The mosses were sprayed in the morning to avoid drought damage.

### Porosity, analysis of gases and solutes

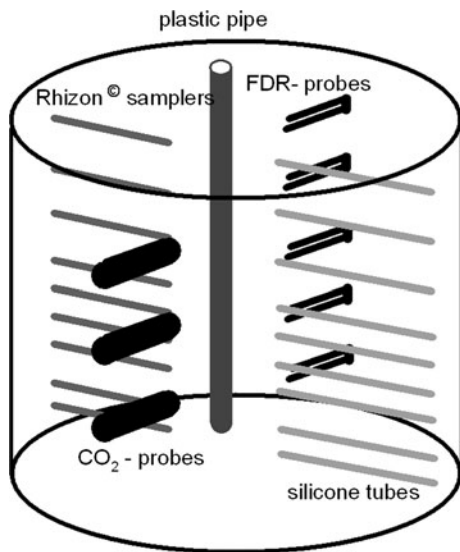
Total porosity was measured by oven drying of 100 cm<sup>3</sup> samples and was much lower in NR compared to MB (Table 1). In F-MB and F-NR, water content was hourly recorded by Function Domain Reflectometry (FDR) probes (ECH<sub>2</sub>O EC-5, Decagon Devices, USA) at five depths (5, 10, 15, 20 and 25 cm below peat surface, Fig. 1). The probes were calibrated in the peats by installing the sensors in additional peat samples that were gradually saturated, redried, and weighed during the procedure.

CO<sub>2</sub> probes (Vaisala Oyi, Finland, GMH70), covered with silicon membranes, were installed at three depths (10, 15, 20 cm below peat surface; Fig. 1) for hourly measurement of CO<sub>2</sub> in the range of 0–5,000 ppm (upper probes) and 0–100,000 ppm. Due to sensor malfunction, reliable data were obtained for –10 and –15 cm in MB peat, and for –10 and –20 cm in NR peat only.

Rhizon<sup>®</sup> samplers (polymer, <0.2 μm pore size, Eijkelkamp, The Netherlands) for soil solution sampling were horizontally installed in nine depths (3, 7, 11, 15, 17, 19, 21, 25 and 27 cm below the peat surface; Fig. 1). Values of pH were measured with a glass electrode in a 1 ml aliquot. Soil gas was

**Table 1** Bulk density and porosity in Mer Bleue (MB) and Niwot Ridge (NR) peat

Depth (cm)	Bulk density		Porosity	
	MB	NR	MB	NR
5	0.020	0.23		0.78
10	0.022	0.18–0.25		0.78
15	0.028	0.26–0.32	0.94–0.97	0.78
20	0.032	0.31		0.74–0.76
25	0.038	0.47–0.56		0.60–0.70



**Fig. 1** Schematic of sampling devices in the mesocosms. CO<sub>2</sub> probes were installed in three depths (10, 15 and 20 cm), rhizon and gas samplers in nine depths (3, 7, 11, 15, 17, 19, 21, 25 and 27 cm), and FDR probes in five depths (5, 10, 15, 20 and 25 cm) in the F-treatments. In C-treatments only rhizon and gas samplers were installed

sampled in all peat cores using silicone tubes (modified after Kammann, et al. (2001)) inserted at the same depths as rhizon<sup>®</sup> samplers (Fig. 1). Gas samples were collected in plastic syringes connected to the samplers by three way valves. Silicone tubes were filled with nitrogen gas after sampling. Pore water and gas phase were sampled 2–4 times a week, always sampling before and after irrigation. CO<sub>2</sub> and CH<sub>4</sub> extracted from gas samplers were analyzed within 30 min on a gas chromatograph with flame ionization detector (FID) and CO<sub>2</sub> methanizer (8610C, SRI Instruments, USA). Pore water concentration of dissolved inorganic carbon (DIC) and CH<sub>4</sub> were calculated from measured concentrations in the gas phase, using Henry's law constants corrected for temperature [ $K_{\text{CO}_2} = 0.0389 \text{ mol l}^{-1} \text{ atm}^{-1}$ ,  $K_{\text{CH}_4} = 0.0014 \text{ mol l}^{-1} \text{ atm}^{-1}$  (Sander 1999)]; DIC speciation was calculated using measured pH of the soil solution and speciation constants taken from Stumm and Morgan (1981).

#### Chamber flux measurements

Fluxes of CO<sub>2</sub> and CH<sub>4</sub> were measured using transparent and opaque static chambers (29 cm

diameter, 28 cm height) and calculated from linear regression of concentration over time. Fluxes with  $R^2 < 0.9$  (CO<sub>2</sub>) and  $< 0.8$  (CH<sub>4</sub>) were discarded. Daytime net ecosystem exchange (NEE) was derived from transparent chambers and ecosystem respiration (ER) from opaque chamber measurements. These terms were kept for reasons of consistency with common notation, although we only analyzed fluxes from mesocosms. Fluxes were measured in triplicates 2–4 times a week. In the MB cores, CH<sub>4</sub> fluxes were additionally measured on some dates for longer intervals due to low emissions. Concentration of CO<sub>2</sub> and CH<sub>4</sub> was measured as described above. Photosynthesis was calculated as the difference between ER and NEE. Fluxes out of the peat were defined to be positive, negative fluxes represent CO<sub>2</sub> or CH<sub>4</sub> uptake.

#### Diffusive fluxes and production rates in the peat

Air filled porosity was derived from measured volumetric water content and total porosity. Diffusive fluxes across the water table were calculated from Fick's law and diffusion coefficients ( $D$ ) corrected for temperature and porosity ( $\varphi$ ) with  $D = D_{\text{H}_2\text{O}} \varphi^{-2}$  (Lerman 1988), and the respective maximum gradient observed at the transition of saturated and unsaturated zone at the time of sampling. In the unsaturated zone, diffusion coefficients were corrected for air filled porosity (afp) using  $D_p = D_{\text{air}} \text{afp}^2 \varphi^{-2/3}$  (Millington and Quirk 1961) as proposed by Jin and Jury (1996). A calculation of diffusion coefficients in the unsaturated zone in MB peat was not possible due to water contents being too low for application of this function. Diffusion coefficients were  $0.15 \text{ cm}^2 \text{ s}^{-1}$  for CO<sub>2</sub> and  $0.21 \text{ cm}^2 \text{ s}^{-1}$  for CH<sub>4</sub> in air and  $1.75 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$  for CO<sub>2</sub> and  $1.57 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$  for CH<sub>4</sub> in water. Air filled porosity in NR peat below the water table was set to zero assuming that air filled pores were disconnected and diffusion limited to the water phase.

Turnover rates ( $R_N$ ) of CO<sub>2</sub> and CH<sub>4</sub> were calculated from the change in storage of the corresponding species ( $\Delta S/\Delta t$ ), diffusion coefficients ( $D_p$ ) in peat and the concentration gradients (in CO<sub>2</sub> and CH<sub>4</sub> per peat volume) at the lower and upper boundaries of the corresponding layer ( $\Delta C/\Delta x$ ) applying Eq. 1

$$R_N = \frac{\Delta S}{\Delta t} + \left[ D_p \frac{\Delta C_{\text{upper}}}{\Delta x} \right]_{\text{upper}} z^{-1} - \left[ D_p \frac{\Delta C_{\text{lower}}}{\Delta x} \right]_{\text{lower}} z^{-1}. \quad (1)$$

Neglecting transport, we used the hourly logged  $\text{CO}_2$  concentration from  $\text{CO}_2$  probes, corrected for pressure, pH and ratio of dissolved and gaseous phase in soil, to calculate minimum production rates by multiple linearization (Tome and Miranda 2004).

Illustration of  $\text{CO}_2$  and  $\text{CH}_4$  concentration over time were plotted by contour plots; Kriging was used for gridding with an anisotropy ratio of 2 as time and depth are not comparable and results were plausible (Surfer 8, Golden Software, USA).

## Results

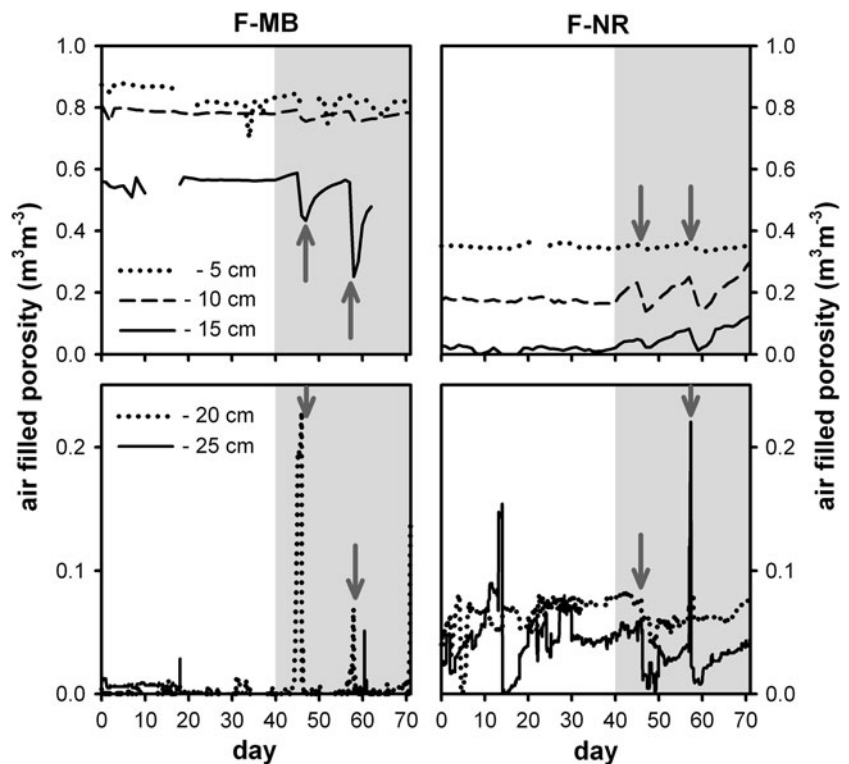
### Soil water and air

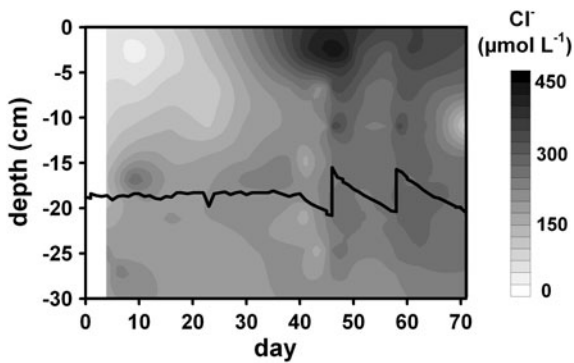
The MB and NR peats strongly differed in their response to irrigation and drying. Water table fluctuations were about 0.5 cm in the C-MB peat and about

2–3 cm in C-NR peat due to daily irrigation and about 5 cm (F-MB) and 11 cm (F-NR) due to the drying-rewetting cycles. Air filled porosity (afp) decreased with depth from >82–92% (F-MB) and 14–36% (F-NR, 5 and 10 cm) in the unsaturated zone to values of <0.01 (F-MB) and 0–9% (F-NR) in the saturated zone (Fig. 2). In F-MB, afp sharply increased within a distance of 1 cm above the water table by 20%, whereas in F-NR such high afp only occurred at about 10 cm above the water table; in the NR peat the change between unsaturated and saturated conditions thus occurred much less abrupt. Drying and rewetting cycles substantially changed afp in both peats (Fig. 2). The effects were most distinct in 10–15 cm where difference between pre- and post-irrigation was up to 20% (F-MB) and 10% (F-NR). The MB peat rapidly dewatered at 20 cm depth when the water table passed this depth during drying, whereas this was not the case in NR peat. In NR peat, afp > 0 was also detected below the water table (Fig. 2).

Chloride concentration in the MB peat was used to trace soil water movement (Fig. 3). Increasing concentrations in the surface peat during drought phases

**Fig. 2** Air filled porosity in F-MB (left) and F-NR (right) in different depths over time. Upper figures show air filled porosity in the mostly unsaturated zone at 5, 10 and 15 cm depths, lower figures in the mostly saturated zone (20 and 25 cm). Grey fields indicate days without irrigation when water table drawdown occurred. Irrigation events are marked by arrows





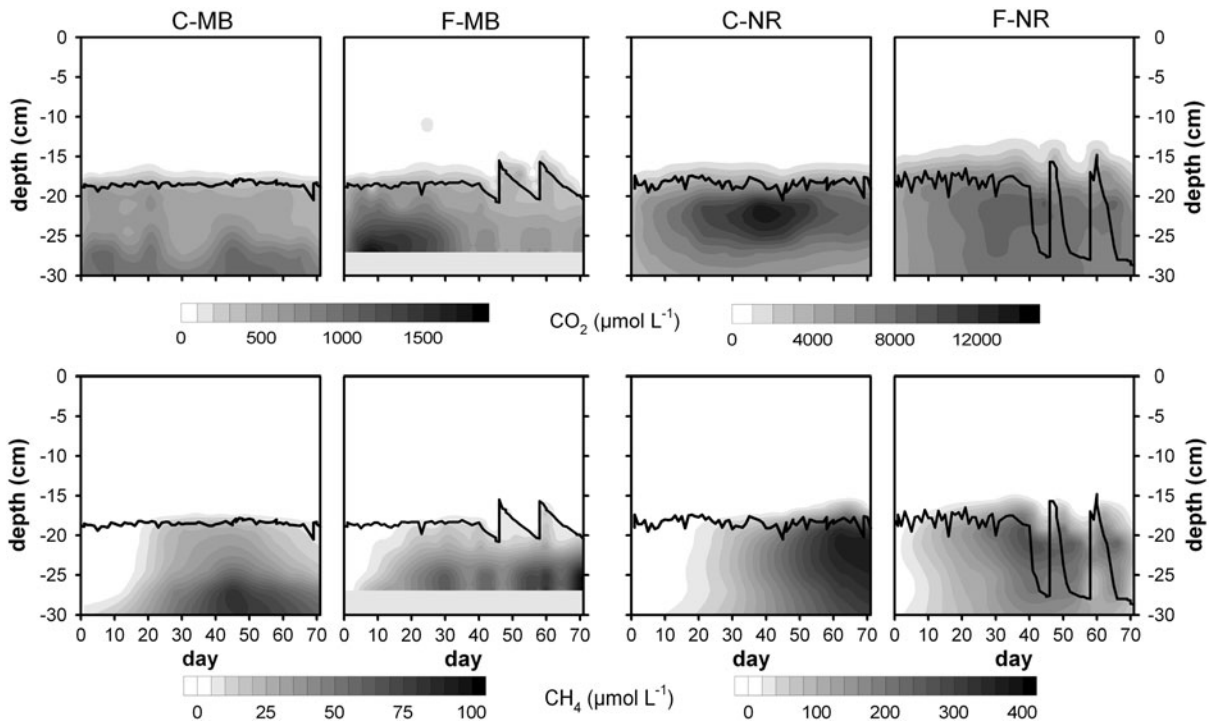
**Fig. 3** Chloride ( $\text{Cl}^-$ ) concentration (grey scale) over time (x-axis) and depth (y-axis) in the F-MB peat core. The solid line represents the depth of the water table.  $\text{Cl}^-$  increases with time in the unsaturated zone because of concentration due to evaporation. Phases of water table drawdown without irrigation were induced from day 40–46, 46–58 and 58–71, irrigation events at days 46 and 58 transported  $\text{Cl}^-$  from the surface into deeper layers

indicated water loss through evapotranspiration, while irrigation events lead to a dilution of the chloride containing pore water in the affected layers.

## DIC and $\text{CH}_4$ concentration and production

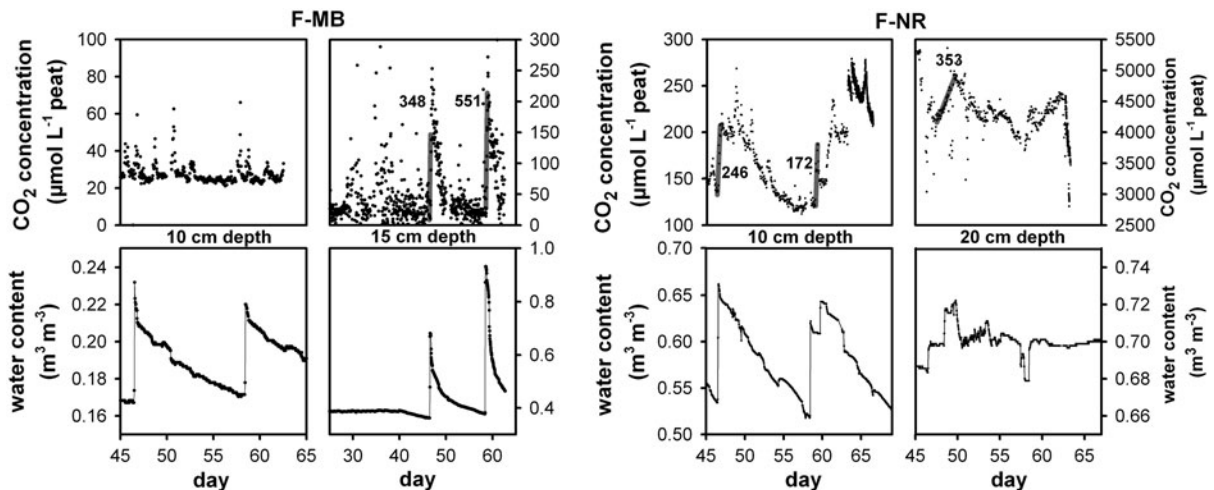
### Carbon dioxide

Concentrations in the uppermost unsaturated zone of all cores were small and generally ranged from 20 to 60  $\mu\text{mol DIC l}^{-1}$  in soil solution. In the transition zone, concentrations strongly increased with depth and peaked at maximum (MB) and intermediate depth (NR) in the saturated zone (Fig. 4). In the MB mesocosms, DIC concentrations were similar in the upper 15 cm and averaged  $26 \pm 6$  (C-MB) and  $30 \pm 13$   $\mu\text{mol l}^{-1}$  (F-MB). In the saturated zone, DIC concentration increased with depth to values of up to 1097  $\mu\text{mol l}^{-1}$  (C-MB) and 1,489  $\mu\text{mol l}^{-1}$  (F-MB). Steepest concentration gradients appeared directly at the water table. In the NR cores, DIC concentration in the unsaturated upper layers were higher and increased from  $53 \pm 11$   $\mu\text{mol l}^{-1}$  (C-NR) and  $57 \pm 10$  (F-NR) in 3 cm depth to values of up to 13,700  $\mu\text{mol l}^{-1}$  (C-NR) and 9,500  $\mu\text{mol l}^{-1}$  (F-NR).



**Fig. 4** DIC (upper row) and  $\text{CH}_4$  (lower row) concentration profiles in soil solution over time in MB and NR cores. The left columns show C-MB (left) and F-MB (middle left), the right columns show C-NR (middle right) and F-NR (right). The solid

line represents the water table position. Note different concentration scales for MB/NR and  $\text{CO}_2/\text{CH}_4$ . The grey field in F-MB below 26 cm stands for missing values for the 27 cm probe



**Fig. 5** CO<sub>2</sub> concentration from CO<sub>2</sub> probes based on total soil volume (*top*) and water content (*bottom*) in 10 and 15 cm depth of F-MB (*left*) and in 10 and 20 depth in F-NR. Numbers at *grey* lines give calculated CO<sub>2</sub>-production rates in nmol cm<sup>-3</sup> day<sup>-1</sup>

The impact of drying and rewetting on DIC concentrations differed between F-MB and F-NR cores. In F-MB, DIC concentration rapidly decreased in layers that became unsaturated and recovered after rewetting within about 2 days (Figs. 2, 4). In contrast, DIC concentration was hardly affected by the much larger water table fluctuations in F-NR. Small peaks in DIC concentration even appeared to occur in the newly unsaturated peat during drying. Concentration decreased only when the water table fell further, and minima occurred shortly before or after irrigation.

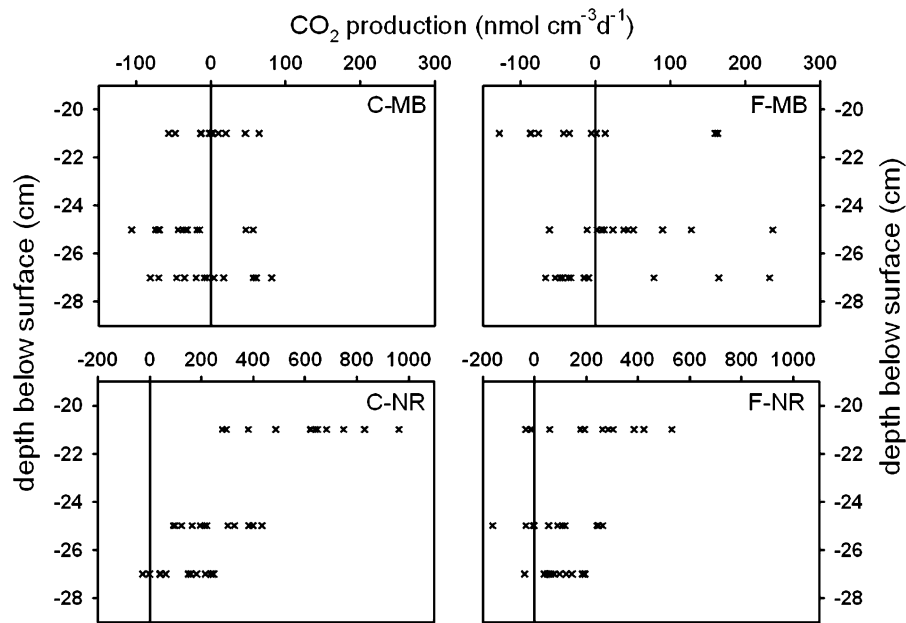
The immediate response in DIC and gaseous CO<sub>2</sub> concentrations (total CO<sub>2</sub>) over time induced by the irrigation and drying could be traced with the CO<sub>2</sub> probes. In F-MB, total CO<sub>2</sub> concentration in 10 cm (F-MB) was relatively constant and not influenced by water table fluctuations. In 15 cm, both irrigation events resulted in a rapid increase of total CO<sub>2</sub> concentration when the water table almost reached the sensor and water content was 72% (1st event) and 98% (2nd) of total porosity (Fig. 5). Concentrations also declined very quickly with the subsequent decrease in water content. Total CO<sub>2</sub> concentrations in F-NR varied similarly in 10 and 20 cm depth but in a more complex manner. Daily maxima in water content after irrigation coincided with minima in total CO<sub>2</sub> concentration, suggesting a dilution with irrigate before CO<sub>2</sub> accumulated again at a particular depth.

Respiration rates in the water saturated zone calculated between individual sampling dates and

during the initial phase of constant water table strongly varied (Fig. 6) and tended to decline over time, partly with apparent consumption later on. Mean respiration rate below the water table during initial constant water table was 25 nmol cm<sup>-3</sup> day<sup>-1</sup> in F-MB and 120 nmol cm<sup>-3</sup> day<sup>-1</sup> in F-NR. Net production rates of CO<sub>2</sub> calculated from entire depth profiles in C-NR averaged 372 mmol m<sup>-2</sup> day<sup>-1</sup> (C-NR) and 392 mmol m<sup>-2</sup> day<sup>-1</sup> (F-NR; Fig. 7) and were in the range of flux measurements, albeit without showing the same temporal variation. Calculated net production decreased strongly with water table drawdown in F-NR (Fig. 7). This can, however, not be interpreted as a decline in production, because degassing under unsaturated conditions translates into an apparent consumption when using a mass balance approach. Production rates derived from CO<sub>2</sub> concentration increase quantified with CO<sub>2</sub> probes shortly after irrigation mostly ranged from 90 to 580 nmol cm<sup>-3</sup> day<sup>-1</sup>; they were in the same range in MB and NR cores.

### Methane

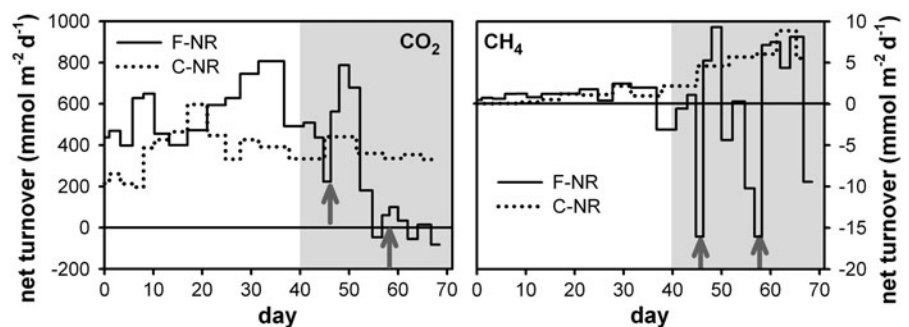
After an initial period of CH<sub>4</sub> build-up in the saturated zone, CH<sub>4</sub> concentration showed a depth pattern similar to CO<sub>2</sub> concentration (Fig. 4) and reached up to 105 µmol l<sup>-1</sup> in MB and 376 µmol l<sup>-1</sup> in NR. Concentration of CH<sub>4</sub> above the water table remained mostly below 0.1 µmol l<sup>-1</sup> in MB and



**Fig. 6** CO<sub>2</sub> production rates (x-axis) at different depths (y-axis) of the saturated zone of Mer Bleue (MB) and Niwot Ridge (NR) mesocosms during the initial phase of constant water table level (first 40 days of the experiment) calculated from mass balances and between single sampling dates. C and

F treatments did not differ during this phase of the experiment. Note different scales for x-axes. The high rates in MB mesocosms occurred in the first week after water table was set to approx. -19 cm

**Fig. 7** Calculated net production rates of CO<sub>2</sub> (left) and CH<sub>4</sub> (right) integrated over depth segments in C-NR (dotted line) and F-NR (solid line). Grey areas indicate times of water table drawdown, arrows mark irrigation events



0.5  $\mu\text{mol l}^{-1}$  in NR above -11 cm, but reached much higher values below. Steepest concentration gradients occurred at the water table in MB and about 2 cm above the water table in NR cores. In MB, CH<sub>4</sub> concentrations in the thin peat layer affected by changing water table declined with falling and increased with rising water table. In F-NR, this relationship was weaker and a decrease in concentration occurred also with irrigation, as seen at day 60 cm and 25 cm depth (Fig. 4). Methane was produced in the entire saturated zone in C-MB during the first 4 weeks, at mean production rate of 0.66  $\text{nmol cm}^{-3} \text{ day}^{-1}$ , and depleted afterwards. In

F-MB, this value was 0.88  $\text{nmol cm}^{-3} \text{ day}^{-1}$ . In NR cores, CH<sub>4</sub> production rates were highest near the water table and averaged 4.7  $\text{nmol cm}^{-3} \text{ day}^{-1}$  during the phase of constant water table in F-NR and 2.4  $\text{nmol cm}^{-3} \text{ day}^{-1}$  in C-NR. Afterwards production accelerated in C-NR to 13.4  $\text{nmol cm}^{-3} \text{ day}^{-1}$ . With water table drawdown in F-NR, production rates were diminished or switched to consumption (Fig. 7). Methane production accounted for <1% to the total CO<sub>2</sub> production during the phase of constant water table in all mesocosms and up to 25% of anaerobic CO<sub>2</sub> production in F-MB, up to 6% in C-MB, 16% in F-NR and 6% in C-NR.



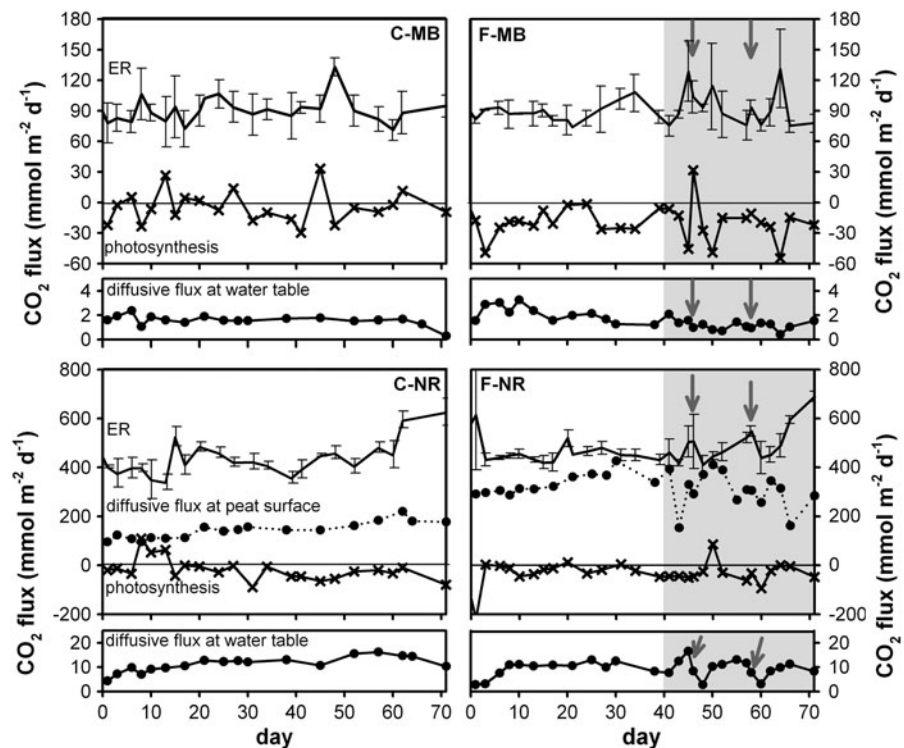
Fluxes of CO<sub>2</sub> and CH<sub>4</sub>

Mean ecosystem, i.e. mesocosm, respiration (ER) was  $91 \pm 13 \text{ mmol m}^{-2} \text{ day}^{-1}$  in both MB mesocosms and  $481 \pm 65 \text{ mmol m}^{-2} \text{ day}^{-1}$  (F-NR) and  $440 \pm 71 \text{ mmol m}^{-2} \text{ day}^{-1}$  (C-NR). Water table fluctuations had no clear impact on CO<sub>2</sub> exchange rates, as differences with time occurred in both controls and treatment cores (Fig. 8). Some increase of ER may have occurred during drying periods in the NR mesocosm, interrupted by a decrease just after rewetting (Fig. 8). Photosynthesis was low in all peat cores with  $-19.2 \pm 16.7 \text{ mmol m}^{-2} \text{ day}^{-1}$  (F-MB),  $-5.5 \pm 15.2 \text{ mmol m}^{-2} \text{ day}^{-1}$  (C-MB),  $-31.4 \pm 46.1 \text{ mmol m}^{-2} \text{ day}^{-1}$  (F-NR) and  $-19.1 \pm 43.6 \text{ mmol m}^{-2} \text{ day}^{-1}$  (C-NR) and did not systematically vary with time (Fig. 8). Differences were in the range of standard deviation. Diffusive fluxes of CO<sub>2</sub> at the water table ranged from  $1.5 \text{ mmol m}^{-2} \text{ day}^{-1}$  in MB soils to  $12.5 \text{ mmol m}^{-2} \text{ day}^{-1}$  in NR soils and accounted for only 0–4.3% of chamber surface fluxes. This was qualitatively confirmed by the estimated CO<sub>2</sub> diffusion at the peat surface (Fig. 8), which averaged  $139 \pm 34 \text{ mmol m}^{-2} \text{ day}^{-1}$  in C-NR and

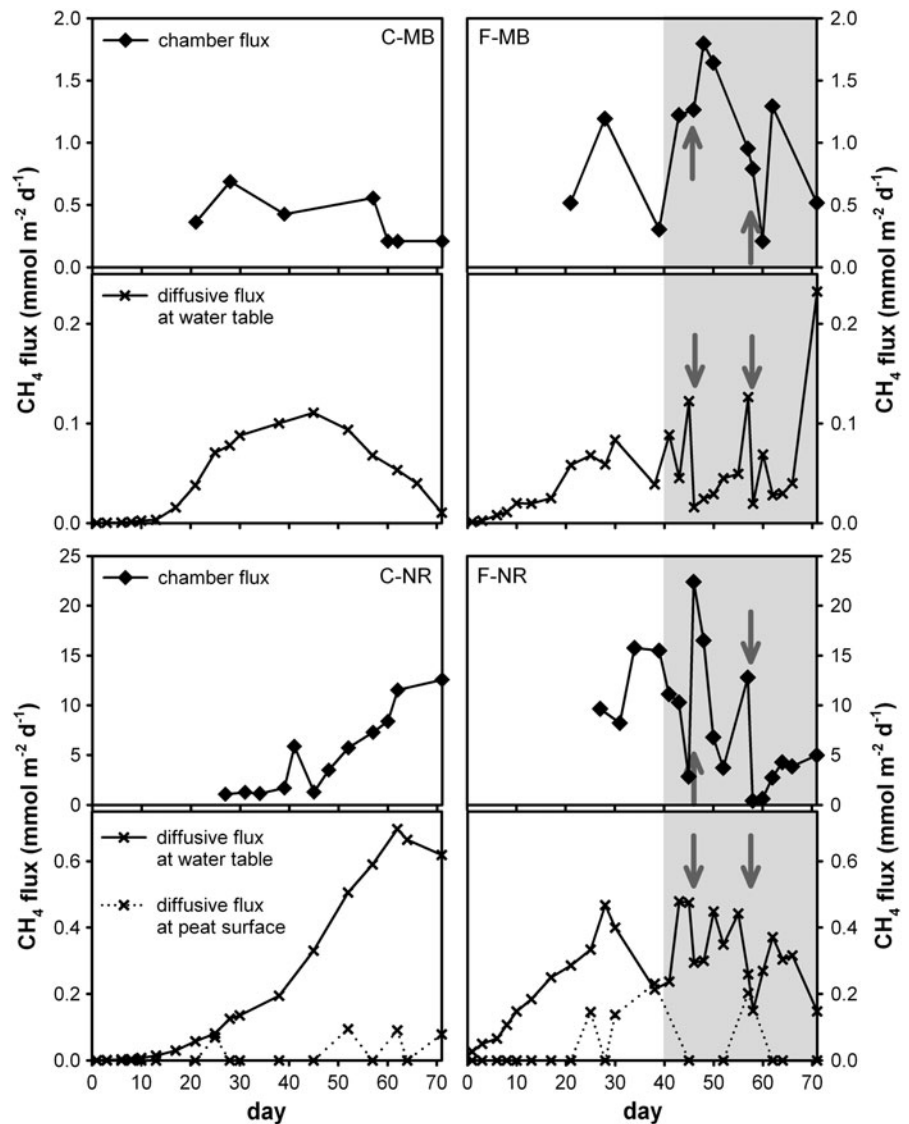
reached  $426 \text{ mmol m}^{-2} \text{ day}^{-1}$  in F-NR before the drying-rewetting period began. The comparison of calculated diffusion rates at the water table and measured fluxes at the peat surface thus shows that CO<sub>2</sub> production was dominated by the unsaturated zone; an estimated 95–100% of the total emitted CO<sub>2</sub> stemmed from above the water table.

Mean CH<sub>4</sub> emission was  $0.5 \pm 0.14 \text{ mmol m}^{-2} \text{ day}^{-1}$  (C-MB) and  $1.1 \pm 0.48 \text{ mmol m}^{-2} \text{ day}^{-1}$  (F-MB; Fig. 9). Highest fluxes occurred after irrigation in F-MB but fluxes did not vary systematically. In F-NR mean CH<sub>4</sub> emission was  $8.5 \pm 6.3 \text{ mmol m}^{-2} \text{ day}^{-1}$  once a CH<sub>4</sub> flux could be detected and peaked at  $22.4 \pm 5.0 \text{ mmol m}^{-2} \text{ day}^{-1}$  (day 46) after the first irrigation event (Fig. 9). With continued drying and rewetting CH<sub>4</sub> efflux appeared to decrease overall. In C-NR, CH<sub>4</sub> fluxes increased to  $12.6 \pm 6.0 \text{ mmol m}^{-2} \text{ day}^{-1}$  at day 71. This increase ( $R^2 = 0.79$ ) was consistent with CH<sub>4</sub> accumulation in the soil. Diffusive flux of CH<sub>4</sub> at water table level reached a maximum of  $0.11\text{--}0.12 \text{ mmol m}^{-2} \text{ day}^{-1}$  in MB cores and  $0.48\text{--}0.70 \text{ mmol m}^{-2} \text{ day}^{-1}$  in NR cores. CH<sub>4</sub> diffusion at the water table explained only parts of the measured CH<sub>4</sub> efflux (0–56% for F-MB,

**Fig. 8** Measured and calculated fluxes of CO<sub>2</sub> for MB (top) and NR (bottom) cores. ER stands for “ecosystem respiration”, respectively, mesocosm respiration. Error bars indicate  $\pm$  one standard deviation of measured flux. Grey fields show periods of water table drawdown and arrows days of irrigation. Note different scales of the y-axes for MB and NR cores



**Fig. 9** Chamber flux and calculated diffusive flux of  $\text{CH}_4$  in MB (*upper figures*) and NR (*lower figures*) over time. Values are means of three measurements over 12 min in NR and single measurements over longer time periods in MB. Grey fields indicate water table drawdown, arrows irrigation events. Note different scales for fluxes



0.2–2.2% for C-MB, 1.3–43% for F-NR and 2.4–6% in C-NR), and diffusion at the peat surface was too small to be quantified.

## Discussion

### Carbon fluxes: the effect of drying and rewetting

We found no clear effect of water table level fluctuations on  $\text{CO}_2$  fluxes from both the fen and the bog peat studied. A weak response was reported previously for much larger water table level changes in experiments or ecosystem observation. Applying

micro-meteorological techniques, Lafleur et al. (2005) found a weak correlation between water table and ER in Mer Bleue bog when water table fluctuated between 30 and 75 cm below peat surface. In fen sites, increasing ecosystem respiration with experimental drought was documented by Strack et al. (2006), but mesocosm experiments simulating intense drought and rewetting showed no significant reaction to drought and only weak decrease in  $\text{CO}_2$  exchange after rewetting (Knorr et al. 2008b). Chimner and Cooper (2003) reported increasing  $\text{CO}_2$  flux with water table drawdown of a few to 60 cm in an alpine fen in the Rocky Mountains. In a bog nearby,  $\text{CO}_2$  efflux increased when water table dropped below peat

surface but not when it fell further (Chimner and Cooper 2003). The investigators suggested that a thin layer of easily degradable material at the peat surface, which was always unsaturated in our study, dominated most of the surface carbon fluxes.

Autotrophic respiration usually contributes between 35 and 50% to ecosystem respiration (Crow and Wieder 2005; Silvola et al. 1996) but it must have been low in this study because of low light intensity and low rates of photosynthesis. A mechanism to compensate for increased heterotrophic respiration in the newly unsaturated volume of peat during dry periods could have been drought stress of autotrophic and heterotrophic respiration at the peat surface in MB cores, because water content in 5 cm depth was mostly lower than 10%. Such an effect would be in agreement with findings reported earlier. Lafleur et al. (2005) reported decreasing respiration rates with decreasing volumetric water content in the uppermost 5 cm of *Sphagnum* peat from Mer Bleue. Tuittila et al. (2004) found a dependency of *Sphagnum* respiration rates on water table levels and highest rates when water table was 12 cm below the surface. Drier conditions led to a decline in *Sphagnum* respiration. Thus, shifting the water table from about -16 cm to -21 cm (MB) and -16 to -27 cm (NR) may have increased heterotrophic respiration but reduced autotrophic respiration, entailing no net effect on CO<sub>2</sub> flux. In the *Sphagnum* rich MB mesocosm, the roughly stable CO<sub>2</sub> fluxes during drying and rewetting (Fig. 5) may be explained by such a mechanism. In the NR mesocosm, predominance of vascular plants and the much higher water content presumably prevented such a compensation effect. The CO<sub>2</sub> flux tended to increase somewhat during drying and to decrease just after rewetting. These effects were small, also when compared to variation in the treatment with constant water table (Fig. 5).

Unlike CO<sub>2</sub> production, methanogenesis is restricted to anaerobic conditions. Methane emissions are controlled by production, transport and oxidation of CH<sub>4</sub> and thus by shifts in the vertical extent of aerobic and anaerobic peat. In agreement with this concept, a strong dependence of CH<sub>4</sub> emissions on water table level has been established in many studies, in fen soils for instance by White et al. (2008) who could explain 77% of variance in CH<sub>4</sub> fluxes from fen mesocosms with water table depth,

and in field studies by Smemo and Yavitt (2006), and Chimner and Cooper (2003). Some studies on bog peat have emphasized the importance of the coupling of production, storage and transport (Blodau and Moore 2003) and of the magnitude of water table change. Shannon and White (1994), for example, found significantly lower CH<sub>4</sub> flux during a dry summer but no significant effect in two other years in a Minnesota bog. In the mesocosm study of White et al. (2008) only 33% of the variance in CH<sub>4</sub> emissions from bog peat could be explained with water table depth. Our study illustrates that CH<sub>4</sub> fluxes in the mesocosms exposed to periodic irrigation and drying can become more variable compared to fluxes when water table is constant (Fig. 9). The irrigation pattern further led to predictable methane production and loss in the fen (Fig. 7), and overall emissions from F-NR decreased when the water table fluctuated, both compared to the days before the fluctuations began and compared to the control core C-NR.

#### Gas transport and respiration: the effect of drying and rewetting

Transport of gases was most likely dominated by diffusion in MB bog peat, though sporadic efflux of CH<sub>4</sub> from F-MB between days 29 and 35 was much higher than diffusive flux at the water table. Concentration changes in the saturated zone were high during this period and fluxes more variable. Plants that have been reported to mediate transport were absent, but incomplete saturation and trapped air were reported in *Sphagnum* peat (Baird and Waldron 2003). Ebullition of gas bubbles may thus have contributed to a decoupling of water table, production, and transport of gases in this peat. In NR cores some gas filled porosity was detected in the saturated zone, possibly due to trapped air when the peat was rapidly wetted by irrigation (Baird and Waldron 2003). A comparison of CO<sub>2</sub> concentration and water content in Figs. 5 and 2 show that strong changes in CO<sub>2</sub> concentration in F-NR were accompanied by abrupt decrease in water content in 10 cm depth. These patterns may suggest that water did move in fronts of intruding water or that abrupt filling and drainage of pores occurred. As air filled porosity increased over time, bubble formation has to be considered as well, although, in theory, bubbles form

only if partial pressure of  $\text{CH}_4$  reaches at least 0.2 atm at standard conditions (Fechner-Levy and Hemond 1996), in our case about  $250 \mu\text{mol l}^{-1}$  of dissolved  $\text{CH}_4$ . This concentration was not reached in MB peat but after about 5–7 weeks in NR cores. Baird et al. (2004) showed experimentally that  $\text{CH}_4$  bubbles build-up was initiated at concentrations of  $10\text{--}100 \mu\text{mol l}^{-1}$ , though ebullition started only at concentrations that were about 10-fold higher. The monotonously increasing  $\text{CH}_4$  concentrations in our chamber measurements speak for limited importance of ebullition and argue for plant transport as the more important transport mechanism in the NR cores (Updegraff et al. 2001; White et al. 2008). A high proportion of emission could have been mediated by the abundant sedges (e.g., Thomas et al. 1996).

The assumption that the water table is the boundary between aerobic and anaerobic zone, as found, e.g., by Nedwell and Watson (1995), was legitimate in the more fibric MB peat. However,  $\text{CH}_4$  production rates above the water table in F-NR show that anaerobic conditions are not always restricted to water saturated conditions. NR cores had much higher water content above the water table, caused possibly by a higher proportion of fine and medium pores. The fast decrease in water table depth in NR (e.g., Fig. 4) indicates that water was removed only from few large pores, leading to a broad transition between oxic and anoxic zone. Evidence is accumulating that such transitions occur in many peatlands. Anaerobic conditions can prevail some decimeters above the water table level (Silins and Rothwell 1999) and the existence of anoxic microniches in peatlands has been inferred before in both bog and fen peat (e.g., Blodau and Moore 2003; Knorr et al. 2008b). The slow reaction of  $\text{CH}_4$  and  $\text{CO}_2$  concentrations in NR peat to water table drawdown was thus likely related to a high bulk density and predominance of fine and medium pores, which caused a large water table drawdown but weak or absent aeration. Methanogenesis continued and respiration rates did not appear to change. The sharp increase in air filled porosity in F-NR at day 58 (Fig. 5) indicates that air intruded only after the water table fell below the respective depth for some days. Drainage in forested peatlands by Silins and Rothwell (1999) showed that the depth of the aerobic zone dropped less than the water table, which was explained with decreasing porosity with depth and capillary rise and increasing bulk density due to

shrinkage. The dependence of respiration and methanogenesis on the position of water table is thus more complex in peatlands than often assumed.

Production rates of  $\text{CO}_2$  and  $\text{CH}_4$  were seldom quantified in intact soil before and not at all during short term drying and rewetting. Some preliminary indications can be derived, keeping the large uncertainties in the mass balance approach in mind. In F-NR, respiration rates derived from  $\text{CO}_2$  probes were on the order of  $100\text{--}350 \text{ nmol cm}^{-3} \text{ day}^{-1}$  at 10 and 20 cm after irrigation. Such values are in a similar range as mean soil respiration rate of  $120 \text{ nmol cm}^{-3} \text{ day}^{-1}$  in the saturated zone calculated from mass balance and data of gas samplers during constant water table conditions. Short term drying and irrigation thus had little effect on soil respiration in the fen peat, likely because afp remained low with 5–25% and changed little during drying and rewetting (Fig. 2). The missing reaction of soil respiration suggests that either effects were too local to be detected by our coarse methodology, or that the intensity of drying and rewetting in such dense peat soils matters. In an earlier mesocosm study of a minerotrophic fen soil exposed to an intense 50-day drought period respiration rates after rewetting did strongly increase (Knorr et al. 2008b). In the less dense and better aerated F-MB bog soil, respiration rates derived from  $\text{CO}_2$  probes after rewetting and at 15 cm depth were  $300\text{--}500 \text{ nmol cm}^{-3} \text{ day}^{-1}$  (Fig. 5) and by a factor of 10 or more higher than during constant water table and when calculated from mass balancing and silicone gas sampler data. Furthermore, as the soil was not fully saturated and advective transport neglected, true respiration after irrigation in this depth was likely even faster. The data hence suggest some sensitivity of soil respiration to short drying–rewetting cycles at least in the intact bog peat.

Interestingly,  $\text{CH}_4$  concentrations rebuilt quickly after resaturation of peat, even in the F-MB core, where drying led to fairly high air filled porosity of 20% one centimeter above the water table (Fig. 4). The potential for methane production was therefore little affected by the short drying and rewetting cycles. In a mesocosm experiment by Blodau and Moore (2003) little time lag in methanogenesis occurred in deep peat layers after resaturation, but in surface layers it took 10–30 days until methane production rates of  $3\text{--}4 \text{ nmol cm}^{-3} \text{ day}^{-1}$

reestablished. In this experiment, water table draw-down was intense (>60 cm) and the drought lasted for 4 months. Knorr et al. (2008b) also observed time lags of <20–50 days in methanogenesis after resaturation in a rich fen soil; here, water table drawdown of about 40 cm took some weeks. The discrepancy between the results from these earlier studies and this one is in line with a dependency of the methane production potential on the duration and intensity of drying, as already reported (Kettunen et al. 1999), and on the soil moisture history of the peat (Oquist and Sundh 1998). In MB peat, the observed increase in methane concentration in newly saturated peat after irrigation could be also explained by mixture of irrigate with CH<sub>4</sub>-rich water from below. However, chloride concentration in the deeper profile increased from 200 μmol l<sup>-1</sup> at day 45 to 260 μmol l<sup>-1</sup> at day 46 (Fig. 3). Water rich in chloride and poor in CH<sub>4</sub> thus moved downward suggesting that the increase in CH<sub>4</sub> concentration seen after rewetting in Fig. 4 was driven by production.

The resilience of methane production is in agreement with the idea that the activity of methanogenic consortia is to a varying degree shielded from short periods of oxygen intrusion, as proposed by Kettunen et al. (1999). The mechanisms leading to this resilience cannot be elucidated by this study. Local anaerobic structures in the peat likely play a role, rather than physiological adaptations of methanogens, which are obligate anaerobes and sensitive to both exposure to oxygen and drying (Fetzer et al. 1993). The existences of anaerobic microniches in fen and even bog peats has been inferred before from the spatial distribution of CH<sub>4</sub> and H<sub>2</sub> concentration (Blodau and Moore 2003; Knorr et al. 2008a, b) and by explicit identification of the distribution of organisms in wetland soils (e.g., Wachinger et al. 2000). Soil physical structures such as roots, which were abundant in both peats, moreover increase local heterogeneity by exudation of labile organic carbon from root exudates and fine root production and decay (Thomas et al. 1996).

## Conclusions

Periodic drying and rewetting between rainfall, as it normally occurs during summer in continental peatlands, had limited impact on processes within the

carbon cycle in an ombrotrophic and shrub dominated bog with fibric porous peat and a minerotrophic, alpine, and sedge dominated fen with much denser peat. A systematic change in C fluxes could not be identified and fluxes became primarily more variable; some impact occurred with respect to CH<sub>4</sub> emission, which is in agreement with accepted knowledge. Changes in the frequency of precipitation on the scale of a day to a week are thus unlikely to have a strong impact on C fluxes in these wetlands, as long as a similar water balance is maintained, and assuming our results can be extrapolated to the field. The interplay between evaporation, transpiration, and irrigation induced clear fluctuations of soil water content and water table position, and it did so quite differently among the two peat soils. The response of gas concentrations to these disturbances differed as well. Large variations in water table in NR peat had almost no impact on respiration patterns and gas transport, but smaller variations in MB had a much larger impact on gas concentrations; the potential for methanogenesis was apparently not affected. The results highlight the importance of physical peat properties and question the assumption that water table position is a reliable predictor of aerobism and anaerobism in peatlands with dense soil. Depth distribution of volumetric water content should thus be tested as a predictor for respiration and methanogenesis. The stability of fluxes during water table changes of 5–10 cm further suggests that time-point measurements of water table are not a useful predictor of trace gas emission and should be replaced by averages of repeated water table measurements.

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