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Carbon turnover in peatland mesocosms exposed to different water table levels

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Abstract. Changes of water table position influence carbon cycling in peatlands, but effects on the sources and sinks of carbon are difficult to isolate and quantify in field investigations due to seasonal dynamics and covariance of variables. We thus investigated carbon fluxes and dissolved carbon production in peatland mesocosms from two acidic and oligotrophic peatlands under steady state conditions at two different water table positions. Exchange rates and CO_2, CH_4 and DOC production rates were simultaneously determined in the peat from diffusive-advective mass-balances of dissolved CO_2, CH_4 and DOC in the pore water. Incubation experiments were used to quantify potential CO_2, CH_4, and DOC production rates. The carbon turnover in the saturated peat was dominated by the production of DOC (10–15 mmol m^{-2} d^{-1}) with lower rates of DIC (6.1–8.5 mmol m^{-2} d^{-1}) and CH_4 (2.2–4.2 mmol m^{-2} d^{-1}) production. All production rates strongly decreased with depth indicating the importance of fresh plant tissue for dissolved C release. A lower water table decreased area based rates of photosynthesis (24–42%), CH_4 production (factor 2.5–3.5) and emission, increased rates of soil respiration and microbial biomass C, and did not change DOC release. Due to the changes in process rates the C net balance of the mesocosms shifted by 36 mmol m^{-2} d^{-1}. According to our estimates the change in C mineralization contributed most to this change. Anaerobic rates of CO_2 production rates deeper in the peat increased significantly by a factor of 2–3.5 (DOC), 2.9–3.9 (CO_2), and 3–14 (CH_4) when the water table was lowered by 30 cm. This phenomenon might have been caused by easing an inhibiting effect by the accumulation of CO_2 and CH_4 when the water table was at the moss surface.

Introduction

Peatlands cover about 450 million ha of land worldwide (Kivinen and Pakarinen 1981) and play an important role in the global biogeochemical cycles. They store large quantities of carbon (C), which is sequestered into organic matter through the synthesis of plant biomass. Peatlands have functioned as sinks for C since the end of the last glaciation because rates of plant production generally exceed rates of organic matter decomposition over millennia (Clymo 1984). Peatlands are also sources of methane (CH_4), contributing about 5% to the atmospheric CH_4 burden (Fung et al. 1991), and sources of dissolved organic matter to surface waters (Urban et al. 1989).

The important controls on organic matter decomposition and C mineralization are soil temperature, plant community structure, position of redox boundaries associated with the water table, and the chemical composition of plant tissues and peat (Whiting and Chanton 1993; Bubier et al. 1993; Bubier 1995; Yavitt et al. 1997). The effects of water table position on C turnover in peat soils have been established by the determination of aerobic and anaerobic potential CO_2 and CH_4 production rates in flask experiments with disturbed peat samples (Yavitt et al. 1987, 1990, 1997; Öquist and Sundh 1998; Kettunen et al. 1999) and by measuring the exchange of CO_2 and CH_4 with the atmosphere in peat columns devoid of vegetation (Moore and Knowles 1989; Moore and Dalva 1993; Aerts and Ludwig 1997). These studies documented that lower water tables increase C mineralization rates, and decrease CH_4 emissions from peat soils. In mesocosm experiments it was also shown that *Sphagnum* mosses grow more slowly when the water table is lowered (Williams et al. 1999).

Process rates within the intact peat soils leading to these changes, however, have not been quantified yet. The simultaneous response of processes in the C cycle, such as photosynthetic CO_2 uptake, mineralization of organic C and release of dissolved organic carbon (DOC), to different water tables, and their net effect on the C balance have not been investigated in studies that are based on controlled experiments with intact peatland mesocosms. This is, however, desirable because a difficulty in the interpretation of CO_2, CH_4 and DOC exchange data from field studies arises from the covariance of environmental controls and the interaction of production, storage and transport of dissolved C (Walter and Heimann 2000; Blodau and Moore 2002b).

In recognition of this situation our specific objectives were (I) to quantify the processes involved in the carbon cycle of intact peat soils and (II) to examine the short-term effect of water table levels on these processes, the carbon fluxes and the carbon balance. To these ends vegetated mesocosms were used, which left the soil structure intact and allowed for the simultaneous determination of export, production and storage of dissolved carbon and the exchange of CO_2 and CH_4 with the atmosphere. The mesocosms were kept under controlled conditions and exposed to different water table levels. The results of this study should provide useful baseline information about CO_2, CH_4, and DOC production and emission from acidic and oligotrophic peatlands.

Methods

Sites

We used peat cores from two peatlands in central and eastern Canada. The first site at Mer Bleue (MB), near Ottawa, eastern Ontario, Canada, is an open, slightly domed, acidic and oligotrophic peatland that is dominated by mosses (e.g., *Sphagnum capillifolium, S. angustifolium, S. magellanicum* and *Polytrichum strictum*) and shrubs (e.g., *Ledum groenlandicum, Chamaedaphne calyculata, Kalmia angustifolia, Vaccinium myrtilloides*). The second site in the Experimental Lakes Area (ELA), near Kenora, northwestern Ontario, Canada, is a small acidic and oligotrophic peatland located in the northwestern watershed of Lake 239 on the Precambrian Shield (Bayley et al. 1986). The peatland is dominated by black spruce (*Picea mariana*) and mosses (*S. magellanicum, S. angustifolium* and *S. fuscum*).

Definitions and conventions

The term *mesocosm* is used for the experiments with intact peat soils. The term *incubations* is used for flask experiments with peat taken from the peat cores following mesocosm experiments. Rates in mesocosms, obtained from mass balances, are referred to as *in situ*, whereas rates in flask incubations are referred to as *potential* turnover rates. Carbon dioxide is used synonymously with dissolved inorganic carbon (DIC), because dissolved CO_2 was, at pH values of below 3–5, the predominating carbonate species. The term water table refers to the depth at which water could be extracted by suction with a syringe. Losses of CO_2 and CH_4 from the peat to the atmosphere or due to drainage have been given a positive sign. All indicators of variability in the text and figures are standard deviations. The term soil respiration is used for the sum of decomposition and plant respiration. All production values are based on dry weight or volume of peat.

Mesocosm experiments

Peat cores, 20 cm in diameter and 75 cm long, were collected in PVC tubes from hollows in fall, and a drainage mesh and cap attached at the bottom. The vegetation, consisting primarily of *Sphagnum* mosses, minor numbers of *Polytrichum* and small specimens *of Ledum groenlandicum, Chamaedaphne calyculata, and Kalmia angustifolia*, was left intact. Pore water samplers (Bev-Line IV, Cole Parmer, 7 mm outer diameter, 3 mm inner diameter, ca. 30 perforations per sampler) were inserted horizontally at 2-cm intervals. The water table was adjusted with distilled water to 2–6 cm below the moss cover and kept constant. The temperature was initially 22 °C during the day and 8 °C during the night. After day 50 the temperature was lowered to 12 °C (day) and 8 °C (night) to slow down the abundant *Sphagnum* growth and the C mineralization rates. Humidity was kept at 70% rH. Light intensity was adjusted to 250 μmol m^{-2} s^{-1}. Solution was added with a sprinkler 5 to 6 days a week, and water manually retrieved at 2 to 3 mm d^{-1} from the base of the mesocosm.The inflowing solute contained H_3O^+ (92/358 μmol L^{-1}), SO_4^{2-} (26/104 μmol L^{-1}), NO_3^- (40/120 μmol L^{-1}), NH_4^+ (40/120 μmol L^{-1}) at two concentration levels, and Ca^{2+} (30 μmol L^{-1}), Mg^{2+} (15 μmol L^{-1}), Na^+ (50 μmol L^{-1}) and K^+ (5 μmol L^{-1}) and Cl^- (150–265 μmol L^{-1}). These concentration levels were due to the mesocosms being part of a N and S deposition study. The analyses showed that the concentrations of DIC, dissolved CH_4 and DOC and the CO_2 and CH_4 fluxes from the mesocosms were unaffected by the different treatments (Blodau 2001). Thus the N and S treatments are not discussed.

Measurements started after an initial equilibration period of 60 days, and were subsequently carried out for about 220 days on an approximately monthly basis. About 60 days after beginning of the experiment the water table level was lowered to ca. 36 cm below the surface in 8 mesocosms by drainage through a pore water sampler. The lower water tables lead to decreased evaporation rates so that water tables temporarily increased again in this treatment. We resorted to a permanent drainage at 36 cm. Between day 143 and 223 the water table level in the mesocosms was between 0 and 2 cm and 30 and 33 cm, respectively, below the original moss surface.

The total moss biomass in the mesocosms was between 200 and 600 g m^{-2} (dry weight). This value is an upper estimate, since the *Sphagnum* were pulled from the mesocosms and all lower parts of living *Sphagnum* stems were included in the measurement. Carbon dioxide and CH_4 exchange rates between the top of the mesocosms and the atmosphere were calculated from linear regressions of 4 to 6 measurements of gas concentrations in the chamber headspace at 8-minute intervals. Rates of photosynthesis were determined from the difference in CO_2 exchange between opaque and transparent chambers. Due to the opaque sides of the transparent chamber the light levels were somewhat attenuated, so that the rates of photosynthesis represented minimum estimates. Regressions with $R^2 < 0.75$ and obvious artifacts (e.g., exponential concentration increase) were eliminated even when $R^2 > 0.75$. Moss growth was determined at intervals of ca. 3 months with the cranked wire technique (Clymo 1970) with 5–7 wires per core.

Differences between treatments were statistically analyzed with t-tests using the software package SPSS, release 5.0 after examination of the data distribution with normality plots.

Incubation experiments

Incubations with peat were carried out after the end of the mesocosm experiments at room temperature (20°–22 °C). Anaerobic potential production rates of CO_2, CH_4, and DOC were determined in four depth increments (8–12, 22–26, 32–36 and 58–62 cm). Peat cores were extruded, dissected and sampled under N_2 in a glove chamber. The peat (50–100 g wet weight, 7.2 ± 3.2 g (s.d.) dry weight) was placed in 125–250 mL, rubber-stoppered Erlenmeyer flasks and fully immersed in deaerated water. No gas headspace was left in the flask except from a small bubble. The flasks were not shaken, but occasionally turned over to avoid a chemical stratification within the flasks. The water was sampled through suction samplers inserted through the rubber stoppers. Over 7 to 9 days, 10 mL of water were extracted on 5 to 6 occasions and CO_2, CH_4, and DOC determined as described below. The extracted water was replaced with the deaerated solutions. Rates were determined by linear regressions of concentration over time corrected for the replacement of water sampled from the flasks with the deaerated solution.

Potential CO_2 production under aerobic conditions was determined for peat removed from 8 depths in 6 to 12 cm increments in each core following the *in situ* experiments. Approximately 5 g of peat (wet weight) from each depth was placed into a 50 ml Erlenmeyer flask. Twenty milliliters of deionized water was added to create a slurry that helped to eliminate any local regions of anoxia in the peat. Flasks were sealed with rubber stoppers and shaken on a rotary shaker at 200 RPM for 3 days. Gas from the headspace was sampled daily and analyzed to determine CO_2 concentrations. Rates were determined as the volume corrected linear regression of concentration over time.

Determination of extractable microbial carbon

Extractable microbial C was determined in peat taken from the same locations used for aerobic CO_2 production potential measurements. Fumigation with $CHCl_3$ and extraction with 0.5 M K_2SO_4 was carried out with slight modifications according to Voroney et al. (1993). Approximately 40 g of peat (wet weight) from each bulk sample were split into two 20 g samples. One sample was placed in a vacuum dessicator and fumigated with ethanol-free $CHCl_3$ in absence of light for 24 hours. Chloroform vapor and residue was then removed through repeated evacuation. All samples were sealed in plastic containers containing K_2SO_4 solution, shaken for 1 hr at 200 RPM on an oscillating shaker, and filtered with 0.45 μm glass fiber filters. Dissolved organic carbon (DOC) was measured with a TOC analyzer after pH adjustment to 2.5 and sparging with CO_2-free N_2 for 10 min. Extractable DOC was measured directly in extracts from the non-fumigated samples. Microbial biomass C was calculated by subtracting the non-fumigated extractable DOC from the fumigation-extractable DOC. No extraction efficiency coefficients were used in our calculations as we were interested in differences among samples, and because there have been reports of a large range of C extraction efficiency coefficients (K_{EC}, K_{EN}) (Sparling et al. 1990; Brookes et al. 1985) for different soils.

Pore water and air analyses

About once a month 5–10 ml of pore water or air was extracted from the suction samplers from zero to 12 centimeter below the water table in 2-cm and below in 6-cm or 12-cm increments with stoppered syringes. DOC was determined after filtration of extracted pore water with a syringe micro-filter (0.45 μm, nylon) on a Shimadzu 5050 TOC analyzer. Dissolved inorganic carbon (DIC), and CH_4 were determined on a Shimadzu Mini 2 gas chromatograph with methanizer (CO_2) in the gas phase of 1.8 mL vials after addition of 20 μL of 4 M HCl and 0.5 mL sample. Losses of CO_2 and CH_4 from the GC vials were corrected with exponential loss functions (n = 16, $R^2 = 0.99$; concentration of CO_2: $C = C_0\ 10^{(-0.0264\ t)}$ and concentration of CH_4: $C = C_0\ 10^{(-0.00635\ t)}$ with t: (h). The original dissolved concentration was reconstructed using the head space concentrations, the volumes of headspace and water phase and Henry's law ($K_H = 10^{-1.5}$ (mol L^{-1} atm^{-1}) for CO_2 and $K_H = 2 \times 10^{-3}$ (mol L^{-1} atm^{-1}) for CH_4. In the unsaturated zone of the mesocosms CO_2 and CH_4 were directly determined on gas samples that were extracted from the sampling ports with syringes. O_2 was determined amperometrically with a low-current electrode and pH potentiometrically on 0.5 to 3 mL of sample with a conventional meter (Orion). O_2 contamination due to the sampling procedure was ca. 0.5 mg L^{-1}. In a few mesocosms concentrations of formate, acetate, propionate, butyrate were determined by HPLC, at the end of the experiment, but in all samples the concentrations were below the detection limit of ca. 50 µmol L^{-1}.

Calculation of in situ *production rates*

The water movement in the peat cores was sufficiently described by advective-diffusive transport (Blodau and Moore 2002a). Variability in concentration profiles through the use of suction samplers was minimized by averaging concentration data within 6 cm or 12 cm depth segments. For these segments, vertical advective-diffusive mass balances were calculated, using temperature-corrected diffusion coefficients for dissolved CO_2, CH_4 and O_2 (Lerman 1979). Net turnover is then given by Equation (1):

$$R = \Delta S_A/\Delta T - (D_{in}\Delta C_A/\Delta X)_{in} + (D_{out}\Delta C_A/\Delta X)_{out} - v(C_{A,in}C_{A,out}) \qquad (1)$$

in which

R = turnover rate (nmol cm^{-3} d^{-1}),

C_A = concentration of component A,

$\Delta S_A/\Delta T$ = change in storage of component A in a segment (nmol cm^{-3} d^{-1}),

D = whole peat diffusion coefficient (cm^2 d^{-1}),

$\Delta C_A/\Delta x$ = concentration gradient of component A (nmol cm^{-4}),

v = advection rate (cm d^{-1}) The effect of bulk density on diffusion coefficients was taken into account by using separately determined bulk density profiles, which were fitted against a power function (Bd = 0.0107 × 0.567 with Bd = bulk density (g cm^{-3}); x: depth (cm); $R^2 = 0.79$; Blodau and Moore (2002a)). Based on preliminary calculations with tabulated diffusion coefficients (Cornel et al. 1985), diffusion was neglected for the calculation of DOC turnover. The concentration profiles were treated as a series of steady states and rates calculated from advective-diffusive mass balances. Diffusive exchange with the atmosphere was calculated using Fick's 1st law. For this calculation, it was assumed that gaseous concentrations 1–2 cm above the water table were in equilibrium with the dissolved concentration at the water table.

To obtain turnover rates under unsaturated conditions, we separately determined water content and bulk density of the depth segments under identical conditions and fitted the data to linear (water content, $R^2 = 0.97$) and square functions (bulk density, $R^2 = 0.79$). Equation (2) (Jin and Jury 1996; Millington and Quirk 1961), and gaseous, temperature-corrected diffusion coefficients (Lerman 1979) were used to estimate unsaturated diffusion coefficients in the peat:

$$\alpha(a) = a^2\beta^{-2/3} \qquad (2)$$

in which

α = diffusion coefficient correction factor (),
a = volumetric air content ()
β = soil porosity ()

Ambient atmospheric concentrations and diffusive mass balances were used to calculate turnover and diffusive exchange rates of CO_2 and CH_4 with the atmosphere.

Results

Pore water concentrations

1–3 cm below the water table, the pore waters became anoxic (Figure 1A). The pH values in the pore water ranged from 3.9 to 4.2 both at high and low water table levels. DOC was the predominant form of C in the pore water with concentrations increasing with depth from about 2.5 to 7.5 mmol L^{-1} (Figure 1B). DIC concentrations increased from 0.1–0.6 mmol L^{-1} at the water table to 2–5 mmol L^{-1} at larger depths and were on average fairly similar in ELA and MB mesocosms (Figure 1C).

Lowering of the water table resulted in degassing of CO_2 from the unsaturated zone and volumetric concentrations of 190–10000 ppmv (8–440 µmol L^{-1}) at and above the water table. In these mesocosms, the DIC gradient was very steep so that outflow concentrations were nearly identical in the treatments (Figure 1C). In the unsaturated zone, CO_2 concentrations were generally smallest below the *Sphagnum* moss surface (402 ± 140 ppmv, with air background of ca. 504 ppmv), indicating uptake from the atmosphere and the soil. Methane concentrations generally ranged from 10–190 µmol L^{-1} just below the water table to 500–1000 µmol L^{-1} at depths of 40 to 70 cm (Figure 1D). In the unsaturated zone concentrations were generally between 2 and 30 ppmv (0.1–1.3 µmol L^{-1}) and increased towards the water table to 13–100 ppmv.

Carbon fluxes and in situ *production rates*

The *Sphagnum* grew on average between 2 mm and 20 mm $month^{-1}$, being faster at the beginning of the experiments and in the ELA cores, and when the water table was kept high (Figures 2A and B). Carbon dioxide uptake by photosynthesis was higher in Mer Bleue mesocosms than in ELA mesocosms and decreased when the water table level was lowered (Table 1, Figures 2C and D) by an average of 24% (MB) and 42% (ELA). Soil respiration fluxes were greater in the ELA than the MB mesocosms, and increased with lowered water table levels (Figures 2E & F). Methane emissions were significantly larger from ELA than MB mesocosms, at both high and low water table levels and strongly decreased after lowering the water table (Figures 2G & H). In the mesocosms with a high water table level, the average *in situ* DIC production was about 7.3 mmol m^{-2} d^{-1} of which ca. 1.6 mmol m^{-2} d^{-1}

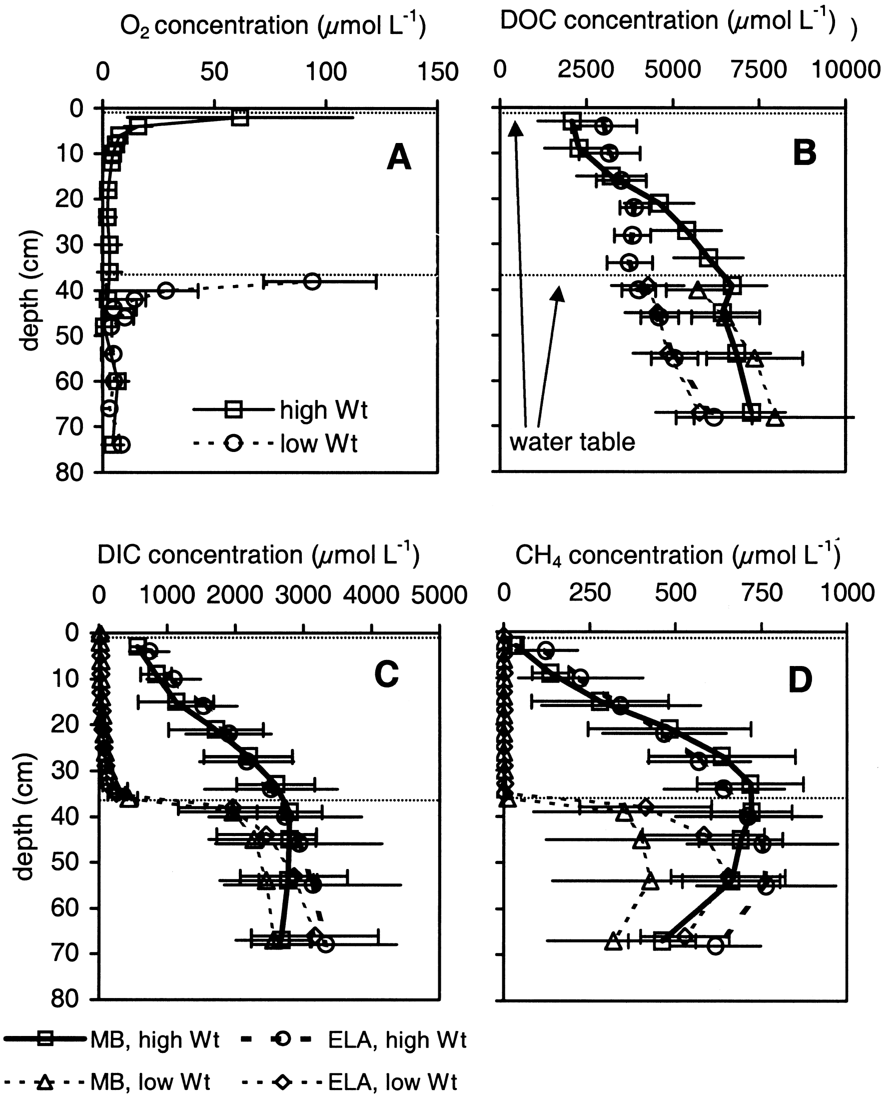

Figure 1. Average concentrations of dissolved O_2, DOC, DIC and CO_2, and CH_4 during the experiment. Bars indicate the average standard deviations of concentrations in mesocosms at individual sampling dates. Note the strong concentration increase in DIC and CH_4 concentrations at 35–45 cm depth in the low water table treatments.

was due to oxic respiration. Most of the DIC produced left the mesocosms with the outflow (average 68–72%) and the remainder by diffusion across the water table (Table 1). The calculated fluxes and the production rates were nearly identical (Table 1).

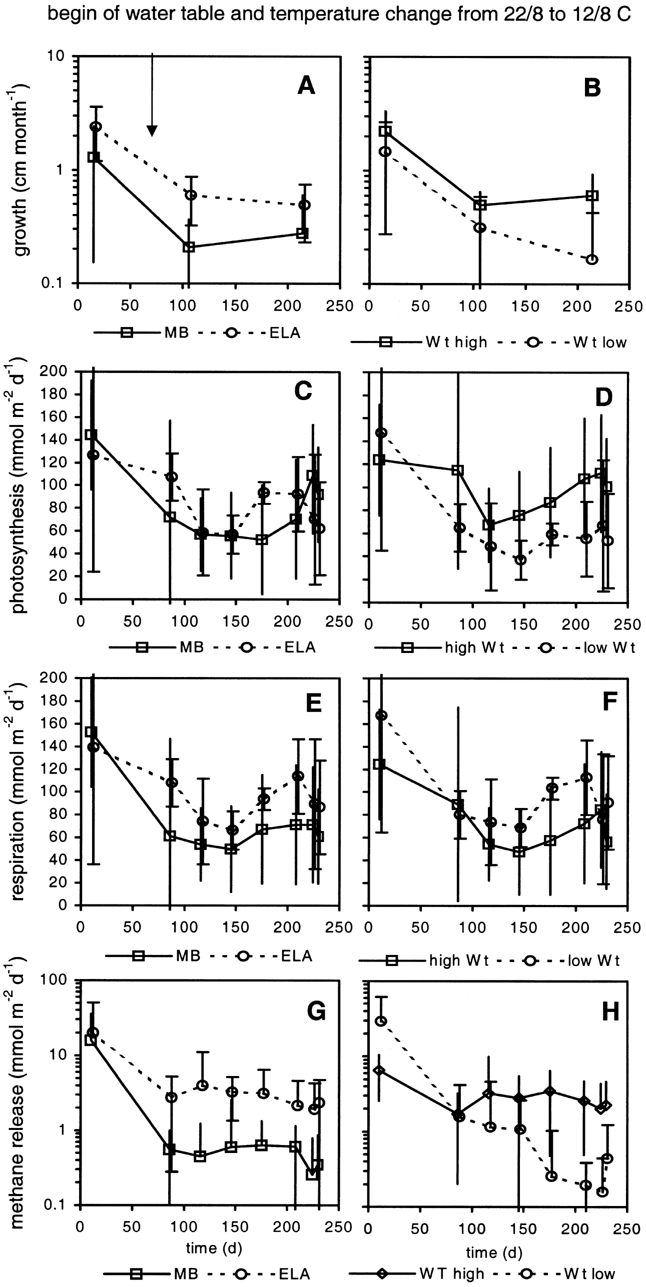

Figure 2. Moss growth, rates of photosynthesis at "daylight", soil respiration and CH_4 emission during the experiment. Bars indicate standard deviations. The water table levels was varied after the first measurement. The figures show that that the impact of the water table change was largest on the CH_4 emission and smallest on the respiration.

Table 1. Depth-aggregated net in situ CO_2, CH_4 and DOC production rates and fluxes, as calculated from pore water profiles and chamber measurements (mmol m^{-2} d^{-1}). Means and standard deviations are presented. Dissolved fluxes represent the outflow from the mesocosm, and diffusive fluxes the estimated diffusive flux across the water table.

Site	MB			ELA		
Species	CO_2	CH_4	DOC	CO_2	CH_4	DOC
High water table[§]						
Net production	6.1 ± 0.8	1.1 ± 0.7	15.4 ± 3.9	8.5 ± 1.6	1.5 ± 0.5	9.7 ± 2.3
Flux, dissolved[a]	4.4± 0.6	0.88 ± 0.12	13.3 ± 0.9	5.8 ± 2.0	1.2 ± 0.2	10.1 ± 1.8
Flux, diffusive[b]	2.1 ± 0.8	0.08 ± 0.05	–	2.3 ± 1.2	0.37 ± 0.30	–
Flux, chamber[c]	47 ± 8	0.94 ± 0.30	–	85 ± 15	3.2 ± 2.3	–
photosynthesis[d]	41 ± 9			54 ± 16		
Low water table[§]						
Net production	170 ± 460	n. q.[e]	n. q.[e]	139 ± 239	n. q.[e]	n. q.[e]
median	152			117		
Flux, dissolved	4.2 ± 0.9	0.58 ± 0.37	14.1 ± 3.9	5.1 ± 2.7	1.02 ± 0.23	9.4 ± 1.9
Flux, chamber	77±15	0.01±0.25	–	95±10.2	0.88±1.15	–
photosynthesis	31±15			23±12		

[§] at 8/12 °C; [a]advective removal from the mesocosmsms; [b]diffusive export to the water table; [c]measured flux from the moss surface; [d]difference between chamber fluxes under shrouded and non-shrouded conditions; [e]n.q. = not quantified due to unknown contribution of the unsaturated zone

In situ DIC production rates strongly decreased with depth (Figure 3C). The *in situ* CO_2 production rates in the unsaturated zone (Equation 2) were, on average, between 1200 and 12000 nmol g^{-1} d^{-1}, and peaked at a depth of 18 cm. The resulting, very poorly constrained, estimate of net production for these mesocosms was 139 ± 239 mmol m^{-2} d^{-1} (ELA) and 170 ± 460 mmol m^{-2} d^{-1} (MB) (Table 1). *In situ* CH_4 production rates decreased from an average of 200 ± 36 nmol g^{-1} d^{-1} at 0–6 cm to a net consumption of 8 ± 2 nmol g^{-1} d^{-1} at a depth of 60 to 74 cm. The calculated diffusive flux across the water table (Table 1) was much smaller (0.08–0.37 mmol m^{-2} d^{-1}) than the measured CH_4 emission rate (0.94–3.2 mmol m^{-2} d^{-1}). This implies that the release of bubbles was the primary mechanism of CH_4 emissions, and that the diffusive-advective mass balances probably accounted only for ca. 35–50% of the total CH_4 production rate. The *in situ* CH_4 production rates in the unsaturated zone (Equation 2) indicated a CH_4 sink of −174 ± 211 nmol g^{-1} d^{-1} between the water table and a depth of 32 cm. Average *in situ* DOC production rates were 15.4 ± 3.9 mmol m^{-2} d^{-1} (MB) and 9.7 ± 2.3 mmol m^{-2} d^{-1} (ELA, Table 1). Rates decreased with depth from 2220 ± 670 nmol g^{-1} d^{-1} (MB) and 2960 ± 810 nmol g^{-1} d^{-1} (ELA) to 3 ± 31 nmol g^{-1} d^{-1} and 21 ± 9 nmol g^{-1} d^{-1} (Figure 4A).

With lower water table levels, average production rates increased at depths below the new water table, DIC by a factor 2.9 to 3.9 (t-test, $^{*}P < 0.05$, n = 8; Figure 3C), CH_4 by a factor 3 to 14 (t-test, $^{*}P < 0.05$, n = 8; Figure 5B) and DOC by a

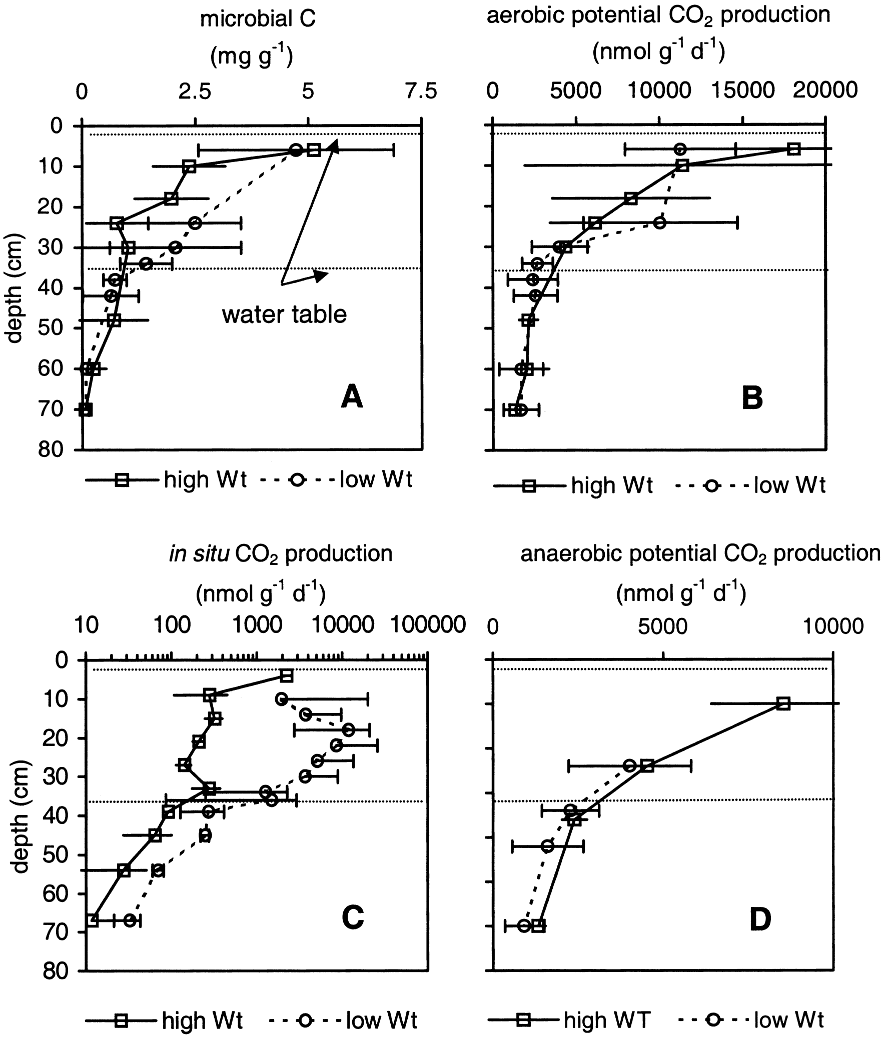

Figure 3. Average microbial C (A), aerobic potential production rates (B), in situ CO_2 and DIC production rates (C), and anaerobic potential CO_2 production rates (D). The figure illustrates the influence of depth and water table level on the C mineralization rates and microbial C concentrations.

factor 2 to 3.5 when compared to the high water table treatment (t-test, *P = 0.05, n = 8; Figure 4).

Potential production rates

The aerobic potential CO_2 production rates followed the same depth trend as the *in situ* rates (Figure 3B) but were, on average, between 8 (0–6 cm) and 112 times (70 cm) larger. The anaerobic potential DIC production rates also decreased with depth

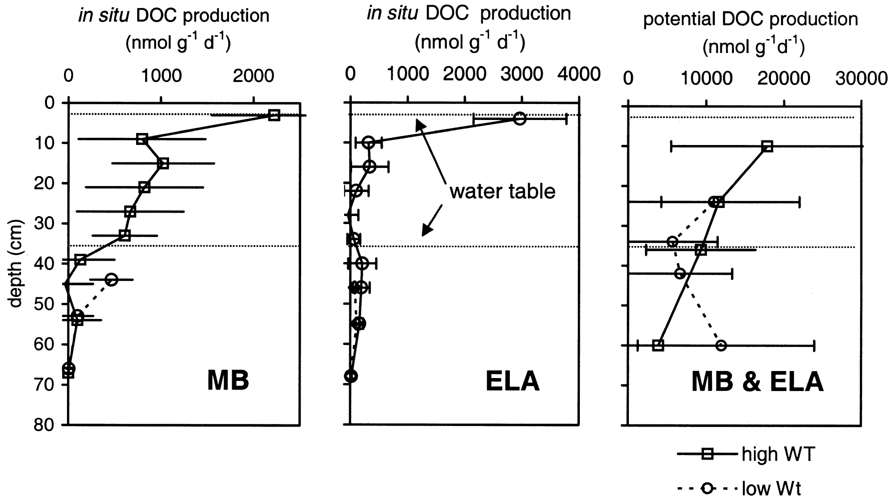

Figure 4. Average *in situ* (A) and potential (B) DOC production rates.

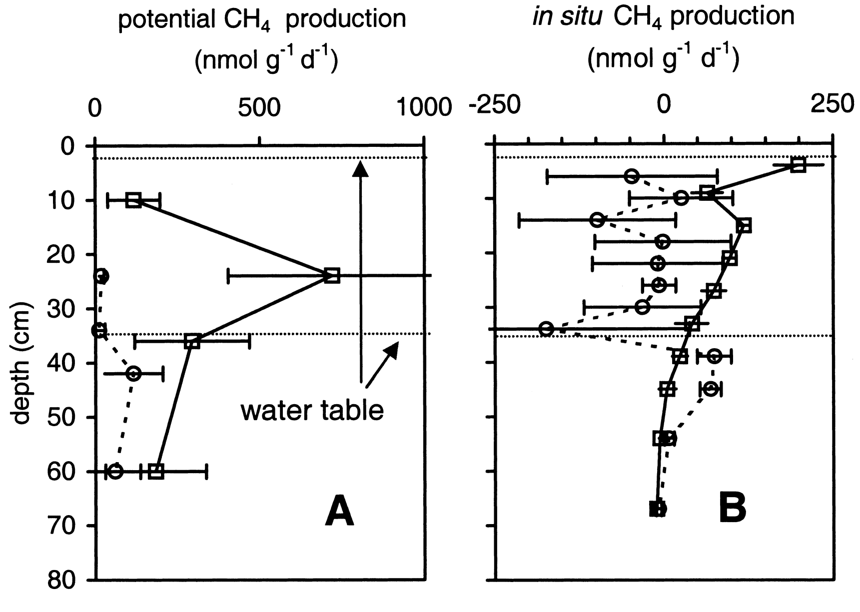

Figure 5. Potential (A) and average *in situ* (B) CH_4 production rates. Note the effect of a lowered water table on the CH_4 production rates at 35–45 cm depth.

(Figure 3D) and were on average 1.4 times smaller than the potential aerobic rates. The potential CH_4 production rates peaked on average at 24 cm and at 750 ± 320 nmol g^{-1} d^{-1} (Figure 5A). Decreasing the water table significantly reduced this rate

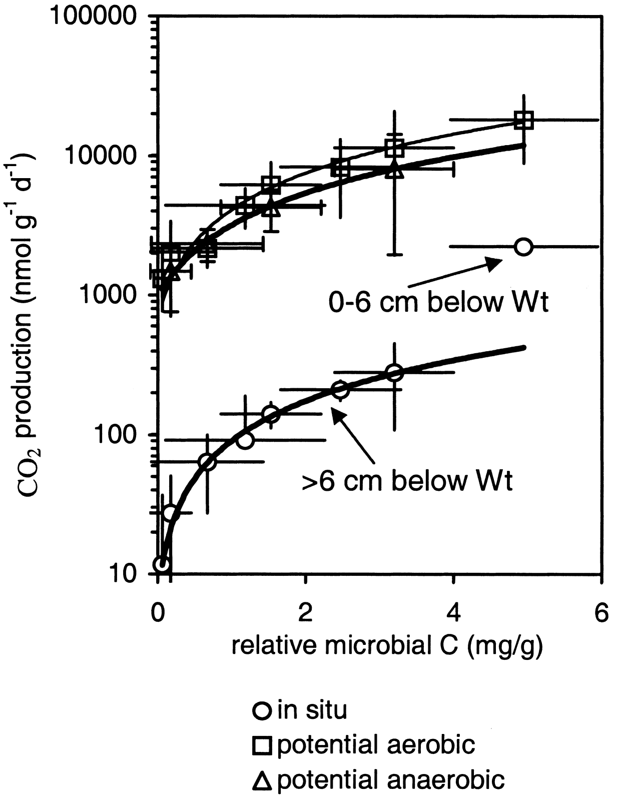

Figure 6. In situ DIC production rates, potential anaerobic DIC production rates, and potential aerobic production rates vs. relative microbial C. Bars indicate standard deviations.

in the unsaturated peat by a factor of 42. Potential rates were on average larger than the corresponding diffusive-advective *in situ* rates by a factor of 2 (10 cm) to 26 (60 cm). Potential DOC production rates decreased on average from 17000 to 4000 nmol g^{-1} d^{-1} with depth (Figure 4). The water table treatments had no effect on potential DOC production rates.

Microbial biomass

Microbial C concentrations were largest at the surface (3.7–8.0 mg g^{-1}, Figure 3A) and decreased with depth. With exception of the surface layer, concentrations were larger in the unsaturated peat of the low water table treatments (Figure 3A). Microbial biomass C concentrations were correlated to *in situ* and potential rates of CO_2 production (Figure 6).

Discussion

As in studies with peat columns devoid of vegetation (Moore and Knowles 1989; Moore and Dalva 1993; Aerts and Ludwig 1997), lowering of the water table level resulted in strong changes of C fluxes from the mesocosms (Table 1). A water table level decrease by 30 cm reduced rates of photosynthesis by 24% (Mer Bleue) and 42% (ELA). Previously a reduction of 25% in *Sphagnum* mass growth with the same water table level decrease was described by Williams et al. (1999). Rates of CO_2 production and emissions increased as found by Moore and Dalva (1993) and rates of CH_4 production and emission decreased as described by Aerts and Ludwig (1997).

When the water table level was high, C mineralization rates were small compared to photosynthesis and plant respiration. Plant respiration was estimated by subtracting the mineralization rates, as calculated from the pore water mass balances, from the CO_2 exchange rates (Table 1). The relative importance of C mineralization, however, increased when the water table was lowered. Under these conditions, the average photosynthesis rates decreased from 48 to 27 mmol m^{-2} d^{-1} ($n = 8$, $^{*}P < 0.05$, t-test), whereas the sum of respiration and mineralization increased from 66 to 86 mmol m^{-2} d^{-1}, compared to the high water table treatment ($n = 8$, $^{*}P < 0.05$, t-test). Assuming a jointly response of photosynthesis and plant respiration in response to the change in environmental conditions (Proctor 1982; Chapin and Oechel 1983) and a constant ratio between photosynthesis and plant respiration, plant respiration would have decreased from 66 to 33 mmol m^{-2} d^{-1} and mineralization would have consequently increased from 7.3 to 53 mmol m^{-2} d^{-1}.

When the water table level was low, C mineralization thus probably became the process with the largest rate in the system. This is qualitatively confirmed by the net CO_2 production rates that were calculated using the mass balance approach (Table 1, ″CO_2 net production″). Along with the increase of C mineralization rates in the unsaturated zone the microbial biomass-C also increased (Figure 3A) suggesting that part of the processed carbon was not mineralized but utilized for microbial biomass synthesis. This was not so in the uppermost layer of the peatland mesocosms, where in both water table treatments C mineralization proceeded under oxic conditions. In accordance with earlier findings oxic respiration apparently allowed for the build up and maintenance of a larger microbial biomass (McLatchey and Reddy 1998).

The outlined changes in the relative importance of process rates within the C cycle should be realistic, since a compilation of CO_2 and CH_4 emission data from column experiments showed that an average water table decrease of 22 cm resulted in an increase of the median of CO_2 fluxes from unvegetated peat columns from 60 to 270 mmol m^{-2} d^{-1} (Figure 7). Such effects are caused by the higher efficiency of aerobic vs. anaerobic C mineralization. In incubation and column studies aerobic-anaerobic ratios typically range from 1.2 to 6 (Figure 7; Moore and Dalva (1993) and Updegraff et al. (1996), Aerts and Ludwig (1997), Yavitt et al. (1997), Öquist and Sundh (1998)).

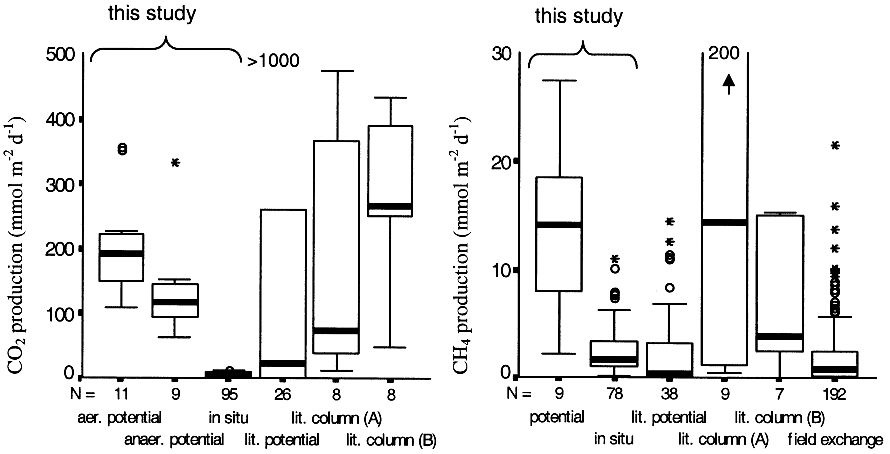

Figure 7. Summary of *in situ* rates, potential rates, and reported rates of DIC/CO_2, and CH_4 turnover. The graph displays median, quartiles, 90% quantiles, and extreme values. Reported potential rates were recalculated for a 40 cm profile (bulk density 0.08 g cm^{-3}), and molar units. "Wt" stands for water table. The "literature" denoted rates were taken from: Aerts & Ludwig 1997; Aerts & Toet 1997; Bellisario et al. 1999; Bubier et al. 1993; Bubier 1995; Freeman et al. 1993; Funk et al. 1994; Hall et al. 1996; Liblik et al. 1997; Moore & Dalva 1993; Moore & Knowles 1989; Moore et al. 1994; Nykaenen et al. 1998; Schimel 1995; Hogg 1993; Valentine et al. 1994; van den Pol-van Dasselaar & Oenema 1999; Yavitt et al. 1990; Yavitt et al. 1997

The *in situ* rates of DOC release obtained in the mesocosms are fairly typical for peatlands although most studies on DOC dynamics in wetlands were carried out on the watershed scale, so that fully comparable *in situ* and potential DOC production rates are not available. Peatlands have been found to export between 0.2 and 11.5 mmol m^{-2} d^{-1} to discharging streams (Moore 1987, 1988; Urban et al. 1989; Koprivnjak and Moore 1992; Dillon and Molot 1997). DOC release from Thoreau's Bog, an ombrotrophic peatland in the northeastern United States, was 5–10 mmol m^{-2} d^{-1} (McKnight et al. 1985), which is somewhat lower than the figures obtained in this study (Table 1, "DOC flux dissolved"). In incubations with peats from different depths, Moore and Dalva (2001) reported average release rates of 2.6–3.8 μmol g^{-1} d^{-1} over a 60 day period with a threefold flushing with distilled water. These rates are similar to the rates in the uppermost peat layers in the MB and ELA cores (2.2 to 2.9 μmol g^{-1} d^{-1}) but are much higher than rates at lower depths.

Below the water table DOC release dominated the C export from peat under the chosen vertical through-flow rate, which represents about twice the average runoff rate at Mer Bleue (ca. 1 mm d^{-1}, based on a 8 month unfrozen period; Fraser et al. (2001)). Also, most of the DOC was released by or just below the vegetation layer (Figure 4). This confirms results from incubation experiments showing that the potential DOC release is highest for plant tissues and decreases with an advancing state of decomposition (Moore and Dalva 2001). The water table level had little influence on the *in situ* and potential DOC production rates (Table 1) and initial rates in flask incubations were, particularly at lower depths, one or two orders of magnitude faster than *in situ*. Previous work has shown that DOC release is strongly correlated with run off from wetlands (Mulholland and Kuenzler 1979; Urban et al. 1989) and that contact of peat with water low in DOC releases DOC from the peat matrix (Moore and Dalva 2001). These and our results suggest that the DOC release from peat is constrained by the accumulation of DOC in the pore water.

Methane production and fluxes followed previously reported patterns. Methane consumption, as observed in the unsaturated peat (Figure 5B), has frequently been reported from field and laboratory studies (Klinger et al. 1994; Yavitt et al. 1990) and occurred primarily at the water table (Figure 5B). When the water table was low, methane production was reduced by a factor of 2.5 (ELA) to 3.5 (MB), and the chamber emissions by a factor of 3.6 (ELA) and about 100 (MB). A compilation of available studies shows that in column experiments a difference in water tables of 22 cm changed the median of CH_4 emission rates by factor of 3.8 (Figure 7)

In field studies and in the Mer Bleue mesocosms differences in CH_4 emissions with variation in water table levels were much larger than in the ELA mesocosms. On average the logarithm of seasonal CH_4 emissions in peatlands changes by 2–5% per 1-cm difference in average seasonal water table level (Blodau 2002). A plausible explanation for the relatively small effect of the water table change on CH_4 emission rates in the ELA mesocosms would be continued ebullition from the saturated into the unsaturated zone, even when the water table was low. According to the difference between fluxes measured with the chamber technique and calculated from concentration profiles (Table 1, diffusive flux vs. chamber flux), the release of bubbles was a primary mechanism of CH_4 emissions in the high water table level treatment. When the water table was low at the ELA site dissolved CH_4 concentrations also remained in a range (> 500 μmol L^{-1}) often allowing for ebullition (Chanton et al. 1989; Chanton and Dacey 1991; Shannon and White 1994). In the Mer Bleue mesocosms, showing much smaller rates of CH_4 emission, this was not the case (Figure 1D).

Due to the changes in process rates the C net balance of the mesocosms shifted from a loss of C of about 21 mmol m^{-2} d^{-1} (Mer Bleue) and 47 mmol m^{-2} d^{-1} (ELA) in the high water table treatment to losses of about 60 mmol m^{-2} d^{-1} (Mer Bleue) and 83 mmol m^{-2} d^{-1} (ELA) in the low water table treatment. According to our estimates the C mineralization contributed most to this change. Rates of photosynthesis and CH_4 production changed less and rates of DOC production did not change (Table 1). It has to be kept in mind though that light intensities in this experiment were low and probably partly responsible for the low rates of photosynthesis and the net loss of carbon from the mesocosms in the high water table treatment.

In addition to the described changes in C fluxes, an important finding of this study is that changes of the water table level can have *in situ* effects on CO_2 and CH_4 production rates that are not controlled by a distinction in aerobic/anaerobic conditions: Lowering of the water table resulted in increased anaerobic *in situ* rates of CO_2, CH_4 and DOC production at larger depths (Figures 3C and 5B). This was also indicated by the steep concentration gradients of CO_2 and CH_4 at low water table level compared to the high water table treatments (Figures 1C and D). As a result advective fluxes of dissolved CO_2, CH_4 and DOC from the mesocosm base decreased only slightly, or not at all, when the water table was lowered (Table 1).

This phenomenon might have been caused by the *in situ* accumulation of CO_2 and CH_4 in the deeper peat when the water table was at the surface because large end-product concentrations of biogeochemical processes decrease the available energy from these processes. Under high CO_2 and CH_4 concentrations the microbial community might thus operate at the thermodynamic limit of metabolism, which is 1/4 to 1/3 of the energy necessary for ATP generation and biomass synthesis (Rothfuss and Conrad 1993; Conrad 1999). For H_2-dependent methanogenesis, a Gibbs free energy of -20 KJ mol^{-1} (CH_4) represents the approximate energetic boundary of CH_4 production (Conrad 1999). Indirect support for a thermodynamically controlled decrease of C mineralization rates comes from the observation that in long-term closed anaerobic incubations, rates decrease but can be fully restored by flushing the incubation flask headspace with N_2 (Magnusson 1993).

Potential and *in situ* CO_2 production rates significantly correlated with the microbial biomass C (Figure 6), but *in situ* rates were between 8 to 100 times smaller than the potential aerobic and anaerobic rates obtained in the flask incubations, when CO_2 and CH_4 concentration levels were still low. This also suggests that the microbial efficiency to process C was greatly reduced under *in situ* conditions, either by the accumulation of CO_2 and CH_4, or by some other reason, which would be related to the physical and chemical disturbance involved in incubating peat. Increased C mineralization rates may for instance be caused by enhanced substrate release due to redox and enzyme induced chemical breakdown, as well as enhanced recycling of biomass after cell lysis due to aeration of previously anaerobic peat (Freeman, pers. communication, Kieft et al. (1987) and Aller (1994)).

Constraining C mineralization by accumulation of CO_2, CH_4 and DOC in the pore waters would have implications for the long-term development of peatlands and for the C dynamics under changed hydrologic conditions. Slowing of the decomposition process due to this accumulation would be a inherent result of the build up of deep peat deposits, in which CO_2 and CH_4 concentrations typically reach levels as high as, or higher than, measured in the mesocosms (Nilsson and Bohlin 1993; Romanowicz et al. 1995; Liblik et al. 1997; Blodau et al. 2002). *Vice versa*, it can be inferred that decreases in concentrations of decomposition products would accelerate the anaerobic decomposition process. This could, for instance, be caused by water table fluctuations and increased flushing of pore water (Siegel et al. 1995) or by the seasonal removal of CH_4 by conduit transport in annual plants containing aerenchyma (Shannon and White 1994; Schimel 1995).

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