Belowground carbon turnover in a temperate ombrotrophic bog

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[1] To examine belowground carbon (C) turnover in peatlands, we measured fluxes of carbon dioxide (CO2) and methane (CH4) by chamber measurements, estimated respiration by in situ incubations of peat, and in situ production of dissolved carbon (CO2; CH4; and dissolved organic carbon, DOC) by pore water modeling at an ombrotrophic temperate bog. Ecosystem respiration (ER) averaged 205 mmol m−2 d−1 in summer and was related to temperature, but not water table position, and in situ rates of heterotrophic respiration in the unsaturated zone were also temperature-dependent, with Q10 = 5.0–6.4. In the saturated zone, concentrations of 0.1–2.5 mmol L−1 (CO2), 0 to 0.6 mmol L−1 (CH4), and <10–120 mg L−1 (DOC) were recorded. Turnover was dominated by DOC unrelated to respiration, which ranged from <0.5 to 7 mmol m−2 d−1 and amounted on average to <1% of ER. Peat decomposition constants kd were 0.060 yr−1 to 0.034 yr−1 in the unsaturated and <0.002 yr−1 in the saturated zone. Monthly averages of CH4 fluxes ranged from 0 to 1.6 mmol m−2 d−1 and were higher than modeled diffusive fluxes when threshold concentrations for CH4 ebullition were recorded closer to the peatland surface. Our results suggest that the saturated zone is of little relevance to ER in this dry temperate bog and that mobilization of DOC is a potentially more relevant process. Temperature is a more important control on ER than water table position because most of the ER is generated close to the peatland surface. Concurrent, moderate increases in temperature and soil moisture are thus likely to increase losses of CO2 from ER and of CH4 from this type of peatland.


1. Introduction

[2] Peatlands cover about 450 million ha of land worldwide [Kivinen and Pakarinen, 1981], have functioned as sinks for C since the end of the last glaciation with average sequestration rates of 20–30 g C m−2 yr−1, and currently store between 250 and 450 Gt of C [Turunen et al., 2002]. Furthermore, peatlands are also sources of methane (CH4), contributing about 4–10% to the atmospheric CH4 burden [Mikaloff Fletcher et al., 2004], and sources of dissolved organic matter to surface waters [Urban et al., 1989]. The role of peatlands in the global C cycle and their location in regions that are anticipated to undergo significant changes in climate over the next decades [Moore et al., 1998] has generated a considerable interest in their C budgets and the ecological and climatic controls on C exchange with the atmosphere and discharging waters.

[3] Ecosystem respiration represents a large component of the C budget and is the emission of CO2 to the atmosphere from autotrophic (vegetation) and heterotrophic (soil organism) respiration. The environmental controls on ER and the relative contribution of aboveground and belowground autotrophic respiration, and heterotrophic respiration in the saturated and unsaturated zone to ER, are still poorly constrained in northern peatlands [Frolking et al., 2002]. Hydrologic and thermal regimes, as reflected by soil temperature and water table position, have been found to correlate to ER to a varying degree in most studies but their relative importance seasonally and in different types of peatlands is debated [e.g., Carroll and Crill, 1997; Roehm and Roulet, 2003; Bubier et al., 2003; Lafleur et al., 2005]. Studies employing incubations and columns with peat soils and litter bag studies demonstrated that higher temperatures, aerobic conditions, a larger content of more easily decomposable litter, and a smaller degree of humification facilitate heterotrophic respiration and may thus increase the contribution of heterotrophic respiration to ER [Moore and Dalva, 1993; Updegraff et al., 1995; Verhoeven and Toth, 1995; Yavitt et al., 1997]. Experiments with intact peatland soils including some or all of the vegetation suggested, on the other hand, that the respiratory processes are modulated by yet poorly understood interactions with soil moisture, tem-
perature, and biological and chemical conditions, and that results obtained from in vitro experiments cannot easily be extrapolated to intact peat soils [Blodau et al., 2004; Udegraaff et al., 2001].

[3] Understanding the response of northern peatlands to potential climate change by ecosystem modeling will thus depend on a quantification of process rates involved in ER and on constraining the circumstances under which environmental controls are effective [Frolking et al., 2002]. To achieve this progress, ER and the contribution of autotrophic and heterotrophic respiration to ER have to be quantified under varying environmental conditions simultaneously and in situ. In particular, we lack information about the relative contribution of the saturated zone to ER [Frolking et al., 2002] and the consequences of saturation for the rates of autotrophic and heterotrophic respiration. To rectify these knowledge deficiencies at an ombrotrophic bog, our objectives are (1) to estimate rates and fluxes of C in the saturated and unsaturated zone, (2) to examine the effect of removal of the foliage of vascular vegetation on the concentrations and the turnover of C in the saturated zone of peat soils, and (3) to refine the belowground component of the C budget presented by Moore et al. [2002]. We carried out chamber gas flux measurements, in situ incubation experiments and quantified dissolved C concentrations, and used these to estimate production, storage, and export of dissolved C in the peat and the exchange of CO$_2$ and CH$_4$ with the atmosphere.

2. Site, Materials, and Methods

2.1. Site

[5] Mer Bleue, near Ottawa in eastern Ontario, Canada, is a mostly ombrotrophic peatland of 2180 ha. The mean annual precipitation of the Ottawa International Airport (about 10 km southwest of the site) is 953 mm, of which 25% fall as snow. From April to November mean air temperatures exceed 0°C, the mean annual air temperature is 6.0°C, and the mean annual growing season 193 d. A peat deposit of up to 6 m has developed within the last 7000 years [Mott and Camfield, 1969].

[6] Two separate sampling areas were established: a “permanent” area and a “defoliated” area, both representative of the bog portion of the peatland. The areas were dominated by the mosses Sphagnum capillifolium, S. magellanicum and Polytrichum strictum, with shrubs such as Ledum groenlandicum, Chamaedaphne calyculata, Kalmia angustifolia, and Vaccinium myrtilloides [Moore et al., 2002]. The permanent area was equipped with 20 round PVC collars, 0.0556 m$^2$ with 18 L chamber volume, in hummocks and hollows. In this area we quantified ER, the heterotrophic respiration in the unsaturated zone by in situ incubation experiments, and the total respiration, encompassing the heterotrophic and autotrophic component, in the saturated zone. This was accomplished by obtaining pore water concentration profiles and subsequent pore water modeling of the profiles (see below).

[7] In the defoliated area, the leaves of shrubs were removed from six plots to determine the effects of vascular plants on C cycling, as described by Stewart [2006]. The plots contained 0.366 m$^2$ aluminum collars and three hollows were further equipped with pore water peepers and suction cups. Shrubs were defoliated within the collars and a 30 cm belt surrounding the collar, to reduce boundary effects from surrounding vegetation and pore water. The leaves were removed on a weekly basis, as some regrowth occurred. The shrub foliage was replaced with nylon “foliage”, maintaining a similar leaf area index, in an attempt to maintain natural ground shade and microclimate. The mosses were not treated. Six collars (3 hummocks and 3 hollows) were used as reference plots (“control”). Water table position and soil temperature profiles were continuously recorded in the vicinity [Lafleur et al., 2001] and in addition determined occasionally at the areas.

2.2. Respiration, CH$_4$, and DOC Production and Consumption

[8] Ecosystem respiration and CH$_4$ fluxes were quantified using chamber measurements. Heterotrophic respiration of the unsaturated zone was estimated using in situ incubations of peat bags in three depth layers (0–30 cm) and total (heterotrophic + autotrophic) respiration in the saturated zone by inverse pore water modeling of dissolved CO$_2$ concentration profiles. To separate the autotrophic and heterotrophic components, respiration rates were estimated at defoliated plots vs. control plots, not distinguishing between “true” autotrophic respiration and the contribution of root exudates to heterotrophic respiration. CH$_4$ production and consumption was not included in total respiration and estimated by inverse pore water modeling, as was production and consumption of DOC. A set of auxiliary data, such as pore water concentrations of short-chained organic acids, hydrogen and sulfate, was collected from the saturated zone and presented in the auxiliary material$.1$

2.2.1. Ecosystem Respiration

[9] To determine ER, CO$_2$ surface flux measurements were made at the plots on several occasions during day time beginning late April 2003. CO$_2$ surface flux measurements were made using a static closed system with a portable infrared gas analyzer EGM-1 or EGM-3 from PP-Systems connected to dark chambers placed inside the groove of collars, which were filled with water before each measurement to assure the seal was airtight. Air circulates from the chamber to the analyzer and CO$_2$ flux was determined using the rate of increase of CO$_2$ concentration in the chamber for a period of 3 to 5 minutes. CH$_4$ surface fluxes were determined using the static chamber approach, sampling headspace air 5 times over a period of 20 minutes and correcting for differences in air temperature. The samples were analyzed on a Shimadzu Mini 2 gas chromatograph with FID.

2.2.2. Heterotrophic Respiration in the Unsaturated Zone

[10] Heterotrophic CO$_2$ in situ production in the unsaturated zone was determined in peat from 3 depths (10, 20 and 30 cm) by placing about 5 g (d.w) of peat into a gauze bag, in triplicate. These bags remained at their original depth of

$^1$Auxiliary materials are available in the HTML. doi:10.1029/2005GB002659.
extraction under the moss cover in the peat, were repeatedly recovered and then placed in a 250 ml flask and incubated for a period of 2–3 days in situ in their original location. Temperatures and wet weights were recorded in the field. Additionally, in 2004 another set of samples was incubated at laboratory room temperature (22° ± 2°). Rates of CO₂ production were determined from the headspace volume corrected linear regression of 3 to 4 samples over time. Annual decomposition constants (kₐ) of the peat were calculated from averaged respiration rates and carbon contents of the peat [Scanlon and Moore, 2000].

2.3. Total Respiration, CH₄, and DOC Production and Consumption in the Saturated Zone

[11] From June 2003 to December 2004, pore water was sampled on 12 occasions using pore water peepers. The peepers were inserted in screened frames that were installed in the peat. This design allowed for the repeated, nondestructive sampling of an individual location and avoided confounding spatial and temporal variability at the site. Selectively screened PVC tubes and a multilevel piezometer were used down to a depth of 400 cm with sampling intervals of 10 cm (supplemental information). Upon retrieval of pore water peepers and samples from piezometers, subsamples were filled into GC vials for the determination of dissolved CO₂ and CH₄ as previously described [Blodau et al., 2004]. Subsamples were used for dissolved organic carbon (DOC) analyses. Other samples intended for ion and gas chromatography were frozen at −18°C and stored until analyzed.

[12] From the concentration profiles obtained we calculated stocks of CO₂, CH₄ and DOC down to a depth of 60 cm using porosity calculated from bulk density reported by Blodau and Moore [2002]. The model PROFILÉ [Berg et al., 1998] was used to estimate steady state production rate depth profiles of CO₂ and CH₄ below the water table and diffusive flux rates of CO₂ and CH₄ across the water table by inverse modeling of concentration profiles. In brief, the model is based on finding the simplest production rate depth profile that provides an explanation to an observed concentration profile of a dissolved species, using a numerical solution of the mass conservation equation (1):

$$\frac{d}{dx}(\phi \cdot D_i \cdot \frac{dC_i}{dx}) + R_i = 0$$

(1)

with $\phi$ : porosity; $D_{si}$: sediment diffusion coefficient for dissolved species i; corrected for temperature; $C_i$: concentration of dissolved species i; $R_i$: production rate of dissolved species i.

[13] Fluxes across the water table were calculated with Fick’s first law. Diffusion coefficients of CO₂ (1.93 × 10⁻⁵ cm⁻² s⁻¹) and CH₄ (1.73 × 10⁻⁵ cm⁻² s⁻¹) at 25°C were corrected for temperature, using linear interpolation, and for the effect of porosity $\phi$ by $D_i = D \cdot \phi^2$ [Lerman, 1979], using bulk density reported by Blodau and Moore [2002].

[14] Pore water movement in the shallow peat of the Mer Bleue bog is mostly horizontally oriented and vertical advection for this reason small [Fraser et al., 2001]. To examine the relative importance of vertical advection vs. diffusion for solute transport, we modeled porewater concentration profiles of chloride, determined on three occasions in the summer of 2004, using a simple hydraulic box model (auxiliary material, Figure S1). The model results suggested that vertical transport was dominated by diffusion and the pore water model thus applicable. It should be considered that under non–steady state conditions the pore water model results deviate from true production rates, as for example be seen from the occurrence of negative CO₂ production rates (see section 3). The magnitude of such artifacts, however, can be assessed by comparison to diffusive fluxes across the water table, when production is standardized to the peatland surface. Diffusive fluxes are independent of the assumptions for calculation of production rates and were mostly similar to them (see section 3). Incomplete anaerobic soil organic matter decomposition, i.e., accumulation of fermentation products, also contributes to CO₂ and CH₄ production [Blodau et al., 2002; Shannon and White, 1996]. Concentrations of acetate and other fermentation products remained <50 μmol L⁻¹ (auxiliary material, Figure S2). The determined CO₂ and CH₄ profiles thus reflect total respiration. Values of $k_a$ were calculated as described. Net DOC turnover was estimated from change in storage over time, as diffusion coefficients for the predominating humic moieties are only in the range of 10⁻¹⁰ to 10⁻¹⁰⁵ m² s⁻¹ [Cornell et al., 1986] and diffusive transport is thus negligible.

2.4. Analytical Procedures

[15] Dissolved CO₂ and CH₄ concentrations were determined on unfiltered samples on a Shimadzu Mini 2 gas chromatograph equipped with a methanizer and a flame ionization detector or on a HP6890 equipped with a TCD and FID. A headspace technique was used to measure dissolved CO₂ and CH₄ (0.5/1.8 mL volume, rubber stoppered GC vials). Losses of CO₂ and CH₄ from the vials were not detectable over the period of storage (~2 days). The original dissolved concentration was reconstructed using the headspace concentrations, the volumes of headspace and water phase and Henry’s law [$K_{H} = 3.89 \times 10^{-2}$ (mol L⁻¹ atm⁻¹) for CO₂ and $K_{H} = 1.3 \times 10^{-3}$ (mol L⁻¹ atm⁻¹) for CH₄]. DOC was determined after filtration of extracted pore water with a syringe microfilter (0.2 μm, nylon) or on samples directly obtained with pore water peepers on a Shimadzu 5050 TOC analyzer. Concentrations of sulfate, fermentation products, and H₂ were determined as auxiliary parameters (auxiliary material).

3. Results

3.1. Water Tables, Temperatures, ER, and CH₄ Fluxes

[16] The seasonal pattern of soil temperatures was similar in both years, with slightly cooler conditions in 2004 (Figure 1a). Temperatures in the hollows (10 cm depth) were about 0°C until the end of April and peaked at 14°–15°C in July and August. In hummocks, temperature at 10 cm depth was slightly below 0°C from early January to mid-April and reached up to 21°C in summer (not shown). The water table remained high until the end of July in 2003, after...
Figure 1. (a) Summary of soil temperatures at 10 cm depth (hollow), (b) water table levels below an arbitrary datum, and (c) CO\textsubscript{2} and (d) CH\textsubscript{4} fluxes, as determined by static chamber measurements at the “permanent” area. Fluxes were averaged for sampling date and all collars at the permanent area. Error bars indicate standard deviation (n = 20).

Figure 2. CO\textsubscript{2} production of peat bags in situ at the permanent area in (a) 2003 and (b) 2004 at depths of 10, 20, and 30 cm, and at constant temperature in the laboratory (22 ± 2°C). Figure 2c shows the temperature dependency of rates as obtained in situ. Temperatures were recorded during the incubations. Error bars indicate standard deviation (n = 3).
which it temporarily fell by 25 cm (Figure 1b). This water table drawdown was weak in 2004 and ended by a rain storm raising the water table by 15 cm in mid-September.

Average daily surface CO$_2$ fluxes (ER) ranged from 40 to 90 mmol m$^{-2}$ d$^{-1}$ in early May and October 2003 to 250 to 350 mmol m$^{-2}$ d$^{-1}$ in mid summer and strongly varied among the collars (Figure 1c). The seasonal average flux was 205 mmol m$^{-2}$ d$^{-1}$. Average daily CO$_2$ fluxes were well explained by differences in temperatures in the shallow peat, particularly in hummocks (Flux (CO$_2$) = 19.89 $\times$ T - 124.9; $R^2$ = 0.81; units in mmol m$^{-2}$ d$^{-1}$ and $^\circ$C, T at depth 10 cm). In 2003, surface CH$_4$ fluxes were on average $<$0.01 mmol m$^{-2}$ d$^{-1}$ and in 2004 fluxes reached on average 0.78 mmol m$^{-2}$ d$^{-1}$, with the only larger flux (2.7 mmol m$^{-2}$ d$^{-1}$) recorded on 16 September (Julian day 259), shortly after a major rainfall (Figure 1). Methane emissions were not significantly correlated with water table position and temperature.

3.2. Heterotrophic Respiration in the Unsaturated Zone

Temperatures in the in situ incubation ranged from 1$^\circ$ to 18$^\circ$C and water contents from 40% to 100% of saturation. CO$_2$ production rates ranged from 0.3 $\mu$mol g$^{-1}$ d$^{-1}$ at a depth of 30 cm in December 2004 to 13.8 $\mu$mol g$^{-1}$ d$^{-1}$ at a depth of 10 cm in August 2004 and generally decreased.

Figure 3. Dissolved CO$_2$ concentrations (open symbols), fitted concentration profiles, and associated production rate profiles at the permanent area. Rates were determined by inverse modeling using PROFILE. The approximate water table at the time of sampling is shown by the dashed line. Negative rates likely reflect non-steady state conditions of profiles, i.e., disequilibrium between production and resulting concentration profile, for example due to changes in the water table.
with depth (Figure 2). Values of $k_2$ decreased with depth from 0.060 yr$^{-1}$ (10 cm) over 0.050 yr$^{-1}$ to 0.034 yr$^{-1}$ (30 cm). Part of this pattern was apparently caused by decreasing temperatures with depth, because at constant incubation temperatures of 22°C more CO$_2$ was produced at 20 cm than at 10 cm (Figure 2). Production rates were exponentially related to temperature ($R^2 = 0.52$ (30 cm), 0.69 (20 cm), 0.86 (10 cm); $P < 0.05$). Q$_{10}$ values were 6.4 (10 cm), 5.1 (20 cm) and 5.0 (30 cm). Using multiple regression with log-transformed rate data, water saturation explained a significant fraction of the variance in the data in the uppermost layer only, where less CO$_2$ was produced during saturation. The seasonal pattern with peak rates in midsummer was, therefore, mainly caused by seasonal differences in temperature (Figure 2). Part of the pattern was due to a factor that covaried with temperature. In June and August, higher rates than at other times were also determined in samples that were incubated at constant temperature at the sampling dates throughout the year.

### 3.3. Total Respiration, CH$_4$, and DOC in the Saturated Zone

#### 3.3.1. Carbon Dioxide

[19] Concentrations increased below the water table and reached maximum concentrations between 1 and 2.5 mmol L$^{-1}$ in the pore water peepers (Figure 3). Concentrations continued to increase down to a depth of 1 m and decreased below that depth in the piezometers (auxiliary material, Figure S3). Diffusive CO$_2$ fluxes across the water table, calculated with PROFILE, amounted to $\leq 1.6$ and $\leq 2.4$ mmol m$^{-2}$ d$^{-1}$ in 2003 and 2004, respectively, with maximum fluxes in July. On the basis of a comparison between diffusive fluxes across the water table and chamber fluxes in 2003 (Table 1), the saturated zone thus contributed less than 1 % to ER. Production rates mostly peaked close to the water table at rates of 15 to 25 mmol cm$^{-3}$ d$^{-1}$ in summer. In spring and winter, rates were $< 10$ mmol cm$^{-3}$ d$^{-1}$ and ranged mostly between 5 and 10 mmol cm$^{-3}$ d$^{-1}$ at depths of 40–60 cm. The maximum of production shifted downward from summer to winter. Depth-integrated rates ranged from 0.01 and 0.03 mmol m$^{-2}$ d$^{-1}$ in May and December 2004, to 2.7 mmol m$^{-2}$ d$^{-1}$ in July 2004 (Table 1), not considering changes in storage. Excluding profiles with apparent negative CO$_2$ production, and not correcting for autotrophic respiration (see below), $k_4$ was on average 0.0020 yr$^{-1}$ from 20 to 30 cm and 0.0012 yr$^{-1}$ from 30 to 60 cm. At the interface between saturated and unsaturated zone, around 25 cm depth, $k_4$ was lower by a factor 17 compared to the in situ incubations.

[20] During summer, production rates and diffusive fluxes across the water table were in close agreement (Table 1), whereas winter fluxes were mostly higher, indicating transport from lower depths (Table 1). Depth-integrated production rates of 3 additional peepers employed in July 2004 were $2.1 \pm 0.7$ mmol m$^{-2}$ d$^{-1}$ suggesting that the permanent peeper was reasonably representative for the area.

[21] Depth-integrated rates were linearly related to temperatures at 30 cm (Production (CO$_2$) = $0.20 \times T - 0.67$; $R^2 = 0.61$; units in mmol m$^{-2}$ d$^{-1}$ and °C), resulting in a Q$_{10}$ value of 2.5 between 10° and 20°C. Changes in storage...
in June–July 2003 and June–August 2004, when the water table was sufficiently constant, amounted to a depth-integrated production of 0.4 mmol m$^{-2}$ d$^{-1}$ and from 2.7 to 4.3 mmol m$^{-2}$ d$^{-1}$, respectively. Taking these figures into account, the depth-integrated in situ production probably was on the order of 2 mmol m$^{-2}$ d$^{-1}$ in early summer of 2003, and increased from 3 to 7 mmol m$^{-2}$ d$^{-1}$ from June to August 2004.

### 3.3.2. Methane

Concentrations in the upper 60 cm of the site remained <0.2 mmol L$^{-1}$ until December, 2003 and reached between 0.4 and 0.6 mmol L$^{-1}$ thereafter (Figure 4). Concentrations increased up to 0.85 mmol L$^{-1}$ at a depth of 1 m and up to 1.5 mmol L$^{-1}$ at a depth of 4 m (auxiliary material, Figure S3). In 2003, diffusive fluxes from the unsaturated zone reached maxima of 0.06 and 0.11 mmol m$^{-2}$ d$^{-1}$ in July and October 2003, respectively. In 2004, when surface CH$_4$ fluxes reached on average 0.78 mmol m$^{-2}$ d$^{-1}$, the average diffusive CH$_4$ flux at the water table only amounted to 0.046 mmol m$^{-2}$ d$^{-1}$ and peaked at 0.27 mmol m$^{-2}$ d$^{-1}$. The majority of CH$_4$ emitted in 2004 was thus not transported by molecular diffusion. In 2003, CH$_4$ was only produced at depths of 40 to 60 cm at rates of <2 nmol cm$^{-3}$ d$^{-1}$. May 2004 was characterized by the absence of CH$_4$ production in the shallow peat and through-transport and oxidation of CH$_4$ from greater depths. Subsequently, CH$_4$ was produced at rates of 2 to 5 nmol cm$^{-3}$ d$^{-1}$ in horizons located below the zone of CH$_4$ oxidation. This zone notably moved closer to the water table in summer 2004 and dropped back down to depths of 20 to 35 cm below the water table in December of 2004.

### 3.3.3. Dissolved Organic Carbon

Concentrations ranged from <10 to 120 mg L$^{-1}$ with little effect of water table position (Figure 5). In 2003, concentrations increased in summer and autumn to levels of up to 100 mg L$^{-1}$. A concentration peak developed at...
depths of 20 to 40 cm, but disappeared in winter and DOC concentrations decreased to minima of about 30 mg L\(^{-1}\) in May 2004. In 2004, less of a pattern became visible and concentrations only increased from September to December. Net rates of DOC production or removal were mostly within ±100 nmol cm\(^{-3}\) d\(^{-1}\), much larger than and unrelated to CO\(_2\) production rates (Table 1). CO\(_2\) production thus potentially accounted only for a small fraction of DOC losses between sampling dates.

Little DOC was present in the form of acetate or other short-chain fatty acids (auxiliary material, Figure S2). Acetate concentrations were fairly uniform with depth, ranging from 10 to 50 µmol L\(^{-1}\), with the lowest levels in August 2004.

3.4. Respiration, CH\(_4\), and DOC in the Saturated Zone After Defoliation

Average concentrations of dissolved CO\(_2\) and CH\(_4\) were smaller in the defoliated than control plots (Figure 6). In July 2004 the concentration differences were 400 µmol L\(^{-1}\) (dissolved CO\(_2\)) and 50 to 70 µmol L\(^{-1}\) (CH\(_4\)) at a depth of 20 cm below the water table. DOC concentrations in defoliated plots were larger by 20–40 mg L\(^{-1}\) at depths of 0 to 10 cm below the water table and acetate concentrations higher by an average of 25 µmol L\(^{-1}\) throughout, compared to the control plots (auxiliary material, Figure S5). The variation within the two treatments was large, so these differences may be due to natural var-
iability. Depth-integrated production rates of dissolved CO$_2$ decreased by 28 \%, from 1.34 mmol m$^{-2}$ d$^{-1}$ (control) to 0.97 mmol m$^{-2}$ d$^{-1}$ (defoliated). Production of CH$_4$, which was only produced deeper into the peat, was not visibly affected (0.25 mmol m$^{-2}$ d$^{-1}$, control, and 0.22 mmol m$^{-2}$ d$^{-1}$, defoliated) (Figure 6). A rainstorm raised the water table by about 15 cm, 3 to 7 days before sampling of individual pore water peepers (Figure 6, September). Total respiration rate in the newly saturated depth increment was about 131 mmol m$^{-2}$ d$^{-1}$ (control) and 74 mmol m$^{-2}$ d$^{-1}$ (defoliated) assuming that dissolved CO$_2$ concentrations were negligible before saturation. The difference in total respiration rates in peats of control and defoliated plots was confirmed.

4. Discussion

4.1. Components of Ecosystem Respiration

Rates of ER and heterotrophic respiration in the saturated zone were in agreement with earlier eddy covariance tower measurements, suggesting that the chamber and peat bag incubation measurements were sufficiently accurate, and that the selected plots was adequately representative for the Mer Bleue bog. Yearly ER has been estimated at 105 mmol m$^{-2}$ d$^{-1}$ of C with heterotrophic respiration accounting for 44–66 mmol m$^{-2}$ d$^{-1}$ [Frolking et al., 2002; Lafleur et al., 2001, 2003; Moore et al., 2002]. Similar rates were also found in other peatlands [Lafleur et al., 2001]. We determined an average heterotrophic respiration of 54 mmol m$^{-2}$ d$^{-1}$ in the unsaturated zone and an ER of 40–350 mmol m$^{-2}$ d$^{-1}$ from the flux measurements in summer 2003 (Table 1). Previously determined rates of heterotrophic respiration in intact soil segments [Scanlon and Moore, 2000] also lay within the range of 0.3 to 13.8 \textmu mol C g$^{-1}$ d$^{-1}$ obtained in this study in situ. Such rates are at the lower end of rates (2–110 \textmu mol g$^{-1}$ d$^{-1}$) reported from aerobic incubation studies with intact cores and slurries of similar peats [e.g., Bergman et al., 1999; Bridgham et al., 1998; Moore and Dalva, 1997].
This study demonstrates that only a very small fraction of ER stemmed from the saturated zone of this relatively dry peatland (Table 1). During the summer, or warm temperatures, O2 was consumed within 1 to 3 cm below the water table and rapidly depleted following water saturation [Blodau et al., 2004; Blodau and Moore, 2003]. Anaerobic total respiration, as determined from the pore water profiles, thus contributed on average less than 1% to ER (Table 1). Even in the wet summer of 2004, accounting for changes in dissolved CO2 storage, and with temperatures at the high water table being about 15°C, total respiration in the saturated zone remained at or below 7 mmol C m⁻² d⁻¹. It thus contributed less than 5% to ER, which was recorded at 154 to 310 mmol m⁻² d⁻¹ in the summer months of 2003 (Table 1). Froliking et al. [2002] used the PCARS model to estimate that depths below 50 cm contributed 10 to 20 mmol C m⁻² d⁻¹ and depths between 10 and 50 cm contributed 10 to 60 mmol m⁻² d⁻¹ to ER at the Mer Bleue bog. Our data suggest that these model estimates are probably high for depth increments that are water saturated. Our observed CO2 concentration profiles are fairly typical for peatlands, albeit somewhat at the lower end [Hornibrook et al., 1997; Nilsson and Bohlin, 1993]. Total respiration in the saturated zone of peat bogs should thus be negligible compared to that of the unsaturated zone.

Autotrophic respiration in the saturated zone decreased by defoliation by an estimated 28% [Figure 6] suggesting that root activity contributed to respiration in the saturated zone. This respiration related to root activity (0.37 mmol m⁻² d⁻¹) was only very small compared to the total root related respiration. The latter has been quantified at 162–176 mmol m⁻² d⁻¹ by comparing C emission from control to defoliated plots and recording a difference in emission of 50 to 60% [Stewart, 2006]. Mapping of root biomass in hollows showed that below a depth of 40 cm shrub roots were absent. The depth increments of 10 to 20 cm and 20 to 30 cm contained about 400 g m⁻² each, and the increment of 30 to 40 cm about 150 g m⁻² of root biomass, of which 15–25% consisted of fine roots [Moore et al., 2002]. A considerable fraction of the shrub root biomass was thus located below the water table (20–25 cm) in the wet July of 2004. Since its contribution to total root related respiration was negligible, the saturated conditions apparently inhibited respiratory activity of the submersed roots.

The reduction of heterotrophic and autotrophic respiration by anoxia, and the low k₅ values of 0.002 yr⁻¹ to 0.0012 yr⁻¹ calculated for the saturated zone, emphasize the potential impact of the water table on these processes. However, ER and water table position did not correlate, and did not either in experiments with intact ombrotrophic bog mesocosms [Updegraff et al., 2001], and in a multiyear study of ER at the Mer Bleue bog [Lafleur et al., 2005]. We believe that the lack of correlation is caused by the small contribution of the deeper peat to ER, which is diminished by increasing recalcitrance of the peat, and decreasing soil temperature and availability of oxygen with depth [Lafleur et al., 2005; M. Heitmann and C. Blodau, unpublished data, 2004]. The bog vegetation may also have some capability to relocate activity to the unsaturated zone when only part of the rooted zone is inundated and maintain respiration. Stronger effects of water table level fluctuations on ER should thus be restricted to wetter peatlands. Instructive in this respect are results from earlier experiments with intact Mer Bleue peat soil columns at constant temperature (10°C), and with the water table being either near the moss surface or 35 cm below [Blodau et al., 2004]. Lowering the water table raised “ER” in these phytotron experiments from 47 to 77 mmol m⁻² d⁻¹.

In this dry ombrotrophic bog, soil temperature was thus the more important control on heterotrophic respiration and also ER, as reported by Lafleur et al. [2005]. Under peat temperature ranges, heterotrophic respiration generally increases by a factor of 2–3 for every 10°C temperature increase (Q₁₀) [McKenzie et al., 1998; Moore and Dalva, 1993; Yavitt et al., 1997]. This was also reported for the Mer Bleue bog [Lafleur et al., 2001; Scanlon and Moore, 2000]. Higher Q₁₀ values were mainly derived from field studies that related CO2 fluxes and soil temperatures in shallow peats [Bridgham et al., 1995; Bubier et al., 1998; Silvola et al., 1996], and may reflect the influence of roots and root exudates. In forest soils, Q₁₀ values of 4.6, compared to 3.5 for bulk soil, and 2.5 in root-free soil, have been determined [Boone et al., 1998]. Part of the observed Q₁₀ value of 5–6 for heterotrophic respiration in the unsaturated zone was apparently caused by a factor that covaried with the temperature. When peat was additionally incubated at constant temperature, higher rates were measured in midsummer than at other times (Figure 2). DOC reaching the peat bags with seepage water may have contributed to this effect.

4.2. DOC

DOC was the most important fraction of dissolved C and was net released and consumed at much larger rates than either CO₂ or CH₄ in the peat (Table 1). On the basis of measurements in summer or the ice-free season, peatlands have been estimated to export DOC in the range of 1 to 10 mmol m⁻² d⁻¹ to discharging streams [Koprivnjak and Moore, 1992; Moore, 1987, 1988; Urban et al., 1989; McKnight et al., 1985]. For the Mer Bleue peatland, a value of 2.6 mmol m⁻² d⁻¹ was previously determined from discharge data [Fraser et al., 2001] and has recently been updated to a 6-year average of 3.7 mmol m⁻² d⁻¹ (N. T. Roulet, unpublished data, 2005). Such rates are much smaller than the minimum release and immobilization rates obtained in this study. In earlier mesocosm experiments with intact peat soils from the Mer Bleue bog, net DOC production rates were 14–15 mmol m⁻² d⁻¹, independent of water table levels [Blodau et al., 2004]. In incubations with peats from different depths and temperatures of 22°C, 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. Assuming a bulk density of 0.05 to 0.1 g cm⁻³, these rates were about 1–4 times the maximum release determined in this study. From this collation it may be inferred that internal seasonal production and consumption strongly exceeds net export from peatlands, and that maximum rates of release during short-term incubation of peat are probably seldom reached in situ.
[32] Soil temperature and runoff may control DOC dynamics [Moore and Dalva, 2001]. During summer, increases in DOC concentrations were observed at the Mer Bleue bog in the hydrologically average year of 2003, as previously at other peatlands [Dalva and Moore, 1991; Waddington and Roulet, 1997]. In the wet summer of 2004 we could not observe this pattern and concentrations decreased over time, possibly because of dilution from precipitation.

4.3. Methane
[33] Methane production and diffusive fluxes remained small at the Mer Bleue bog and the gross CH₄ production amounted to only 17% of below water table CO₂ production, when averaged over the sampling period, and to less than 10% in summer. Accordingly, heterotrophic respiration mostly proceeded by utilization of electron acceptors such as sulfate, which can support respiration rates of 1 to 40 mmol m⁻² d⁻¹ in bogs [Nedwell and Watson, 1995; Vile et al., 2003; Wieder et al., 1990]. Decreasing sulfate concentrations coincided with increasing CH₄ concentrations over the sampling period (auxiliary material, Figure S4) but these changes did not affect CH₄ production rates, which remained low. Thus we could not identify an effect of sulfate availability on methanogenic activity.

[34] Particularly in winter, when oxygen penetrated deeper into the peat (C. Blodau, unpublished data, 2001), CH₄ was oxidized below the water table (Figure 4), in agreement with the methanotrophic activity reported from the saturated zone of peatlands [Kettunen et al., 1999]. Production and emission of CH₄ were very low in 2003 and only began increasing in 2004, reaching 0.4–2.7 mmol m⁻² d⁻¹. The chamber fluxes then exceeded diffusive fluxes across the water table and also the gross production of CH₄ in the near-surface peat (Table 1). Emission was at this point probably driven by ebullition, which may occur at partial pressures above 0.21 atm, or 358–389 μmol L⁻¹ at 8° to 12°C, depending on the partial pressure of N₂, which is stripped from the peat pore waters with continuing CH₄ production [Fechner-Levy and Hemond, 1996].

[35] The difference in CH₄ emission rates between 2003 and 2004 may be attributed to the threshold of CH₄ concentrations allowing for ebullition, which drew nearer to the peatland surface in 2004 (Figure 4). The high water table may have also shortened the residence time of CH₄ in the unsaturated zone. In September 2004, emission rates peaked at 2.7 mmol m⁻² d⁻¹ after the water table rose by about 15 cm five days before the flux measurement. Since CH₄ was not produced in the added water column within the first week (Figure 4), the increase in CH₄ flux can only be explained if a larger fraction of the CH₄ escaped oxidation. A similar effect was previously reported by Kettunen et al. [1996], who observed emissions to increase for short periods after rainfall and associated rises in water tables in a boreal pine sedge fen. Such an effect would be opposed to decreases in ebullition with rising water table and hydrostatic pressure in floating mats [Fechner-Levy and Hemond, 1996]. As 3 cm of water column equals a change in atmospheric pressure of about 1 hPa, low atmospheric pressure owing to the storm event in September 2004 might have offset the effect of the rising water table and triggered additional ebullition.

5. Conclusions
[36] At the Mer Bleue bog, the contribution of the saturated zone to ER was negligibly small, and the contribution of CH₄ production was even lower by an order of magnitude. C turnover in the saturated zone was dominated by DOC release and consumption unrelated to respiration, which likely is the more relevant process with respect to the C budget. As much of the ER stemmed from the shallow, never saturated peat, the water table position had little or no influence on ER, which was essentially controlled by soil temperature. In dry ombrotrophic bogs, moderate increases in temperature in summer would likely increase ER more strongly than moderate rises in water table position decrease it. Large relative changes in C turnover rates in the saturated zone of a dry ombrotrophic bog will also be of little consequence for its overall C budget. Effects of water table changes on the belowground C turnover and fluxes can be expected to be greater in wetter peatlands, where the change from oxic to anoxic conditions affects peat layers that are warmer, better aerated, and contain most of the fine root biomass. Our results further suggest that water table rises will increase CH₄ emissions more strongly than expected from diffusive fluxes across the water table, by bringing the zone of high CH₄ concentrations closer to the peatland surface, which may facilitate ebullition. Concurrent, moderate increases in temperature and soil moisture are thus likely to increase losses of CO₂ from ER and of CH₄ from this type of peatland.

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