Ecosystem Respiration in a Cool Temperate Bog Depends on Peat Temperature But Not Water Table

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ABSTRACT

Ecosystem respiration (ER) is an important but poorly understood part of the carbon (C) budget of peatlands and is controlled primarily by the thermal and hydrologic regimes. To establish the relative importance of these two controls for a large ombrotrophic bog near Ottawa, Canada, we analyzed ER from measurements of nighttime net ecosystem exchange of carbon dioxide (CO_2) determined by eddy covariance technique. Measurements were made from May to October over five years, 1998 to 2002. Ecosystem respiration ranged from less than 1 µmol CO_2 m^{-2} s^{-1} in spring (May) and fall (late October) to 2–4 µmol CO_2 m^{-2} s^{-1} during mid-summer (July-August). As anticipated, there was a strong relationship between ER and peat temperatures (r^2 = 0.62). Q_{10} between 5° to 15°C varied from 2.2 to 4.2 depending upon the choice of depth where temperature was measured and location within a hummock or hollow. There was only a weak relationship between ER and water-table depth (r^2 = 0.11). A laboratory incubation of peat cores at different moisture contents showed that CO_2 production was reduced by drying in the surface samples, but there was little decrease in production due to drying from below a depth of 30 cm. We postulate that the weak correlation between ER and water table position in this peatland is primarily a function of the bog being relatively dry, with water table varying between 30 and 75 cm below the hummock tops. The dryness gives rise to a complex ER response to water table involving i) compensations between production of CO_2 in the upper and lower peat profile as the water table falls and ii) the importance of autotrophic respiration, which is relatively independent of water-table position.

Key words: ecosystem respiration; carbon dioxide; peatland; bog; eddy covariance; soil climate.

INTRODUCTION

Northern peatlands occupy about 3.5 million km^2 and contain up to one-third of the world's soil carbon (C) pool (Gorham 1991). These peatlands have accumulated C through an imbalance between plant uptake of atmospheric CO_2 by photosynthesis and the release of CO_2 to the atmosphere through plant respiration and the decomposition of organic matter. The C budget of these systems under a changing climate will depend on the relative response of plant productivity and the rate at which organic matter decomposes, with thermal and hydrologic regimes being of critical importance.

Ecosystem respiration (ER) is the emission of carbon dioxide to the atmosphere from vegetation (autotrophic) and soil (heterotrophic) activities. Compared to photosynthetic uptake, ER is a poorly

understood and modeled part of the ecosystem C budget (Giardina and Ryan 2000; Grace and Rayment 2000; Melillo and others 2002). Although thermal and hydrologic regimes should play a role in determining ER in all ecosystems (Reichstein and others 2003), there are conflicting conclusions about the relative importance of these two environmental controls in peatlands. Although most studies find temperature to be an important control on peatland ER, the influence of soil moisture or water-table depth (WTD) on ER is less clear. Periodic chamber-based measurements of small areas have shown that both peat temperature and WTD are important controls on ER, with their relative importance being dependent on the vegetation, mircrotopography and temperature range. Bridgham and Richardson (1992) made monthly measurements of soil CO_2 emission in three southern peatlands with clipped vegetation in the chambers and showed that temperature was more important than WTD, although the latter was significantly correlated to soil CO_2 emission. In Finland, Silvola and others (1996a) determined soil CO_2 emission from 26 sites and noted that temperature played an important role in controlling emission rates at many sites. They also found that when standardized for temperature, a fall in water-table position resulted in an increase in emission, but that the relative increase was reduced when the water table fell below 30 cm. For a number of boreal peatland types Bubier and others (1998) concluded that trophic status, above ground net primary productivity, and soil temperature were more important than water table in determining ER. Although water table was of minor importance in predicting daily ER, it became more important in predicting seasonal average ER at these sites. In an experimental manipulation of peat temperature and WTD in a bog and a fen, Updegraff and others (2001) showed that ER responded to temperature increases but not to a variation in water-table position of 20 cm. At six sites in the Mer Bleue bog over two summers, Bubier and others (2003a) found that WTD was strongly appelated with ER during a dry summer, but that temperature was more important during a wet summer.

Laboratory incubations are more consistent in their findings than field experiments. In such studies, peat samples or mesocosms of reconstituted peat are subjected to controlled and manipulated temperature and moisture, and the rates of CO_2 production are monitored. Moisture is normally treated in terms of flooded and drained (water table held at depth below the surface) conditions. There is general agreement that CO_2 emissions increase with increasing temperature and are higher under drained than flooded conditions (for example, see Bridgham and Richardson 1992; Moore and Dalva 1993; Funk and others 1994; Moore and Dalva 1997; Scanlon and Moore 2000; Waddington and others 2001).

Chamber and laboratory studies are limited because of infrequent measurements over short sampling periods and small areas, disturbance of the ecosystem, and in many cases only soil CO_2 emissions are measured and not ER. Eddy covariance measurements from towers provide an alternative, allowing an assessment of CO_2 flux under undisturbed conditions with intact vegetation and at larger spatial scales – that is, footprints of several hundreds to thousands of square meters. Despite some issues surrounding sampling under stable atmospheric conditions, carefully analyzed nighttime eddy covariance measurements can be used to estimate ER (for example, see Hollinger and others 1994; Law and others 1999; Valentini and others 2000). Eddy covariance measurements, when collected over a long period, can capture fluxes from a large combination of environmental controls and antecedent conditions and at a larger spatial scale that are difficult if not impossible to obtain in manipulation or chamber-based studies. Very few peatland studies employing the eddy covariance technique have analyzed ER measurements (see Discussion).

In this paper, we investigate ER during the growing season (May through October) at a large ombrotrophic bog as determined by nighttime net ecosystem CO_2 exchange measurements from an eddy covariance tower. Data from five years were available, providing a wide range of environmental conditions and antecedent controls influencing ER. Specifically, we examine relationships between ER and the peat thermal regime and water-table position. These results, combined with laboratory incubation of intact peat samples from the bog under varying moisture content, show that the lowering of the water table accompanied by a drying of the surface layers results in the conclusion that ER is independent of water-table position in this relatively dry bog.

Methods

Site

The measurements were made at Mer Bleue, a large (2800 ha), low-shrub ombrotrophic bog located just east of Ottawa, Ontario, Canada (45.40°N lat., 75.50°W long.). The climate of this area is cool

continental, with a mean annual temperature of 5.8°C and mean annual precipitation of 910 mm. Average May to October temperature and precipitation are 15.5°C and 491 mm respectively. The dominant vegetation types are evergreen shrubs (*Chamaedaphne calyculata, Ledum groenlandicum, Kalmia angustifolium*), a deciduous shrub (*Vaccinium myrtilloides*) and a continuous ground cover of *Sphagnum* mosses (*S. capillifolium, S. fuscum, S. magellanicum*). In 1998, total aboveground and belowground biomass averaged 356 ± 100 and 1820 ± 660 g m^{-2} for vascular species and 144 ± 30 g m^{-2} for the *Sphagnum* capitula (Moore and others 2002). See Moore and others (2002) and Bubier and others (2003a) for further details on ecological characteristics of the site. The peat thickness exceeds 5 m in the central portion of the bog. The surface has a typical hummock-hollow micro-topography.

Ecosystem Respiration Measurements

The overall CO_2 exchange and eddy covariance measurements employed at Mer Bleue have been discussed in detail by Lafleur and others (2001, 2003) and modeled by Frolking and others (2002). Here we give a brief description of the instruments and data processing used in support of the current analysis. A 3-dimensional sonic anemometer (R2 Solent, Gill Instruments, UK) and closed-path infrared gas analyzer (IRGA, LI-6262, Li-COR, NE, USA) were used to measure rapid (10 Hz) fluctuations in vertical wind speed and CO_2 concentration. Eddy fluxes of CO_2 were computed from 30-min covariances of these quantities after accounting for the travel time for the sample air between the intake (located near the anemometer) and the IRGA located in a heated shed at the base of the instrument tower. Air was drawn down the sampling tube and through the IRGA at a rate of 6.5–8.5 L min^{-1}. The sonic anemometer and intake for CO_2 sampling were mounted at 3.2 m above the bog surface. Post processing of the eddy flux data included corrections for changes in air density due to water vapour fluctuations.

Continuous measurements of several environmental variables were also conducted during the study. Incident photosynthetically active radiation (PAR) was measured with a quantum sensor (model QZ190, LI-COR, NE, USA). Air temperature and humidity were measured at 2.0 m with a probe (model HMP35C, Campbell Scientific, UT, USA). Wind speed at 2.0 m was measured with a cup anemometer (model 20120, R.M. Young, MI,

USA). Two arrays of copper-constantan thermocouples were installed to measure soil temperatures at depths of 1, 5, 10, 20, 40, 60, 80, 150, and 250 cm. One array was placed in a hummock and one in a hollow. Precipitation was measured on site with a tipping bucket gauge (model 525 m, Campbell Scientific) during the snow-free period only. Winter precipitation was obtained from a near-by weather station. Water level was measured in two wells, one in a hollow and one in a hummock, with a float and counterweight attached to a potentiometer. In addition, frequent manual measurements were made on both wells. All water level measurements were referenced to the mean height of the hummock surfaces. We also measured soil moisture content with a profile of TDR probes (model CS615, Campbell Sci.). We could not establish a satisfactory calibration for peat soil, but the TDR probes do give an indication of the relative magnitude of changes in soil moisture for a given change in water table at a specific depth. Signals from all of the sensors were monitored on a CR7X and a CR10X data logger every 5 s and averaged every 30 min.

Long-term records of precipitation and air temperature are not available for the Mer Bleue site. To determine the variance of the five years of Mer Bleue data against a longer term record we used precipitation and air temperature recorded at the Ottawa International Airport, 10 km southwest of Mer Bleue.

Flux Data Handling

Flux data were subjected to a series of screening procedures. In the first pass, we discarded data during periods of instrument malfunction (such as during heavy rain) or out of range values. The second screening related to problems arising from eddy covariance theory. Nighttime eddy covariance data continue to be the subject of considerable debate (Aubinet and others 2000; Baldocchi and others 2001). Low wind speeds, thermal stratification of the atmosphere, and incomplete mixing that often occur at night can generally result in inaccurate flux measurements. A common practice used to filter 'bad' data is to plot flux data against friction velocity ($u*$) and then assess a $u*$ cut-off limit below which data are rejected (Goulden and others 1996, 1997). In an earlier paper we examined this problem for the Mer Bleue flux system and determined that the critical value $u*$ was 0.1 m s^{-1} (Lafleur and others 2001). Thus, all CO_2 fluxes were discarded when $u*$ was less than 0.1 m s^{-1}. Data loss from all sources accounted for between

Table 1. Growing Season (May through October) Mean Daily Air Temperature and Total Precipitation for the Study Period compared to Long-term (1961–1990) Averages

	1998	1999	2000	2001	2002	30-y Average
Temperature (°C)	17.2	15.2	15.2	17.3	16.1	15.5
Precipitation (mm)	431	507	508	461	556	491
Water table (cm)	−48.3	−47.4	−34.8	−46.3	−48.8	n/a

Data are from the Meteorological Services of Canada weather observing station at the Ottawa International Airport, 10 km southwest of Mer Bleue. Mean water table data are from the field site and are relative to the mean hummock surface.

33% and 44% of all possible values (on an annual basis).

ER was determined from nighttime flux data obtained during May to October for the years from 1998 to 2002, inclusive. Nighttime was defined as the period when incident PAR = 0 μmol m^{-2} s^{-1}. Each night was defined as the dark period centered on 2400 h EST. For all nights with at least six good 30-min flux measurements mean ER was computed as the average of all available measurements. Nighttime mean soil and air temperatures and water-table depths were also computed.

Laboratory Peat Respiration Measurements

The influence of moisture content on CO_2 production from peat samples was examined by incubating (at 20°C) replicate, small (5 cm height, 5 cm diameter), intact cores of peat collected from depths of 0–5, 10–15, 20–25, 30–35 and 40–45 cm from a hummock at Mer Bleue. The cores were allowed to dry over 10 days, rewetted to field capacity over 1 h and the drying was repeated for 3 drying cycles over 30 days. Drying occurred from the top and sides of the cores to reduce heterogeneity of water content within the core. CO_2 production was determined from changes in the headspace concentration over a 1 h period, by sampling every 15 min. CO_2 concentrations were analyzed using a Shimadzu Mini II gas chromatograph equipped with a methanizer. Volumetric moisture content of the cores was determined by changes in mass of the core and its saturated volume.

RESULTS

Growing season (May to October) air temperatures were warmer than the long-term average by 1.3 to 1.8°C in 1998, 2001 and 2002. Air temperatures were near average in 1999 and 2000 (Table 1). Growing season precipitation totals were highly variable, ranging from 60 mm below

average in 1998 to 65 mm above average in 2002. Mean growing season water table was near −48 cm in all years, except 2000 when it was −34.8 cm (Table 1).

ER followed a roughly symmetrical trend around a broad mid-summer peak in each year, although with high day-to-day variability (Figure 1a). Values ranged from less than 1.0 μmol CO_2 m^{-2} s^{-1} in the spring (early-May) and autumn (late-October) to 2.0 to 4.5 μmol CO_2 m^{-2} s^{-1} in mid-summer (July). The 5 cm hummock soil temperatures followed a similar temporal trend as ER, ranging from 0 to 10°C in the spring, to peak values of 12 to 17°C in July and falling to 3 to 7°C in October (Figure 1b). The same pattern of soil temperatures occurred at depths of −10 and −20 cm but the seasonal amplitude was reduced. Water table was variable in all years (Figure 1c). Based on previous studies the seasonal pattern in water table is driven by the distribution of precipitation relative to the loss of water by evapotranspiration (Fraser and other 2001). In general, water tables were highest in spring and autumn with periods of drawdown occurring in summer. The year with the shallowest (least negative) WTD and the smallest daily variation was 2000, as a result of consistent rainfall in all months. Reduced July/August precipitation in both 2001 and 2002 (40% and 51% below the long-term average) caused prolonged water table drawdowns to develop by mid-summer, lasting approximately 40 and 65 days respectively. The early summer decline of the water table each year was at a rate of about −0.4 cm d^{-1} and the rise in the autumn was at a rate of about 3 cm d^{-1}. When data for all years were pooled, WTD and peat hummock temperature had a weak inverse correlation ($r^2 = 0.26$, $p < 0.001$). Correlation coefficients for individual years ranged from −0.72 (1999) to 0.22 (2000).

The relationship between the position of the water table and relative water content of the peat above the water table is not constant with depth. Peat 28 cm below the hummock surface dewaters
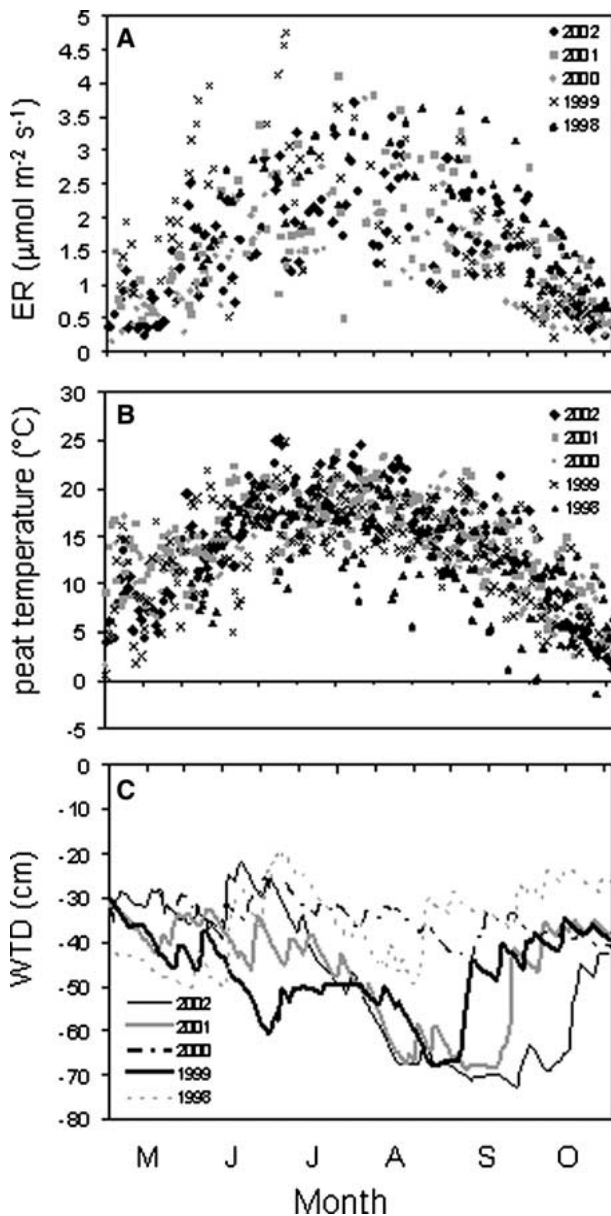
Figure 1. Seasonal trends in **A**) ecosystem respiration, ER, measured by nighttime eddy covariance measurements, **B**) nighttime temperature at 5 cm below the hummock surface, and **C**) water-table depth, WTD, for the period May–October, 1998 to 2002. ER points are mean nighttime fluxes on days with more than six 30-min periods of good data. Soil temperature is nighttime average hummock temperature at −5 cm depth. Daily mean WTD is relative to the hummock surface.

rapidly from about 80 to about 10% once WTD drops below about −33 cm, then decreases marginally with further falls in water table to 70 cm (Figure 2a). In contrast, more decomposed peat 48 cm below the hummock surface loses water very gradually as WTD falls below −50 cm and is
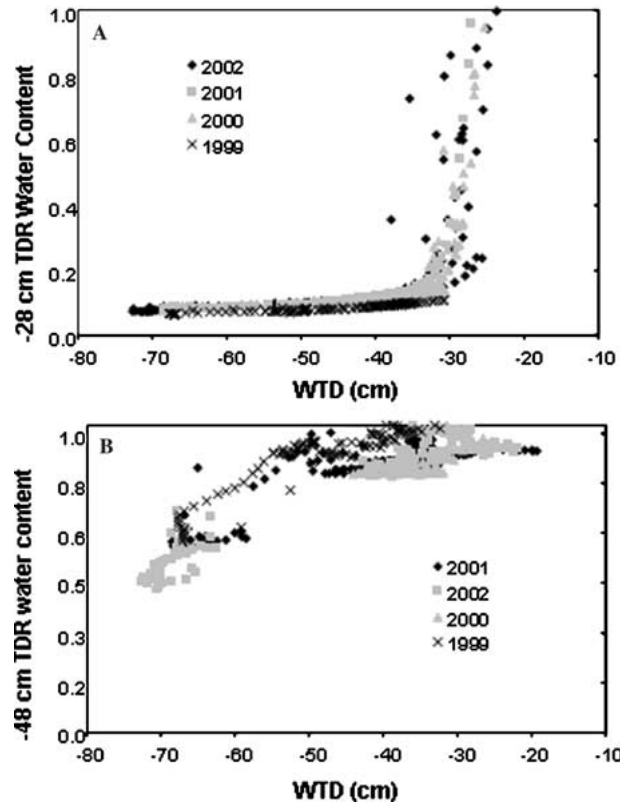

Figure 2. Relationship between peat moisture content as a percent by volume and water-table depth, WTD, below the hummock surface at **A**) −28 cm soil depth and **B**) −48 cm soil depth.

still quite wet (50–60% water content) even when the water table is at −70 cm (Figure 2b).

ER was strongly correlated to air and soil temperatures (Table 2, Figures 3a–c). Employing a first order exponential model, explained variance in ER was similar using the air and upper soil profile temperatures ($r^2 = 0.61$ and 0.62 respectively). Explained variance only decreased appreciably when the deeper hollow temperatures were used. Values of the Q_{10} coefficient generally increased with depth into the soil, and were larger for the peat hollow than for the hummock (Table 2). There was a strong inverse relationship ($r^2 = 0.81$) between the calculated Q_{10} coefficient and the range of temperature measured at each location (not shown).

ER data were sorted into shallow (>−40 cm) and deep (<−60 cm) water table groups and exponential relationships with hummock 5 cm temperature were computed (not shown). The goodness of fit was poorer for the deep water table data ($r^2 = 0.48$) than for the shallow ($r^2 = 0.68$), possibly because of the narrow range of temperatures when the water
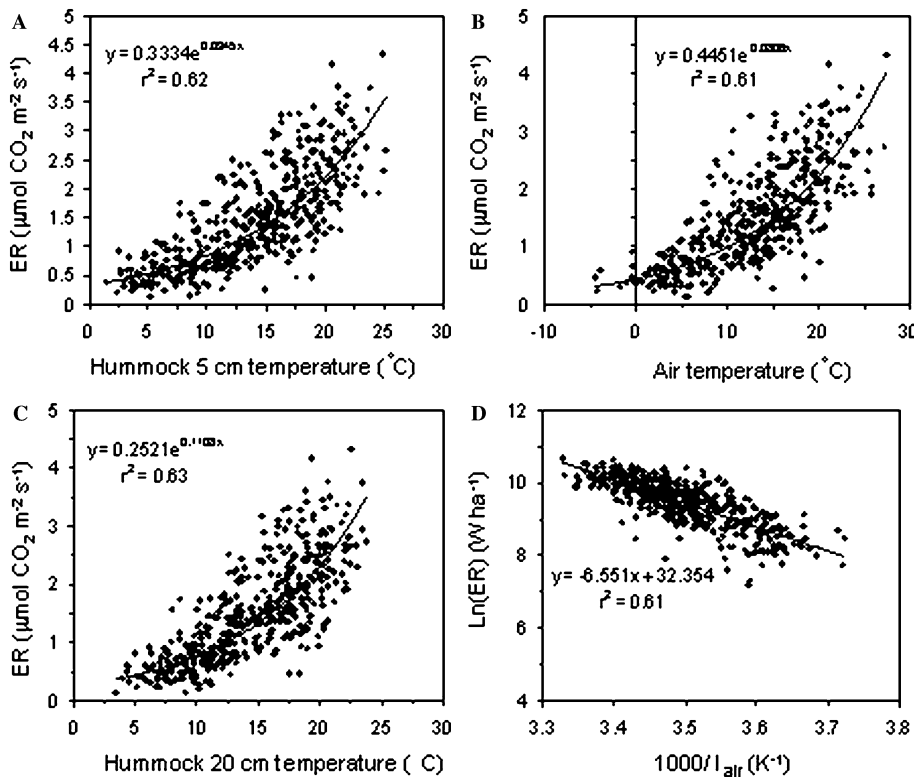
Figure 3. Relationship between ER and selected environmental temperatures: **A**) hummock soil temperature at 5 cm, **B**) air temperature (0.5 m height), and **C**) hummock soil temperature at 20 cm. Points are nighttime averages for all years combined. Equation shown is the best-fit exponential relationship. **D**) Relationship between natural logarithm of ER, ln(ER), with ER in energy units (W ha^{-1}), against inverse temperature (1000/T), T is air temperature at 50 cm height in K. Equation shown is the best-fit linear relationship.

Table 2. Comparison of Statistical Models Relating Ecosystem Respiration, ER, and Various Environmental Temperatures

Location	a	b	r^2	Q_{10}	T_{min}	T_{max}	T_{mean}	T_{range}
Air_50	0.0196	0.0806	0.61	2.24	−4.5	27.4	12.7	31.9
Hum_5	0.0147	0.0945	0.62	2.57	1.4	25.2	13.9	23.8
Hum_10	0.0133	0.0975	0.62	2.65	2.1	25.3	14.5	23.2
Hum_20	0.0112	0.1108	0.63	3.03	3.3	23.8	14.3	20.5
Hol_5	0.0102	0.1364	0.58	3.91	0.6	19.5	12.3	18.9
Hol_10	0.0097	0.1431	0.52	4.18	1.0	18.2	12.0	17.2
Hol_20	0.0106	0.1430	0.38	4.18	1.2	15.8	11.4	14.6

Models were first order exponential equations of the form ER = ae^{bTsoil}, where a and b are fitted coefficients. r^2 is the coefficient of determination. Location indicates where temperature was measured: Air_50 is air temperature measured at 50 cm height, Hum_x and Hol_x are peat temperatures measured below a hummock and hollow respectively, where x is the soil depth at which measurements were made. Q_{10} is the ratio of respiration rates modeled at 5 and 15°C. Minimum (T_{min}), maximum (T_{max}), average (T_{mean}) temperature, and temperature range (T_{range}) are given for each location in °C.

table was deeper. The resulting Q_{10} quotients were 2.58 (shallow) and 2.02 (deep).

There was a weak ($r^2 = 0.11$), but statistically significant ($p < 0.05$), relationship between ER and water-table position, with an increase in ER as the water table falls (Figure 4a). When data were sorted into individual years, some years produced significantly better relationships (that is, $r^2_{1998} = 0.27$, $r^2_{1999} = 0.36$, $r^2_{2001} = 0.35$) and others were poorer and insignificant (that is, $r^2_{2000} = 0.06$, $r^2_{2002} = 0.09$). As with the pooled data set, the slope of these relationships was negative except for 2000, which was positive but not statistically significant. It

is notable that in 2000 the water table was the highest for all years and showed the least variation over the season, whereas in 2002 the water table was the lowest of the five years. There was no apparent relationship between WTD and the residuals from the ER versus T model (Figure 4b).

The laboratory incubation of intact peat cores with varying moisture content showed that CO_2 production rates declined with reduced soil moisture contents (Figure 5). The uppermost samples of peat (0 to 5 cm) had the largest CO_2 production rates, on a per mass basis, and the greatest decline as the moisture content fell. There was also an
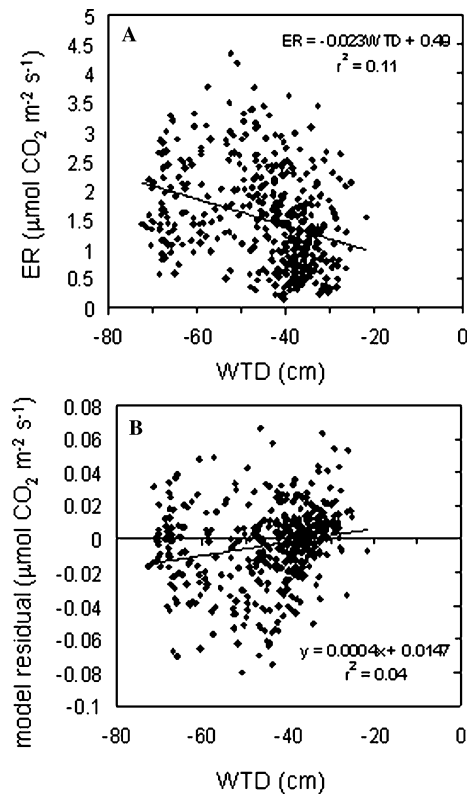
Figure 4. A) Relationship between ecosystem respiration, ER, and water-table depth, WTD, for all years combined. Best-fit linear regression is shown. **B)** distribution of residuals (model ER minus observed ER) for the exponential model shown in Figure 3, as a function of WTD.

overall decrease in CO_2 production rate through the three drying cycles. CO_2 production rates were smallest in the lower samples (from 20–25 to 40–45 cm), decreased little as the volumetric moisture content was reduced from 60 to 20% and showed no difference among the three drying cycles.

DISCUSSION

The strong temperature dependence of ER at the Mer Bleue bog is consistent with findings from field studies that have examined respiration at the plot scale with chambers (Bubier and others 1998; Silvola and others 1996a; Bubier and others 2003a, 2003b). However, we found that near-surface temperatures are better predictors of ER than deeper soil temperatures. Q_{10} values derived for Mer Bleue ranged from 2.24 to 4.18 depending on the depths of the temperature measurements used in the analyses. Larger Q_{10} values were associated with locations with a smaller temperature range,

which occur deeper in the profile. All values fell within the considerable range in Q_{10} for peatlands reported in the literature, 1.8–6.1 (Svensson 1980; Chapman and Thurlow 1996; Silvola and others 1996a). We conclude that at least some of the variation in Q_{10} reported in the literature is likely due to the lack of standardization of the depth at which peat temperature is measured.

Our results suggest that ER was not strongly dependent upon WTD at Mer Bleue bog, despite a considerable range in WTD (−30 to −75 cm). As discussed above most laboratory manipulations on peat soil columns tend to support the notion of a strong dependence of CO_2 emission on WTD, whereas field studies with chambers both support (for example, see Silvola and others 1996a; Oechel and others 1998; Bubier and others 2003b) and refute (for example, Bubier and others 1998; Updegraff and others 2001) the argument that WTD strongly influences ER. Previous tower studies employing eddy covariance at peatland sites shed little light on this issue. Most studies offer no detailed analysis of nighttime data and instead model ER (for example, Shurpali and others 1995; Aurela and others 1998, 2001; Soegaard and Nordstoem 1999). A few studies present temperature-nighttime flux relationships, but do not consider the influence of WTD (for example, Neumann and others 1994; Nieveen and others 1998; Arneth and others 2002). One exception is Vourlitis and Oechel (1999), who provide a response surface for ER as a function of temperature and water table in arctic tussock tundra. The lack of ER analysis in previous eddy covariance studies seems to arise from two factors. First, some peatland systems were quite wet (that is, WTD > −10 cm) and WTD does not vary enough to produce an effect on ER (Suyker and others 1997; Nieveen and others 1998; Nordstroem and others 2001). Second, WTD information was only anecdotal and could not be formally treated (Aurela and others 2001; Arneth and others 2002). We suggest that future eddy covariance measurements can provide valuable information on peatland ER, if combined with an appropriate suite of environmental variables.

At the Mer Bleue bog Bubier and others (2003a) measured daytime ER using opaque chambers from June to August 2000 and 2001 at hummock and hollow microhabitats, representing the vegetation and hydrology within the footprint of the flux tower. They found that the bog hummock showed no statistical difference in respiration between the two years, whereas the hollow had significantly greater respiration in the drier year (2001). Linear relationships between ER and WTD were poor
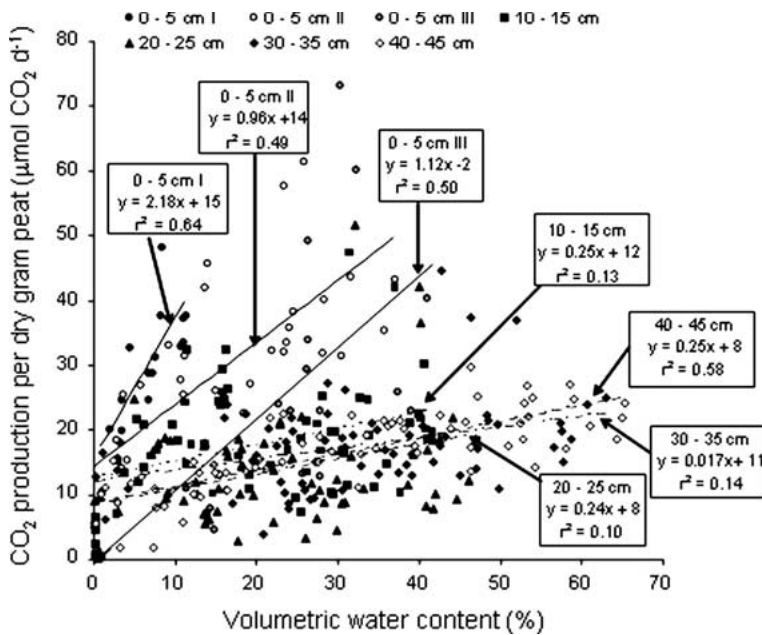
Figure 5. Relationship between CO_2 production during laboratory incubation of intact peat cores, collected from 0 to 45 cm depth at Mer Bleue, as a function of volumetric water content. Three drying cycles for the 0 to 5 cm sample are shown separately; data from the three drying cycles of the deeper samples have been combined into one set. Incubation temperature was 20°C. Lines represent the linear regressions between CO_2 production and volumetric water content. Note that these incubation conditions represent drying from field capacity, but not conditions between field capacity and saturation.

($r^2 \leq 0.12$) for both microsites in the wet year (2000), but improved markedly ($r^2 = 0.62$ for hummock; $r^2 = 0.39$ for hollow) in the drier year. Combining both years resulted in intermediate values of r^2. These values are slightly higher, but in broad agreement with those found in the present study ($r^2 = 0.06$ in 2000, $r^2 = 0.35$ in 2001). Employing multiple regression with various environmental temperatures and water table, Bubier and others (2003a) found that temperature was a stronger determinant of ER than WTD for both hummock and hollow sites.

The lack of a strong ER response to WTD in peatland environments has been reported in other studies (Updegraff and others 2001), but these somewhat counter-intuitive findings are in want of an explanation. We offer the following speculation for the apparent lack of a strong dependency of ER on water table at the Mer Bleue low-shrub bog:

1) Mer Bleue is an inherently dry peatland ecosystem. The 5-year mean growing season WTD was −45 cm below the peat surface of hummocks. Other peatlands studied for CO_2 or CH_4 exchanges are generally wetter, although Mer Bleue does not appear to be atypical based on a broad survey of peatland water tables in Ontario (for example, Riley 1983). Soil moisture characteristic curves for the surface layers of most peatlands indicate that small changes in water-table elevation within a narrow range can result in large changes in soil moisture and hence air filled porosity; peat water content is relatively insensitive to changing water-table depth outside of this narrow range. This sensitivity was also present at Mer Bleue (Fig-

ure 2a). Because WTD was usually below −30 cm (Figure 1c) the surface peat water content was generally low and quite constant. In contrast, the peat water contents are much greater at depth and are less sensitive to changes in WTD (Figure 2b), due to 10 to 1000 fold decrease in hydraulic conductivity and specific yields in the more humified, deeper peat (Letts and others 2000). Our laboratory experiments suggest that CO_2 production is greatest and most sensitive to moisture changes in the uppermost portions of the peat profile (Figure 5). Other studies of peatland soils have found similar results (Updegraff and others 1995; Waddington and others 2001). However, because the soil moisture content was relatively invariant in the upper layers, little change in heterotrophic respiration would be expected to result from observed changes in water-table depth.

2) Respiration is dependent upon oxygen availability; thus to increase substantially heterotrophic respiration in the deeper peat layers there would have to be significant oxygen diffusion into those layers. The change of soil moisture at −48 cm indicates that there is only a small increase in air-filled porosity except when the water table is extremely deep, for example, less than −60 cm. Although we are unaware of any studies of oxygen diffusion in peat soils relative to moisture content, in mineral soils at saturation ratios above 0.6 (that is, volume of water/volume of pores), soil respiration becomes oxygen limited (Linn and Doran 1984; Skopp and others 1990). At −28 cm the peat of Mer Bleue seldom reaches saturation ratios of 0.6, but at −48 cm the saturation ratio exceeds 0.6 much of the

time. Studies of gas diffusion in soils show that increasing the saturation ratio from 0.6 to 0.9, the range observed at −48 cm, results in a three order of magnitude decrease (10^{-1} to 10^{-4} $m^{2/3}$) in normalized gas permeability (Nazaroff 1992). Thus even with a deep water table (for example, <−60 cm), unsaturated peat in the 40–60 cm depth range is probably not well-oxygenated.

3) A number of studies have argued that the substrate quality in peatlands, upon which decomposition and CO_2 production are highly dependent, varies inversely with depth (Updegraff and others 1995; Christensen and others 1999; Waddington and others 2001). Fresh litter and the partially decomposed plant material of the uppermost peat decompose at a faster rate than older peat material lower in the profile. In the upper most peat layers moisture increases respiration, as in the case of our incubation experiments (Figure 5), presumably because of the ready supply of fresh substrate and or nutrient (Skopp and others 1990). The Peat Decomposition Model (Frolking and others 2001), which successfully reproduces peat accumulation over periods of several thousand years, predicts an order of magnitude drop in decomposability due to increasing recalcitrance from the surface to a depth of −40 to −50 cm. Even if this deeper peat is exposed to increasingly oxic conditions, the highly recalcitrant nature of the peat is such that there is little available substrate to decompose. In simulations of the carbon exchanges of Mer Bleue, the Peatland Carbon Simulator (Frolking and others 2002) predicted that there is very little contribution to ER from the peat layers below −35 cm, even when the water table is quite deep.

4) The relationship between ER and water table is not simply dependent on heterotrophic respiration, but also on the response of the living plant respiration to changes in moisture and WTD. The exact proportion of ER attributable to plant respiration at Mer Bleue is unknown, but estimated at about 50% of total ecosystem respiration (Moore and others 2002). Elsewhere it has been estimated that plant roots contributed 35–45% of total soil respiration at a central Finland peatland (Silvola and others 1996b) and a recent model of peatland C exchange estimated autotrophic respiration to be about 50% of total respiration (Frolking and others 2002). This proportioning between autotrophic and heterotrophic respiration is unlikely to be constant, but may vary more with autotrophic production, which would be much less sensitive to changes in water table than to temperature at the leaf surface. Hence a stronger relationship with air temperature

and/or the upper most soil temperature is probable. If so, such behavior would contribute to the similar results found for ER versus temperature relationships for the upper soil and air temperatures, as well as the similarity of the relationships for shallow and deep water tables.

The points discussed above suggest some important differences between peatland and forest ecosystems. The extent to which these differences are reflected in terms of ER may be evident in the recent model by Enquist and others (2003). These authors proposed a generalized model of ER based on an analysis of natural logarithm of ER against inverse temperature. The model is based on metabolic kinetics and, as such, ER fluxes usually reported in units of μmol CO_2 m^{-2} s^{-1} are converted to metabolic energy units of W ha^{-1} by multiplying by 0.272 J $μmol^{-1}$ of CO_2 and scaling to a hectare (see Methods in Enquist and others 2003). Applying the model to data from Mer Bleue produced an inverse linear relationship between ln(ER) and inverse temperature (Figure 3d), as did the forest ecosystems used in the Enquist analysis. However, the slope (−6.50 W ha^{-1} K^{-1}) and intercept (30.89 W ha^{-1}) of the Mer Bleue relationship are smaller than those found for the upland ecosystems. As a consequence, the Mer Bleue peatland becomes an apparent outlier (under-predicted) when the predicted ER at 10°, 15° and 20°C is compared to values from other sites plotted against latitude (see Figure 2b in Enquist and others 2003). This may represent limitations in resource supply at Mer Bleue, such as poor nutrient availability and/or the behavior of an ecosystem with a large anaerobic sub-environment.

CONCLUSION

Growing season ecosystem respiration in a dry ombrotrophic bog was strongly correlated with peat temperature and very weakly correlated with water-table depth. As explained by the four points given above, we believe that the relationship between ER and WTD is the result of complex but predictable interactions among WTD, vertical profiles of peat water content in the unsaturated zone above the water table, and vertical profiles of peat decomposability. A natural hypothesis derived from this reasoning would be that wetter peatlands should have a stronger ER sensitivity to WTD than observed in this study (provided WTD falls below the peat surface). A second hypothesis is that peatland ER will not follow a generalized model of ER such as proposed by Enquist and others (2003). Eddy covariance measure-

ments of ER would be a useful platform for testing both these hypotheses.

Currently, much of our current understanding of ER comes from forest environments, as evidenced by two recent attempts to produce generalized models of ER (or soil respiration) from existing data sets (Enquist and others 2003; Reichstein and others 2003). Peatland ecosystems have received much less attention than upland ecosystems; thus no comparable modeling synthesis exists. Predicting how the C balance of peatlands will respond to anticipated climatic change requires a process-level understanding of how C cycles through peatlands, mapping of the spatial distribution of relevant peatland characteristics, and the ability to predict how climatic change will impact peatland hydrology and water-table depth.

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