Ecosystems (2011) 14: 646–657
DOI: 10.1007/s10021-011-9435-9

ECOSYSTEMS

A Multi-Year Record of Methane Flux at the Mer Bleue Bog, Southern Canada

Tim R. Moore,[1]* Allison De Young,[1] Jill L. Bubier,[2] Elyn R. Humphreys,[3] Peter M. Lafleur,[4] and Nigel T. Roulet[1]

[1]*Department of Geography, and Global Environmental & Climate Change Centre, McGill University, 805 Sherbrooke St. W, Montreal, Quebec H3A2K6, Canada;* [2]*Mount Holyoke College, 50 College Street, South Hadley, Massachusetts 01075, USA;* [3]*Department of Geography and Environmental Studies, Carleton University, Ottawa, Ontario K1S 5B6, Canada;* [4]*Department of Geography, Trent University, Peterborough, Ontario K9J7B8, Canada*

ABSTRACT

The Mer Bleue peatland is a large ombrotrophic bog with hummock-lawn microtopography, poor fen sections and beaver ponds at the margin. Average growing-season (May–October) fluxes of methane (CH_4) measured in 2002–2003 across the bog ranged from less than 5 mg m^{-2} d^{-1} in hummocks, to greater than 100 mg m^{-2} d^{-1} in lawns and ponds. The average position of the water table explained about half of the variation in the season average CH_4 fluxes, similar to that observed in many other peatlands in Canada and elsewhere. The flux varied most when the water table position ranged between −15 and −40 cm. To better establish the factors that influence this variability, we measured CH_4 flux at approximately weekly intervals from May to November for 5 years (2004–2008) at 12 collars representing the water table and vegetation variations typical of the peatland. Over the snow-free season, peat temperature is the dominant correlate and the difference among the collars' seasonal average CH_4 flux is partially dependent on water table position. A third important correlate on CH_4 flux is vegetation, particularly the presence of *Eriophorum vaginatum*, which increases CH_4 flux, as well as differences in the potential of the peat profile to produce and consume CH_4 under anaerobic and aerobic conditions. The combination of peat temperature and water table position with vegetation cover was able to explain approximately 44% of the variation in daily CH_4 flux, based on 1097 individual measurements. There was considerable inter-annual variation in fluxes, associated with varying peat thermal and water table regimes in response to variations in weather, but also by variations in the water level in peripheral ponds, associated with beaver dam activity. Raised water level in the beaver ponds led to higher water tables and increased CH_4 emission in the peatland.

Key words: greenhouse gases; peatlands; wetlands; water table; *Eriophorum vaginatum*; *Castor canadensis*.

INTRODUCTION

Since the early studies (for example, Clymo and Reddaway 1971; Svensson 1980; Harriss and others 1982), over 1100 papers have been published on the exchange of methane (CH_4) between peatlands

---

Received 21 October 2010; accepted 10 March 2011;

Author Contributions: TRM conceived and directed the study; ADY collected and analyzed much of the data; JLB, ERH, PML and NTR contributed data to the study and aided in the interpretation of the results; all six wrote the paper.

**Corresponding author; e-mail:* tim.moore@mcgill.ca

and the atmosphere (ISI Web of Science). Through a combination of field and laboratory studies, the scientific community has been able to define the range of fluxes, with their high spatial variability (several orders of magnitude over short distances) and strong seasonal variability, which helps constrain models (for example Walter and Heimann 2000) and the spatial and temporal contribution of wetlands to atmospheric CH_4. Major controls on fluxes include microbial rates of CH_4 production and consumption, temperature and water table position and vegetation, as well as processes of diffusion, ebullition and transport through the aerenchyma of plants (see Whalen 2005).

Harriss and others (1982) noted almost 30 years ago '… the potential complexity of the problem of quantitatively determining long-term net flux of CH_4 from a wetland system to the atmosphere' and this complexity remains. In particular, many field campaigns have been run over short periods, for 1 or 2 years, and there is little knowledge of the interannual variability in CH_4 emission rates (with the exception of the decadal record at Sallie's Fen, NH, U.S.A., see Treat and others 2007). In addition, many studies focus on only one or two factors controlling the rates and do not address the high degree of small-scale spatial variability that influences scaling-up attempts (see Baird and others 2009).

At large temporal and spatial scales, water table position exerts an important control on CH_4 emission rates, through its control on the distribution of oxic and anoxic parts of the peat profile, and indirectly through vegetation and substrate quality. At the Mer Bleue peatland in south central Canada, we measured the May to October 2002–2003 emission of CH_4 from a series of collars, representing the major range of vegetation and water table position in the peatland, from hummock-lawn-hollow bog through poor fen to beaver ponds. Overall, there was a strong correlation between the seasonal average CH_4 flux and the average water table position (Figure 1A). This pattern has been repeated in many other studies, as illustrated in Figure 1B, where the slopes of the regression between $\log_{10}CH_4$ flux and water table depth are similar, but the intercepts vary. Within any of these relationships, however, there is considerable variation around the best-fit line, showing that factors other than water table depth play an important role, particularly in the intermediate water table depths (at Mer Bleue between -15 and -40 cm).

In this paper, we report on CH_4 fluxes measured at 12 permanent locations in the bog section of Mer Bleue, to better identify the correlates on fluxes. Measurements were made at 1–2 week intervals from May to November over 5 years (2004–2008), to establish the interannual variability in CH_4

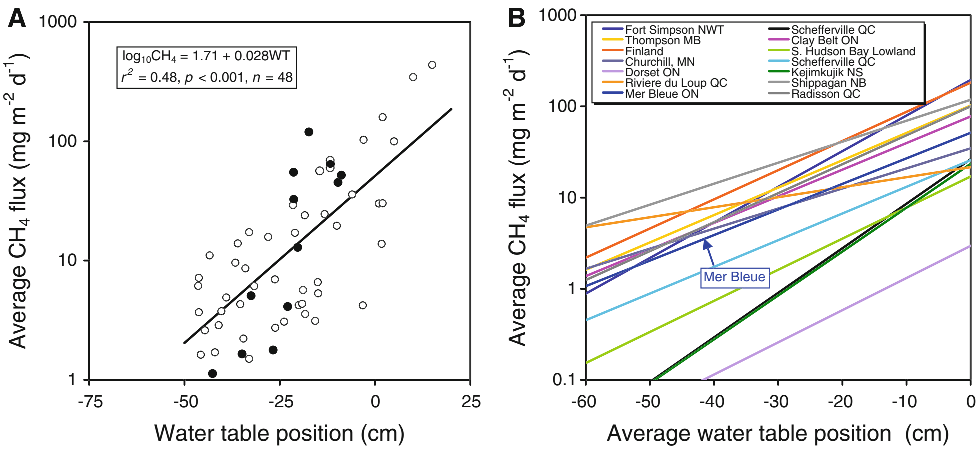

Figure 1. **A** Relationship between the growing-season (May to October) water table position and mean CH_4 flux from sites in the Mer Bleue peatland, 2002–2003. The *filled circles* are the 12 collars that are the focus of this study. **B** Regressions between growing-season water table position and CH_4 flux from locations including Mer Bleue (from **A**). The regressions are based on up to 120 individual collars at each location, with r^2 values ranging from 0.3 to 0.8. Results are drawn from: Churchill, Manitoba: Rouse and others (1995); Clay Belt, Ontario: Bubier and others (1993); Dorset, Ontario: Roulet and others (1992); Finland: Nykänen and others (1995); Fort Simpson, North-west Territories: Liblik and others (1997); Kejimkujik, Nova Scotia: Dalva and others (2001); Mer Bleue, Ontario: this study; Radisson, Québec: Pelletier and others (2007); Rivière du Loup, Québec: Moore (unpublished data); Schefferville, Québec: Bubier (1995); Shippagan, New Brunswick: Moore (unpublished data); Southern Hudson Bay Lowlands: Moore and others (1994); Thompson, Manitoba: Bubier and others (1995).

fluxes. To determine the important controls on these fluxes, we examine their relationship to water table depth and its variations, peat profile temperature, vegetation and the ability of the peat profile to produce and consume CH_4. Finally, we show the magnitude of the CH_4 fluxes relative to the Net Ecosystem Exchange of CO_2 (NEE) for the study period.

Materials and Methods

Site Description

The Mer Bleue peatland, covering approximately 28 km^2, is located 10 km east of Ottawa, Ontario (45.41°N latitude, 75.48°W longitude). The climate of the region is cool continental, with a 30-year (1971–2000) mean annual temperature of $6.0 \pm 0.8°C$ and an annual precipitation of 943 mm, with 235 mm falling as snow. Mer Bleue lies in a post-glacial channel system and formed over the past 8400 years, beginning as a fen, and switching to the bog phase around 7000 years BP. Peat depths vary from 5 to 6 m near the center decreasing to 0.3 m at the margins with a narrow band of beaver ponds surrounding the bog (Roulet and others 2007).

The bog surface has a hummock-lawn-hollow microtopography. The dominant evergreen (*Chamaedaphne calyculata*, *Ledum groenlandicum*, *Kalmia angustifolia*), and deciduous (*Vaccinium myrtilloides*) shrubs have an average height of 0.2–0.3 m and leaf area index of about 1.3 (Moore and others 2002; Bubier and others 2006). Sedges (mainly *Eriophorum vaginatum*) comprise a sparse cover with *Maianthemum trifolium*, and a few small trees (*Larix laricina* and *Betula populifolia*) are present on hummocks. Hummocks, lawns and hollows are covered by mosses (mainly *Sphagnum capillifolium*, *Polytrichum strictum*, *Sphagnum magellanicum* and *Sphagnum angustifolium*).

Field Measurements

Methane flux was measured at 12 locations (Table 1), selected to capture the main variation in water table position and vegetation within the peatland with moderate water table position and high variability in CH_4 flux (Figure 1A). We used a static chamber method with a chamber of 18 l volume placed on permanent collars (water sealed, 25 cm diameter) inserted into the peat to a depth of 10–15 cm. Flux measurements were made once or twice a day on an approximately weekly basis, between 09:30 and 15:00 h, with the following number of sampling dates per year: 2004—17; 2005—25; 2006—14; 2007—25; 2008—18. The air inside the chamber was sampled every 5 min for 25 min through a septum and stopcock, and the samples were analyzed on a Shimadzu Mini II gas chromatograph (Shimadzu Scientific Instruments, Columbia, MD, USA) equipped with a flame ionization detector. The GC was calibrated for each sample period with two standards (1.8 and 2000 ppmv CH_4) and periodically checked to ensure the calibration had a reproducibility of approximately 1%. The fluxes of CH_4 were calculated from the slope of the regression between CH_4 concentration and time, and

Table 1. Plant Species Coverage and Mean Water Table Position (2004-8) for the 12 Collars

Species	Collar											
	1	2	3	4	5	6	7	8	9	10	11	12
S. capillifolium	70	90	95	75	80	80	95	50	90	90	60	95
S. magellanicum	0	10	<1%	25	<1%	<1%	<1%	5	10	0	5	5
S. angustifolium	0	0	0	0	0	0	0	0	0	0	0	5
P. strictum	30	10	5	5	20	25	15	40	15	5	40	5
C. calyculata	0	<1%	<1%	0	0	<1%	5	5	0	<1%	<1%	2
K. angustifolia	<1%	10	0	0	10	30	5	5	<1%	10	5	2
L. groenlandicum	20	1	1	20	10	20	25	0	0	0	0	0
V. myrtilloides	0	20	10	10	0	0	0	0	0	0	10	<1%
Vaccinium oxycoccus	<1%	<1%	<1%	<1%	<1%	<1%	<1%	<1%	<1%	1	2	<1%
E. vaginatum	10	0	100	40	<1%	0	0	0	0	0	0	<1%
Carex trisperma	0	0	0	0	0	<1%	0	0	0	<1%	0	<1%
M. trifolium	0	0	0	0	0	0	20	10	25	10	0	30
Mean water table (cm)	−46	−35	−32	−23	−41	−39	−33	−31	−27	−31	−52	−27
Category	Ev	Hu	Ev	Ev	Hu	Hu	Hu	La	La	La	Hu	La

Hu hummock, La lawn, Ev E. vaginatum.

expressed as mg m^{-2} d^{-1}, with fluxes being rejected when the pattern was poor, such as with a high initial CH_4 concentration or low r^2. The flux rejection rate was 6.9%.

In 2007 and 2008, 2-mm internal diameter metal tubes were inserted into the peat within the collar to depths of 10, 20, 30 and 40 cm. The tubes were attached to Tygon tubing with a stopcock and were used to sample 4 ml of either pore air or pore water, depending on the water table position. Pore air concentration of CH_4 was determined as above. Pore water CH_4 concentration was determined by drawing 4 ml of N_2 gas into the syringe containing the water, shaking for 10 min and determining the headspace concentration of CH_4, the concentration being expressed as μg CH_4 ml^{-1}.

Water table position was measured at the time of CH_4 flux sampling, by determining its height in a 2-cm diameter tube close to the collar. Plant species coverage in each collar was determined in summer, 2005 (Table 1).

An eddy covariance tower was established in 1998, about 200 m SSW of the location of the collars, and has measured air and peat temperature, precipitation, water table position and NEE (see Roulet and others 2007).

Laboratory Measurements

To determine the above- and belowground biomass of *E. vaginatum* and *M. trifolium*, two plants known to have aerenchyma and thus may affect CH_4 flux, five peat cores (30 cm long, 30 cm wide and 50 cm deep) of each were collected in mid-July, 2008, the peak of the growing-season. Aboveground biomass was measured by clipping above the *Sphagnum* surface and separating into live and dead parts. The belowground component was measured by separating the peat core into 10 cm increments, down to 50 cm and removing plant roots, divided into live and dead parts: live when porous, spongy, and white in color and dead when black and no longer fibrous. Samples were oven-dried at 70°C, weighed and the biomass expressed as g m^{-2}.

To determine the potential of the peat profile to produce CH_4 under anoxic conditions and consume CH_4 under oxic conditions, triplicate peat cores down to 50 cm were collected in autumn, 2008, from locations that were either dominated by *E. vaginatum* or were free of this species, near collars 3 and 8, respectively. Peat samples were refrigerated and incubated at 20°C by placing approximately 20 g of wet peat into a 250 ml Mason jar. For the oxic incubations, 2.7 ml of pure CH_4 was added to the jar to produce an initial headspace concentration of 5000–6000 ppmv CH_4. Headspace samples were taken at days 0, 2, 3 and 5 and CH_4 concentration determined as above. For the anoxic incubations, the jars were purged with N_2 gas, water was added to produce a slurry and headspace samples taken at days 0, 4, 6, 9 and 11 for determination of CH_4 concentration, as above. Three replicates at each depth per core were measured. Changes in headspace CH_4 concentration and headspace volume were used to calculate the potential oxic CH_4 consumption and CH_4 anoxic production rates, expressed per mass of dry peat, determined by oven-drying at the end of the incubation.

RESULTS

CH_4 Fluxes and Concentrations, Vegetation and Peat CH_4 Production/Oxidation Potentials

The individual CH_4 fluxes covered a wide range, from small uptake (−2 mg m^{-2} d^{-1}) to large emission (>1000 mg m^{-2} d^{-1}), approximately normally distributed once the fluxes were logarithmic transformed. When expressed as the mean of the 12 collars at each sampling date (Figure 2), a strong seasonal pattern emerges, with small fluxes (10–30 mg m^{-2} d^{-1}) in the spring, reaching a

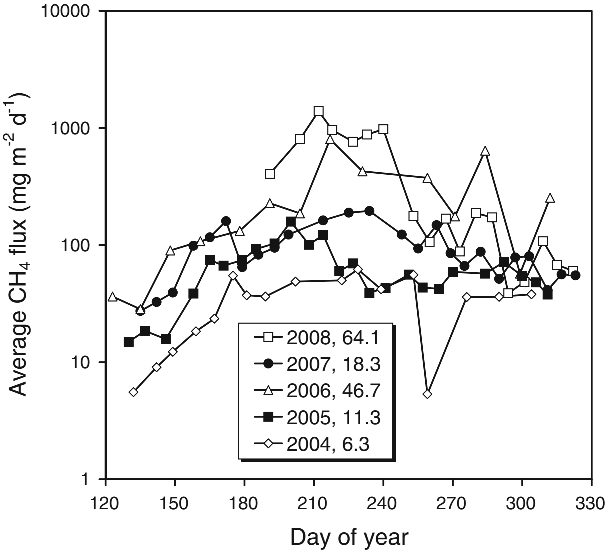

Figure 2. Temporal variation in CH_4 flux, expressed as the average of the 12 collars, from 2004 to 2008. In cases where a flux measurement was missing, an estimate was made as the average of the previous and following sampling dates, to ensure that all collars were included in the overall average flux for that date. The value after the year is the estimated cumulative flux from DOY 120 to 320 for each of the years, as the mean of the 12 collars, expressed in g CH_4 m^{-2}.

maximum in mid-summer (100–1000 mg m^{-2} d^{-1}) and falling to small, but still significant, fluxes in the late-autumn just before the onset of the snow cover (40–100 mg m^{-2} d^{-1}).

These seasonal patterns of CH_4 flux reflect the interaction of the variation in water table position and peat temperature, illustrated by measurements from the nearby eddy covariance tower (Figure 3). During the spring, the water table is relatively high (at −30 to −40 cm in the hummock) and falls during the summer to between −40 and −60 cm, before rising again to −30 to −40 cm in the late-autumn (Figure 3A). Peat temperature recorded at a depth of 40 cm in the hummock (close to the average position of the water table) is around 5°C in the spring, rises to 13–15°C in mid-summer and falls again in the late-autumn to 5–7°C (Figure 3B).

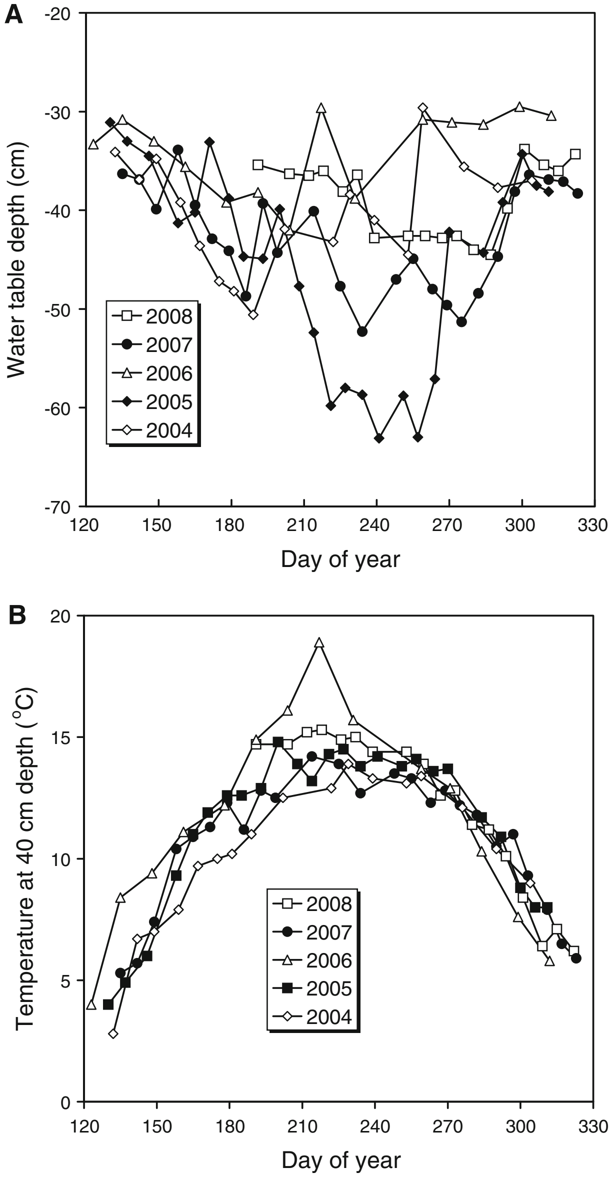

Figure 3. Mean daily water table position (**A**) and temperature recorded at a depth of 40 cm (**B**) in a hummock at the nearby eddy covariance tower site from 2004 to 2008 for dates when CH_4 fluxes were measured.

There was a wide range in the concentration of CH_4 contained in the pore air of the collars (data not shown). At the 10 cm depth, minimum, maximum, mean and median concentrations were 1.4, 7702, 247 and 18 ppmv, respectively, whereas at a depth of 20 cm, values were 1.5, 3232, 189 and 21 ppmv. No consistent seasonal pattern of pore air CH_4 concentration was apparent and concentrations at 10 cm were generally highest in the collars with *E. vaginatum* and where the water table was high. There was no significant relationship between the CH_4 flux and the gradient in CH_4 concentration between the pore air at 10 cm and the atmosphere above the peat surface, suggesting that mechanisms other than diffusion influence the flux.

Pore water CH_4 concentrations measured at the collars also had a high degree of variability (data not shown). Despite a wide range of values, there was a general pattern of small CH_4 concentrations close to the surface (mean, 0.008 mg l^{-1}), increased concentrations at 20 cm depth (mean, 0.082 mg l^{-1}), maximum values at 30 cm depth (mean, 0.141 mg l^{-1}), and elevated but slightly smaller than the maximum values at the 40 cm depth (mean, 0.096 mg l^{-1}). The pore water concentrations were highest at the surface where *E. vaginatum* was present, as found with the pore air samples.

The overall influence of water table position on the seasonal average CH_4 flux is illustrated in Figure 4, which shows the relationship for the 12 collars, by year. In some years, there was a strong correlation but in other years, notably 2006 and 2008, there was no significant relationship ($P > 0.05$). These two years were generally the wettest at the peatland with the average tower hummock water table depth, from May to October, being −34 and −37 cm in 2006 and 2008, respectively, whereas the average depths were −39, −45 and −42 cm in 2004, 2005 and 2007, respectively. Clearly, factors other than water table position influence the seasonal average CH_4 flux.

The influence of *E. vaginatum* cover on CH_4 flux was examined by comparing fluxes in 2005 and 2007 (selected because our flux sampling was densest in these years) from 2 collars with a similar water table depth but varying in *E. vaginatum* cover (Table 1). Collar 3 contained 100% cover of *E. vaginatum*, and had an average water table depth

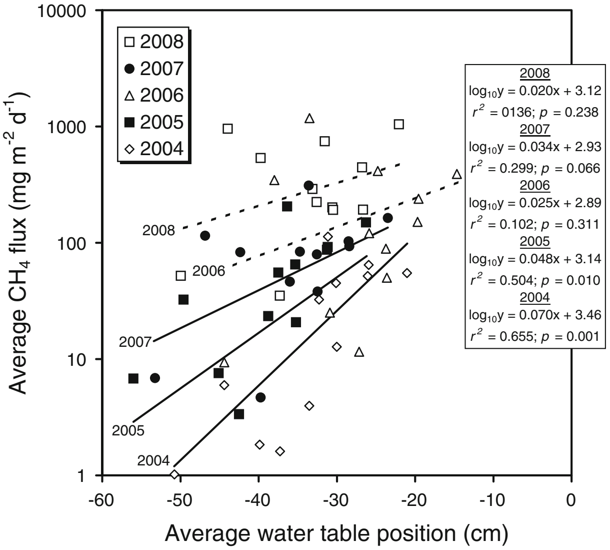

Figure 4. Relationship between the average seasonal water table position and CH_4 flux for the 12 collars for 2004–2008.

of −36.4 and −33.6 cm in 2005 and 2007, respectively, whereas collar 8 had no *E. vaginatum* and was dominated by the shrubs *C. calyculata* and *L. groenlandicum*, with some *M. trifolium*, and an average water table depth of −37.5 and −34.7 cm in 2005 and 2007, respectively. In the early spring, CH_4 fluxes were similar in the two collars, but differentiation occurred in mid-summer with the *E. vaginatum*-dominated collar emitting between 200 and 600 mg m^{-2} d^{-1}, whereas the collar without *E. vaginatum* emitted between 50 and 100 mg m^{-2} d^{-1} (Figure 5). This differentiation continued through to the late-autumn, with collar 3 continuing to emit greater than 200 mg m^{-2} d^{-1}, whereas the CH_4 fluxes from collar 8 fell to 20–50 mg m^{-2} d^{-1}. The seasonal averages for the two collars showed that the presence of *E. vaginatum* resulted in a 3–4 fold increase in CH_4 flux.

Measurement of above- and belowground live *E. vaginatum* tissues down to 50 cm showed that in this ecosystem, about 25–30% of the total live plant biomass was below-ground, ranging from 25 to 100 g m^{-2} (Figure 6A). About one third of this root biomass occurs in the top 20 cm of the peat (Figure 6B), generally above the water table, with the remainder from 20 to 50 cm, in the section where the water table fluctuates during the summer, and thus providing a potential for both CH_4 production and aerenchyma for atmospheric exchange of CH_4 and oxygen. *M. trifolium*, in contrast, has a smaller aboveground biomass but a much larger live root fraction (Figure 6A), though a larger proportion of the roots are located in the top 20 cm (Figure 6B).

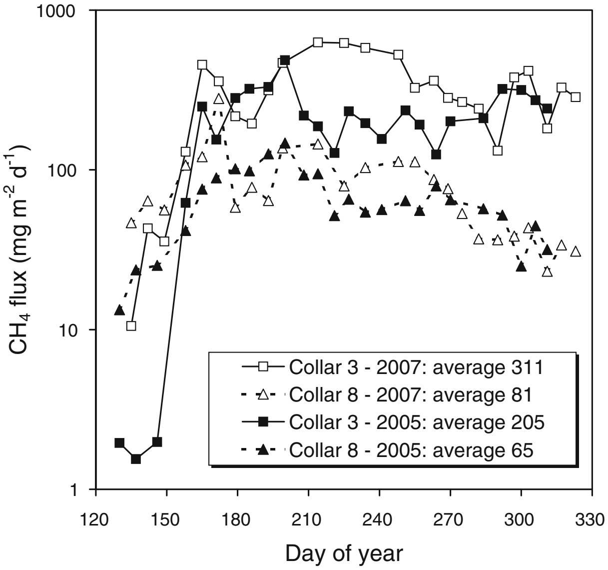

Figure 5. CH_4 flux from collars with a similar water table depth but with either a dense *E. vaginatum* cover (collar 3) or without *E. vaginatum* (collar 8) during 2005 and 2007. Seasonal average fluxes (mg m^{-2} d^{-1}) are given in the *legend*.

M. trifolium may also play a role in CH_4 emission from this system, though it senesces early (August) in this peatland.

The range of anaerobic CH_4 production potentials from the peat cores collected from beneath *E. vaginatum* and beneath shrubs/*Sphagnum* was large, spanning three orders of magnitude, from 0.003 to 1.4 µg g^{-1} h^{-1}, with the shrubs/*Sphagnum* peat potentials being larger in the top 20 cm than the *E. vaginatum* (Figure 7A). This pattern was reversed below 20 cm, where the peat is saturated for most of the year. Aerobic CH_4 consumption potentials had a smaller range, from 2.5 to 12.1 µg g^{-1} h^{-1}, with the potentials from beneath the *E. vaginatum* higher than that beneath shrubs/*Sphagnum* (Figure 7B).

Relationship Between CH_4 Flux and Environmental Variables

The large CH_4 flux data set provides an opportunity to test whether environmental variables can adequately explain both spatial and temporal variations in CH_4 flux in this ecosystem. The fluxes were converted to $\log_{10}$(mg CH_4 m^{-2} d^{-1} + 2.01), to allow all values to be used. The correlations between $\log_{10}CH_4$ flux measurements from all collars and all dates and air and peat temperatures from 1 to 200 cm below the hummock surface at the tower were all significant at the $P \leq 0.001$ level, though

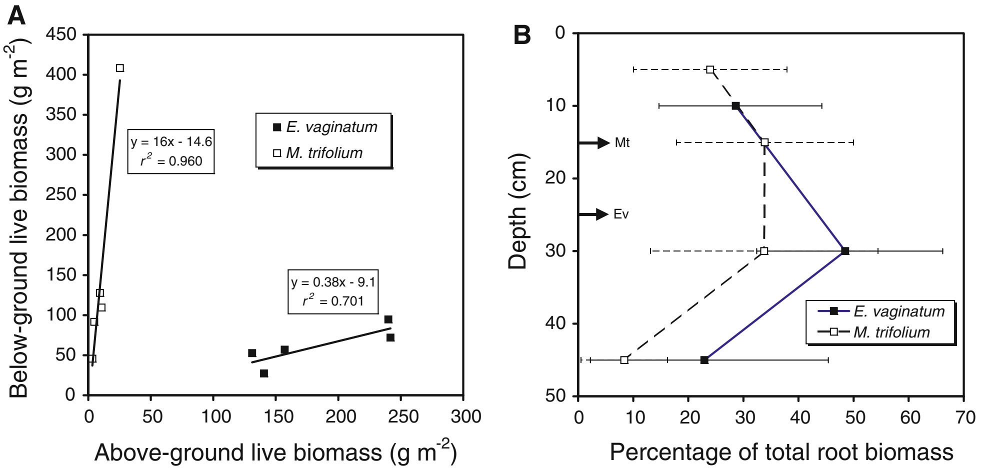

Figure 6. Relationship between above- and belowground biomass in *E. vaginatum* and *M. trifolium* (**A**) and distribution of roots with depth (**B**) (*bars* represent standard deviation of the 5 cores) or as percentage of total. *Arrows* represent average water table depth at time of sampling.

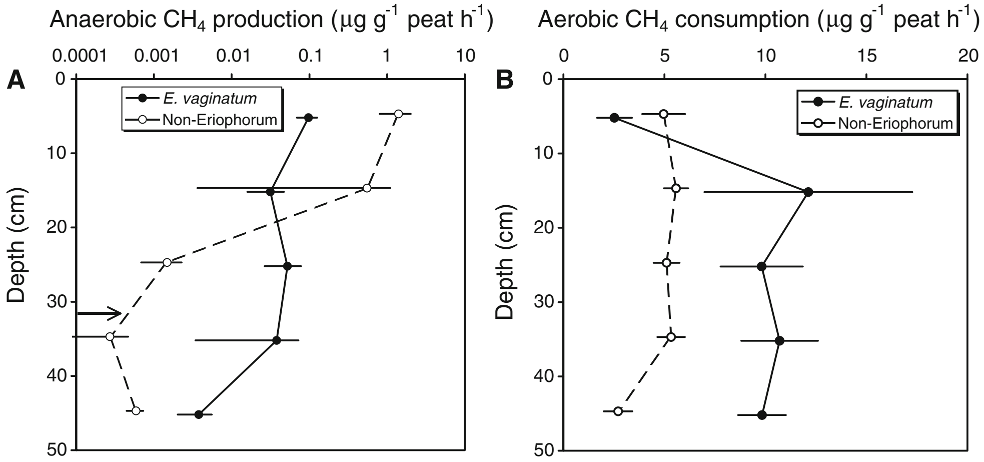

Figure 7. Potential rates of anaerobic CH_4 production (**A**) and aerobic CH_4 consumption (**B**) from peat profiles collected beneath *E. vaginatum* and non-*E. vaginatum* (shrub-*Sphagnum*). *Arrow* represents average water table position in the two sets of cores.

the r^2 values were small, ranging from 0.011 (air) to 0.117 (peat 40 cm), the latter coinciding with the average position of the water table. Similarly, individual water table depth at the collars was also significantly ($P < 0.001$) correlated with $\log_{10}CH_4$ flux, but with an r^2 value of 0.102. The coverage of *E. vaginatum* and *M. trifolium* were both significantly ($P < 0.001$) and positively correlated with $\log_{10}CH_4$ flux, with r^2 values of 0.124 and 0.061, respectively. Forward step-wise multiple regression revealed that the combination of vegetation coverage (*E. vaginatum* and *M. trifolium*) and peat temperature at 40 cm and water table position could explain 44% of the variation in $\log_{10}CH_4$ flux, with a standard error of the estimate of 0.570 (Table 2).

When separated into monthly groupings, the significance of the variables for explaining individual fluxes changed. Across the 5 years, water table was the most significant correlate of CH_4 fluxes in May, June, July and August, whereas *E. vaginatum* became the most important in September, October and November (Table 2). However, using monthly means across the 5 years for each individual collar, peat temperature was the best predictor of CH_4 fluxes with an r^2 of 0.43 ($n = 35$), including water table raises the r^2 to 0.56. When analyzing the study period means for all years and all collars, water table was the most important predictor of seasonal mean CH_4 fluxes ($r^2 = 0.35$, $n = 60$) followed by peat and air temperature (cumulative $r^2 = 0.53$).

When fluxes are separated into the 12 collars (data not shown), regressions of CH_4 flux against water table position and temperature at 40 cm were all significant at $P \leq 0.001$, with r^2 values ranging from 0.07 to 0.41, and standard errors of the estimate of 0.285 to 0.767. The r^2 values of the relationship between temperature and CH_4 decreased with greater water table depths ($r^2 = 0.50$, $P = 0.010$). The standard error of the estimate of the temperature–CH_4 regression model decreased with increasing average water table position ($r^2 = 0.56$, $P = 0.005$).

Table 2. Forward Multiple Regression Equations of $\log_{10}CH_4$ flux (mg CH_4 m^{-2} d^{-1} + 2.01) and Variables Representing Vegetation, Peat Temperature and Water Table

Data set	Equation	r^2	P	s.e.e.
All data	$1.462 + 0.009(0.001) * \mathrm{Ev}$	0.124	<0.001	0.711
	$1.187 + 0.013(0.001) * \mathrm{Ev} + 0.029(0.002) * \mathrm{Mt}$	0.270	<0.001	0.649
	$0.272 + 0.013(0.001) * \mathrm{Ev} + 0.029(0.002) * \mathrm{Mt} + 0.082(0.006) * \mathrm{T40}$	0.387	<0.001	0.595
	$0.806 + 0.011(0.001) * \mathrm{Ev} + 0.020(0.002)*\mathrm{Mt} + 0.099(0.006)* \mathrm{T40} - 0.018(0.002) * \mathrm{WT}$	0.437	<0.001	0.570
May	$1.465 + 0.033(0.005) * \mathrm{WT} + 0.021(0.004)*\mathrm{Mt} + 0.064(0.02) * \mathrm{T40}$	0.502	<0.001	0.443
June	$0.583 - 0.020(0.004) * \mathrm{WT} + 0.012(0.001) * \mathrm{Ev} + 0.028(0.004) * \mathrm{Mt} + 0.113(0.026) * \mathrm{T40}$	0.607	<0.001	0.427
July	$0.712 - 0.024(0.007) * \mathrm{WT} + 0.009(0.002) * \mathrm{Ev} + 0.128(0.033) * \mathrm{T40} + 0.016(0.006) * \mathrm{Mt}$	0.433	<0.001	0.575
August	$1.5 - 0.027(0.005) * \mathrm{WT} + 0.011(0.022) * \mathrm{E} + 0.017(0.005) * \mathrm{Mt} + 0.08(0.040) * \mathrm{T40}$	0.403	<0.001	0.698
September	$1.458 + 0.014(0.001) * \mathrm{Ev} + 0.023(0.004) * \mathrm{Mt}$	0.326	<0.001	0.567
October	$0.533 + 0.012(0.002) * \mathrm{Ev} + 0.013(0.004) * \mathrm{Mt} + 0.111(0.033) * \mathrm{T40} - 0.012(0.005) * \mathrm{WT}$	0.366	<0.001	0.518
November	$2.174 + 0.017(0.002) * \mathrm{Ev} + 0.029(0.005) * \mathrm{Mt} - 0.178(0.055) * \mathrm{T40}$	0.528	<0.001	0.484

The data were analyzed in their entirety (upper box) and separated into months (lower box)

T40 Mean daily peat temperature at 40 cm (°C), measured at eddy covariance tower, WT water table position (cm), Ev E. vaginatum coverage (%), Mt M. trifolium coverage (%).

DISCUSSION

As has been found many times previously, CH_4 flux from peatlands shows great temporal and spatial variability, with fluxes covering 4 orders of magnitude, from small rates of consumption (-2 mg m^{-2} d^{-1}) to greater than 1 g m^{-2} d^{-1}. It is important to note that the very high fluxes recorded are unlikely to be sustained for long periods and may represent ebullition events of short duration.

Similar to many studies, for example Dise and others (1993), Bubier and others (1995), Huttunen and others (2003) and Treat and others (2007), we have found that vegetation, peat temperature and water table are the primary factors influencing CH_4 emission. Moreover, our analysis shows that their relative importance depends on the time scale of measurements. Using the individual fluxes over the 5 years, vegetation was the most important, followed by peat temperature at 40 cm and water table position, though there is collinearity between the latter two. On a seasonal timescale, water table was the best predictor of seasonal mean CH_4 flux, with peat temperature as the second most important factor. This result differs from a 5-year analysis of CH_4 fluxes from Sallie's Fen (Treat and others 2007), which found that air temperature was the best predictor of mean seasonal CH_4 flux, whereas water table did not improve the model. The contrasting results between these results may, in part, reflect the difference between fen and bog ecosystems.

The main differences between Mer Bleue Bog and Sallie's Fen are associated with the hydrologic, nutrient and plant community distinctions. The water table is higher at Sallie's Fen, averaging from 10 to 30 cm below the peat surface in most years from May through August, compared to 20–50 cm during the same time period at Mer Bleue Bog. However, the water table can also drop significantly at the end of summer at Sallie's Fen, sometimes as low as 80 cm below the peat surface. These low water tables at the fen are associated with some of the largest CH_4 fluxes, resulting in poor correlations between CH_4 flux and water table on a seasonal basis, and a positive correlation with CH_4 flux on daily and monthly timescales. At Mer Bleue, all of our correlations between CH_4 flux and water table at all timescales are negative: lower water tables associated with smaller CH_4 fluxes. Although we would expect higher CH_4 fluxes with wetter conditions, owing to the larger anaerobic zone for CH_4 production and smaller zone of CH_4 oxidation, results at Sallie's Fen and other peatlands (Bellisario and others 1999; Strack and others 2004) suggest that episodic fluxes associated with falling water tables, warmer temperatures and increased pressure gradients can result in high CH_4 emissions. Another difference between the Sallie's Fen and Mer Bleue Bog CH_4 flux studies is that measurements were conducted only during the summer (May through August) at the fen site in

Treat and others (2007), whereas we measured from May through November. In addition to water table position, CH_4 fluxes from peatlands are affected by water table dynamics, such as more CH_4 being emitted when the water table is falling than rising (Moore and Dalva 1993). Declines in atmospheric pressure have also been seen to influence the CH_4 flux (Tokida and others 2007).

Eriophorum vaginatum (cotton grass) is an important control on CH_4 fluxes at Mer Bleue. Several studies have reported the importance of vascular plant enhancement of CH_4 emissions through aerenchymous tissue, and that fluxes associated with sedge biomass are often higher than other plant types (for example, Greenup and others 2000; Tuittila and others 2000; Joabsson and Christensen 2001; Ström and others 2003, 2005; Marinier and others 2004; Koelbener and others 2010). We also found that *E. vaginatum* was the most important correlate of daily CH_4 flux in the autumn months, and a significant factor starting as early as June. This suggests that one of the reasons we observe high CH_4 fluxes into the autumn season at Mer Bleue is the continuing contribution of vascular plant transport and root exudation even when the air and peat temperatures are beginning to decline. Water table also rises in the autumn after the late summer drawdown, coupling the rooting zone of *E. vaginatum* with the zone of CH_4 production. *Maianthemum trifolium* (Solomon's Seal) plays a similar role in raising CH_4 fluxes but, unlike *E. vaginatum*, most of its biomass is belowground, with the aboveground portion senescing in late summer.

Our results also showed that *E. vaginatum* influenced the ability of the peat to consume and produce CH_4, with larger aerobic CH_4 consumption and anaerobic CH_4 production potentials in peat beneath *E. vaginatum* tussocks, than in peat derived from shrub and *Sphagnum* plants. As has been shown elsewhere (for example Moore and Dalva 1997), anaerobic CH_4 production potentials vary widely in peats, reflecting substrate quality and microbial community differences, whereas aerobic CH_4 consumption potentials tend to be less variable. Ström and others (2005) showed that rhizosphere CH_4 consumption was an important control on the effect of vascular plant species on CH_4 emission from a wetland in southern Sweden.

The emission of CH_4 to the atmosphere from peatlands involves several complex processes of production, consumption and transport, which are controlled to some degree by environmental variables such as temperature, water table and vegetation. Although regression analyses, such as ours, show that there are significant statistical relationships between CH_4 flux and the variables, when the range of sites is large and the time of measurement long, the strength of these regressions is not strong. In our case, we were able to explain only 44% of the variance in individual CH_4 flux with the four main variables. Aggregating data, by time or site types, improves the explanatory power.

Despite varying environmental controls, water table is always a key determinant of CH_4 flux in space and time. Hence, long-term behavior of the water table is likely to have important implications for wetland-atmosphere CH_4 flux. In this context, variation in precipitation should be linked to peatland CH_4 fluxes, through a strong control on water table height. Yet our measurements show there is no significant relation ($P = 0.20$) between average water table position and the total precipitation (May–October) over the 11 years of record (Figure 8A). The measurements do show an overall rise in the May to October average water table depth from −46 cm during the period 1998–2003 to −39 cm in the period 2004–2008, with a significant difference between the two periods ($P = 0.05$, two-tailed *t*-test). The cause of this apparent step change in water table can be traced to the removal and then reappearance of *Castor canadensis*, the Canadian beaver, in the perimeter of Mer Bleue. In 1998–2000, the National Capital Commission, which manages Mer Bleue, removed beavers from the ponds on the western perimeter of the northwest arm of Mer Bleue, where the eddy covariance tower is located allowing the water table to fall to naturally lower levels. Beavers reestablished themselves around 2005 and their dams raised average water tables. In addition to the rise in the average May to October water table position, there have also been changes in the frequency distribution of daily water table depth (Figure 8B). The early years (1998–2003) were characterized by hummock water table positions lower than −55 cm for 2 or more months each year, whereas in the later years (2004–2008), the water table never fell beneath −50 cm for more than a few days.

The inter-annual variation in seasonal (May–October) average water table position is small (16 cm for the 1998–2003 period), yet interannual differences are largely driven by late summer water table differences, which can be more than 25 cm (Figure 3A). This can, however, have a profound effect on the emission of CH_4, as it occurs at a time when the peatland is warmest, reducing peat profile CH_4 production rates and resulting in significant inter-annual variability in CH_4 fluxes (Figure 2). In a northern Manitoba wetland complex, Bubier and others (2005) showed that a small

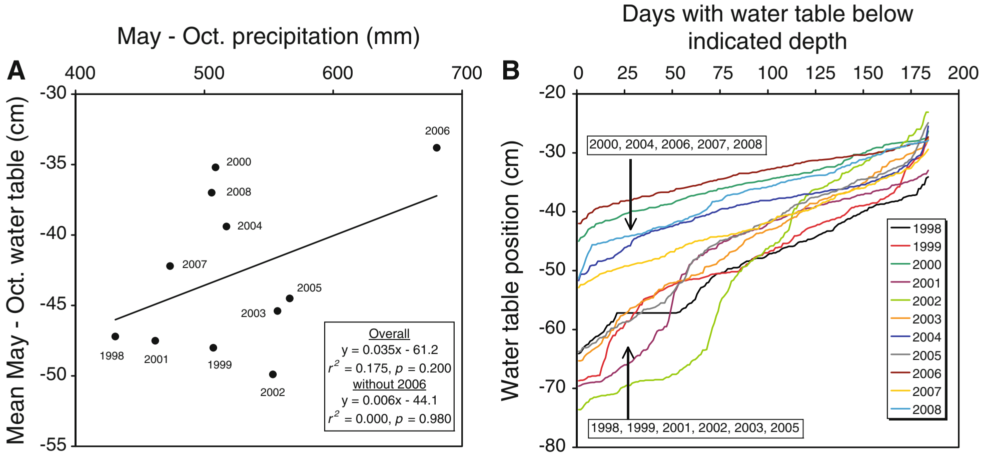

Figure 8. Relationship between May to October precipitation and average water table position in the tower hummock, 1998–2008 (**A**) and frequency distribution of water table position for these years (**B**).

rise in water table (an average of 2–5 cm) between years resulted in a 60% increase in CH_4 emission. Nisbet (1989) estimated that beaver populations were near extinction in Canada in the 1930s and 1940s but have increased five-fold since then. The raising of water levels associated with increased beaver populations may have had a significant effect on CH_4 fluxes from peatlands adjacent to ponds, as well as on the emission from beaver ponds themselves (for example, Dove and others 1999; Billett and Moore 2008).

Dividing the Mer Bleue collars into hummock, lawn and *E. vaginatum* categories (Table 1) allows us to estimate the May to November emission of CH_4. These range from 2004 to 2007 from 1.9 to 8.3 g CH_4 m^{-2} for hummocks, 8.7 to 26.5 g CH_4 m^{-2} for lawns to 11.6 to 76.8 g CH_4 m^{-2} for *E. vaginatum*. Hummocks dominate the bog section of Mer Bleue (~70% coverage) with *E. vaginatum* occupying only a small proportion (~1.5% coverage from air photography and ground truthing in the section near the CH_4 measurements and eddy covariance tower; M. Kalacska and P. Arroyo, McGill University, personal communication). Assigning the overall CH_4 flux into these categories and areal coverage, May to November flux from the peatland as a whole for 2004–2008 ranges from 4.0 to 23.1 g CH_4 m^{-2}. To this could be added another 1–2 g CH_4 m^{-2} representing winter fluxes (see Dise 1992; Melloh and Crill 1996) suggesting a total annual flux of 5–25 g CH_4 m^{-2} y^{-1}.

Roulet and others (2007) estimated the annual C balance of Mer Bleue Nov. 1–Oct. 31 over 6 years (1998–1999 to 2003–2004) using eddy covariance data for NEE, estimated CH_4 emission based on data shown in Figure 1A and on estimated water export of DOC. They reported NEE ranging from −2 to −112 g m^{-2} y^{-1}, with an average of −40 g m^{-2} y^{-1}, whereas CH_4–C emission ranged from 2.8 to 4.4 g m^{-2} y^{-1}, with an average of 3.7 g m^{-2} y^{-1}. Since 2004–2005, under the generally wetter conditions, the NEE values have been larger, ranging from −91 to −148 g m^{-2} y^{-1}, with an average of −112 g m^{-2} y^{-1}. Based on Roulet and others (2007) the CH_4 flux returned a mass of carbon to the atmosphere equivalent to approximately 9% of NEE, but for the years post 2004–2005, between 3 and 16% of the C equivalent to NEE has been returned to the atmosphere as CH_4. Although the increase in CO_2–C uptake is greater than the increase in CH_4–C emission in wet years, the differences in the global warming potentials between the two gases affect the impact on radiative forcing (Frolking and Roulet 2007).

Although there is an inverse correlation between the annual NEE and the average May to October water table position from 1998–1999 to 2008–2009 and 2004–2005 to 2008–2009 ($r^2 = 0.41$, $P = 0.03$, $n = 11$ and $r^2 = 0.99$, $P = 0.00$, $n = 5$, respectively), the estimated annual CH_4 flux for 2004–2005 to 2008–2009 was not significantly correlated with the average May to October water table position ($r^2 = 0.32$, $P = 0.32$, $n = 5$). Although average water table position is an important correlate of many biogeochemical processes in wetlands, variations in the frequency distribution and timing of the water table and other factors affect CH_4 flux.

CONCLUSIONS

In a bog typical of many in northern environments, we have shown the strong spatial and temporal variability in CH_4 flux, over the snow-free season of 5 years. These variations in flux can be related to several environmental and ecological variables, including temperature, water table position, vegetation and the ability of the substrate to produce and consume CH_4. The nature and strength of the relationship between the CH_4 flux and these variables depend on the spatial and temporal range of the observations examined. For example, water table is important when comparing among sites over long periods and temperature relates to the overall seasonal pattern. Vegetation, such as sedges, also enhances CH_4 flux, though their effect is dependent on their phenology. Although the strength of the relationships improve as data are aggregated, on an individual flux measurement basis, less than half of the variance in log-transformed CH_4 flux can be explained by simple environmental correlates. Our results also show that in addition to variations in precipitation, water table can be affected by external controls, such as peripheral beaver dams, which can profoundly affect CH_4 fluxes. The results confirm the complexity of CH_4 fluxes, being dependent on rates of CH_4 production and consumption and a variety of transport mechanisms.

ACKNOWLEDGEMENTS

We thank David Brodkey, Hélène Lesage, Michael Wironen, and especially Mike Dalva for their help in the field and laboratory, and Margaret Kalacska and Pablo Arroyo for estimating cotton grass coverage. We are grateful to the National Capital Commission for their logistic help and permission to use Mer Bleue and to the Associate Editor and an anonymous reviewer for their helpful comments. This work has been supported primarily by a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Mer Bleue facility has also received support from NSERC, the Canadian Foundation for Climate and Atmospheric Sciences and BIOCAP Canada, through the Fluxnet Canada Research Network and the Canadian Carbon Program.

REFERENCES

Baird AJ, Belyea LR, Morris PJ. 2009. Upscaling peatland-atmosphere fluxes of carbon gases: small-scale heterogeneity in process rates and the pitfalls of 'bucket-and-slab' models. In: Baird AJ, Belyea LR, Comas X, Reeve A, Slater L, Eds. Northern peatlands and carbon cycling. Washington DC, USA: American Geophysical Union. pp 37–54.

Bellisario LM, Bubier JL, Moore TR, Chanton JP. 1999. Controls on CH_4 emissions from a northern peatland. Glob Biogeochem Cycles 13:81–91.

Billett MF, Moore TR. 2008. Supersaturation and evasion of CO_2 and CH_4 in surface waters at Mer Bleue peatland, Canada. Hydrol Proc 22:2044–54.

Bubier J. 1995. The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. J Ecol 83:403–20.

Bubier J, Moore TR, Roulet NT. 1993. Methane emissions from wetlands in the boreal region of northern Ontario, Canada. Ecology 74:2240–54.

Bubier JL, Moore TR, Bellisario L, Comer N, Crill P. 1995. Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. Glob Biogeochem Cycles 9:455–70.

Bubier J, Moore T, Savage K, Crill P. 2005. A comparison of methane flux in a boreal landscape between a dry and a wet year. Glob Biogeochem Cycles 19:GB1023. doi:10.1029/2004GB002351.

Bubier J, Moore TR, Crosby G. 2006. Fine-scale vegetation distribution in a cool temperate bog. Can J Bot 84:910–23.

Clymo RS, Reddaway EJF. 1971. Productivity of *Sphagnum* (bog-moss) and peat accumulation. Hydrobiologia 12:81–192.

Dalva M, Arp P, Moore TR, Clair TA. 2001. Methane and carbon dioxide emissions from wetlands, Kejimkujik National Park, Nova Scotia: measurements, predictions and climatic change. J Geophys Res 106:2955–2962.

Dise NB. 1992. Winter fluxes of methane from Minnesota peatlands. Biogeochem 17:71–83.

Dise NB, Gorham E, Verry ES. 1993. Environmental factors controlling methane emissions from peatlands in Northern Minnesota. J Geophys Res 98:10,583–94.

Dove A, Roulet N, Crill P, Chanton J, Bourbonniere R. 1999. Methane dynamics of a northern boreal beaver pond. Ecoscience 6:577–86.

Frolking S, Roulet NT. 2007. Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. Glob Change Biol 13:1079–88.

Greenup AL, Bradford MA, McNamara MP, Ineson P, Lee JA. 2000. The role of *Eriophorum vaginatum* in CH_4 flux from an ombrotrophic peatland. Plant Soil 227:265–72.

Harriss RC, Sebacher DI, Day FP. 1982. Methane flux in the Great Dismal Swamp. Nature 297:673–4.

Huttunen JT, Nykänen H, Turunen J, Martikainen PJ. 2003. Methane emissions from natural peatlands in the northern boreal zone in Finland, Fennoscandia. Atmospheric Environ 37:147–51.

ISI Web of Science. Topic = (methane flux OR methane emission OR methane exchange) AND Topic = (peatland* OR bog* OR fen* OR swamp* OR wetland*). Accessed 19-7-10.

Joabsson A, Christensen TR. 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. Glob Change Biol 7:919–32.

Koelbener A, Ström L, Edwards PJ, Olde Venterink H. 2010. Plant species from mesotrophic wetlands cause relatively high methane emissions from peat soils. Plant Soil 326:147–58.

Liblik L, Moore TR, Bubier JL, Robinson SD. 1997. Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, NWT, Canada. Glob Biogeochem Cycles 11:485–94.

Marinier M, Glatzel S, Moore TR. 2004. The role of cotton-grass (*Eriophorum vaginatum*) in CO_2 and CH_4 fluxes from restored peatlands, eastern Canada. Écoscience 11:141–9.

Melloh RA, Crill PM. 1996. Winter methane dynamics in a temperate peatland. Glob Biogeochem Cycles 10:247–54.

Moore TR, Dalva M. 1993. The influence of temperature and water table position on methane and carbon dioxide emissions from laboratory columns of peatland soils. J Soil Sci 44:651–64.

Moore TR, Dalva M. 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. Soil Biol Biochem 29:1157–64.

Moore TR, Heyes A, Roulet NT. 1994. Methane emissions from wetlands, southern Hudson Bay lowland. J Geophys Res 99:1455–68.

Moore T, Bubier J, Lafleur P, Frolking S, Roulet N. 2002. Plant biomass, production and CO_2 exchange in an ombrotrophic bog. J Ecol 90:25–36.

Nisbet EG. 1989. Some northern sources of atmospheric methane: production, history, and future implications. Can J Earth Sci 26:1603–11.

Nykänen H, Alm J, Silvola J, Martikainen P. 1995. Fluxes of methane on boreal mires with different hydrology and fertility in Finland. In: Laiho R, Laine J, Vasander H, Eds. Northern peatlands in global climate change, proceedings of the international workshop held in Hyytiälä, Finland. Helsinki: Academy of Finland. p 127–35.

Pelletier L, Moore TR, Roulet NT, Garneau M, Beaulieu-Audy V. 2007. Methane fluxes from three peatlands in the La Grande Rivière watershed, James Bay lowland, Canada. J Geophys Res Biogeosci 112:G01018. doi:10.1029/2006JG000216.

Roulet NT, Ash R, Moore TR. 1992. Low boreal wetlands as a source of atmospheric methane. J Geophys Res 97:3739–49.

Roulet NT, Lafleur PM, Richard PJH, Moore TR, Humphreys ER, Bubier JL. 2007. Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. Glob Change Biol 13:397–411.

Rouse WR, Holland S, Moore TR. 1995. Methane emissions from wetlands in the Churchill region. Arct Alp Res 27:146–56.

Strack M, Waddington JM, Tuittila ES. 2004. Effect of water table drawdown on northern peatland methane dynamics: implications for climate change. Glob Biogeochem Cycles 18:GB4003. doi:10.1029/2003GB002209.

Ström L, Ekberg A, Mastepanov M, Christensen TR. 2003. The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Glob Change Biol 9:1185–92.

Ström L, Mastepanov M, Christensen TR. 2005. Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. Biogeochemistry 75:65–82.

Svensson BH. 1980. Carbon dioxide and methane fluxes from the ombrotrophic parts of a subarctic mire. Ecol Bull (Stockholm) 30:235–50.

Tokida T, Miyazaki T, Mizoguchi M, Nagata O, Takakai F, Kagemoto A, Hatano R. 2007. Falling atmospheric pressure as a trigger for methane ebullition from peatland. Glob Biogeochem Cycles 21:GB2003. doi:10.1029/2006GB002790.

Treat CC, Bubier JL, Varner RK, Crill PM. 2007. Timescale dependence of environmental and plant-mediated controls on CH_4 flux in a temperate fen. J Geophys Res Biogeosci 112:G01014. doi:10.1029/2006JG000210.

Tuittila ES, Komulainen VM, Vasander H, Nykänen H, Martikainen PJ, Laine J. 2000. Methane dynamics of a restored cutaway peatland. Glob Change Biol 6:569–81.

Walter B, Heimann M. 2000. A process-based, climate-sensitive model to derive methane emissions from natural wetlands: application to five wetland sites, sensitivity to model parameters, and climate. Glob Biogeochem Cycles 14:745–65.

Whalen SC. 2005. Biogeochemistry of methane exchange between natural wetlands and the atmosphere. Environ Eng Sci 22:73–94.