Temperature Sensitivity of Methane Production in the Permafrost Active Layer at Stordalen, Sweden: A Comparison with Non-permafrost Northern Wetlands

Authors: Lupascu, M., Wadham, J. L., Hornibrook, E. R. C., and Pancost, R. D.

Source: Arctic, Antarctic, and Alpine Research, 44(4) : 469-482

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1938-4246-44.4.469

Arctic, Antarctic, and Alpine Research, Vol. 44, No. 4, 2012, pp. 469–482

Temperature Sensitivity of Methane Production in the Permafrost Active Layer at Stordalen, Sweden: a Comparison with Non-permafrost Northern Wetlands

M. Lupascu§#*
*J. L. Wadham**
E. R. C. Hornibrook† and
R. D. Pancost‡

*Bristol Glaciology Centre, University Road, Bristol, BS8 1SS, University of Bristol, U.K.
†Bristol Biogeochemistry Research Centre *and* Cabot Institute, School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1RJ, U.K.
‡School of Chemistry, University of Bristol, Cantock's Close, Bristol, BS8 1TS, U.K.
§Present address: Department of Earth System Science, University of California, Croul Hall. Irvine, California 92697-3100, U.S.A.
#Corresponding author: mlupascu@uci.edu

Abstract

Relationships were determined between methane (CH_4) production and *in situ* conditions within the permafrost active layer during a single melt season at Stordalen, Sweden, with a specific emphasis on temperature sensitivity of methanogenesis. *In situ* temperature, moisture, pH, dissolved organic carbon, and CH_4 concentration data were measured at three contrasting active layer sites (sedge mire, *Sphagnum* mire, and ombrotrophic bog), and laboratory incubations of active layer material were subsequently employed to determine the sensitivity of CH_4 production to temperature. Q_{10} values, describing the CH_4 production response of peat to a temperature change of 10 °C, ranged from 1.9 to 3.5 and 2.4 to 5.8 for the sedge and *Sphagnum* mire sites, respectively. A wider review of the literature on Q_{10} responses of methanogenesis in northern peatlands shows similar features to the temperature response of CH_4 production in the active layer at Stordalen. In general, Q_{10} values are not significantly different in Arctic permafrost wetlands than non-Arctic northern wetlands; however, *Sphagnum* sites display Q_{10} responses (mean $Q_{10} = 8$) that are notably greater than that of wetter minerotrophic-sedge environments (mean $Q_{10} = 4.3$). This finding has implications for the parameterization of Q_{10} factors in numerical carbon cycling models, and suggests that the use of spatially variable Q_{10} values could be a useful approach for more accurate modeling of CH_4 fluxes from northern wetlands under different climatic change scenarios.

DOI: http://dx.doi.org/10.1657/1938-4246-44.4.469

Introduction

Mean annual Arctic air temperatures have increased at almost twice the rate of the global average during the past 100 years (IPCC, 2007). Future climatic projections suggest that the mean annual air temperature will increase by 2.2 to 3.2 °C in the 60 to 90°N latitudinal zone by 2050, with the potential for significant effects on terrestrial ecosystem processes and carbon cycling. Of particular concern is the impact of such temperature increases on Arctic tundra carbon reserves (Callaghan et al., 2005; Chapin et al., 2005).

Since the last glaciation, organic soils (peatlands) and cryoturbated permafrost-affected mineral soils in the northern permafrost region have accumulated 1600 Pg of C (10^{15} g) due to the sequestration of organic matter (Tarnocai et al., 2009). The fate of these carbon reserves in Arctic tundra regions depends upon rates of aerobic and anaerobic microbial decomposition of organic matter (OM) in the seasonally thawed ''active layer.'' Rates of decomposition are critically dependent on both hydrology and temperature (Christensen, 1991; Gorham, 1991; Hargreaves and Fowler, 1998); whereas dry conditions lead to predominantly aerobic decomposition producing CO_2, waterlogged conditions promote slower decomposition yielding the more potent greenhouse gas CH_4 (as well as CO_2) (Callaghan et al., 2005). Soil temperature is known to have an effect on rates of these microbial processes (Anderson, 1992; Schimel et al., 1993). Although CH_4 budget estimates change year to year, the most recent models of Wania et al. (2010) and Petrescu et al. (2010) for northern peatlands (45–90°N), account for 40–74 Tg CH_4 yr^{-1} and for 37.7–157.4 Tg CH_4 yr^{-1}, respectively, of the total 190–220 Tg CH_4 yr^{-1} from natural sources (IPCC, 2007).

Methane production results from the interaction of different biological and physical processes in the soil (Hogan, 1993; Schimel et al., 1993; Conrad, 1989; Bouwman, 1990; Wang et al., 1996) where decomposition of organic matter takes place under anaerobic conditions. The final step in the process of anoxic decomposition of complex organic matter is methanogenesis (Conrad, 1999) where the main substrates are hydrogen (Equation 1) or acetate (Equation 2).

$$CO_2 + 4H_2 \rightarrow CH_4 + H_2O \quad (1)$$

$$CH_3COO^- + H_2O \rightarrow CH_4 + HCO_3^- \quad (2)$$

Major process-level controls upon CH_4 production in wetland ecosystems are: pH, temperature (Valentine et al., 1994), and substrate quantity and quality (Bridgham and Richardson, 1992; Valentine et al., 1994). Ecosystem-level controls include the presence of water, and the position of the water table (Harriss et al., 1982), and plant composition (Waddington et al., 1996; Bellisario et al., 1999). Controls on CH_4 production in temperate and northern peatlands are well documented (Bergman et al., 2000; Dunfield et al., 1993; Le Mer and Roger, 2001; Segers, 1998; Svensson, 1984), but there is disproportionately less information on the spatial and temporal variation of these controls (especially with respect to soil temperature) in Arctic permafrost environments (Christensen et al., 2003, 2004; Valentine et al., 1994). In addition, most studies derive associations between temperature and CH_4 production from sea-

1523-0430/6 $7.00

sonal field data sets where many other environmental variables also were changing. Few attempts have been made to conduct controlled laboratory experiments to determine the sensitivity of CH_4 production in permafrost wetlands to changing soil temperature (Brouchkov and Fukuda, 2000; Metje and Frenzel, 2005, 2007; Rivkina et al., 2007; Svensson, 1984; Wagner et al., 2003, 2005, 2007), and no studies have compared the sensitivity for methanogenesis in the permafrost active layer to the range of Q_{10} in northern peatlands more generally. This paper aims to assess the variation in the controls of the CH_4 concentration and production in the permafrost active layer of three contrasting peatlands located in a low Arctic discontinuous permafrost environment in northern Sweden. Through a comparison of our own experimental incubations data and those derived from previous studies, we investigate in detail the potential effect of temperature increase on CH_4 production rates in the organic matter rich soils of permafrost and non-permafrost northern wetlands.

Materials and Methods

STUDY SITE

Fieldwork was conducted in Stordalen mire, 10 km southeast of Abisko (68°21′N, 18°49′E) in northern Sweden. The site is 25 ha in area and situated ~200 km north of the Arctic Circle and 385 m a.s.l. on the south shore of Lake Torneträsk (Fig. 1). It is characterized by discontinuous permafrost with small (~2 m) variations in topography. The small-scale topography gives rise to three types of peatland environments that differ in their nutrient and moisture conditions (Rosswall et al., 1975; Sonesson, 1969; Johansson et al., 2006). These three environments formed the focus for this study and are:

(a) Minerotrophic-sedge mire in which water and ion inputs derive from precipitation, surface water, and groundwater sources, leading to a relatively high soil pH and nutrient status. The dominant plant species in this wet mire is *Eriophorum angustifolium* Hock., but with considerable areas of *Sphagnum riparium* Ångst. The mire was not underlain by permafrost at the time of sampling, but the ground surface freezes and thaws seasonally. Fully thawed conditions usually prevail by mid-June.

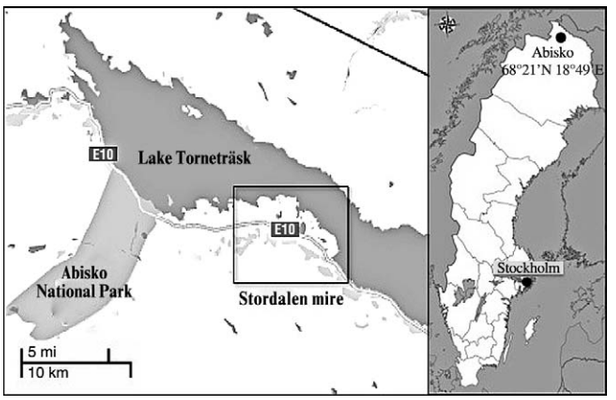

FIGURE 1. Stordalen field site location at Abisko, northern Sweden.

(b) Minerotrophic-*Sphagnum* mire, which is dominated by *Sphagnum* spp. It is underlain by permafrost, with a variable summer active layer depth. The active layer depth in summer 2006 was 22 cm (June) and ~90 cm in August and September.

(c) Ombrotrophic bog, which receives water and associated ions solely from the atmosphere, usually because the accumulation of soil organic matter has caused hydrologic isolation from groundwater inputs, resulting in low soil pH and low nutrient status. The vegetation is dominated by ericaceous and other woody species such as *Rubus chamaemorus* L., *Empetrum hermaphroditum* Hagerup., and *Andromeda polifolia* L. (Johansson et al., 2006). The upper part of the permafrost thaws during summer forming an active layer of variable thickness. Average active layer depths recorded in summer 2006 were 22 cm (June), 32 cm (August), and 53 cm (September).

These three sub-habitats are hereafter designated as sedge (or *Eriophorum*) mire, *Sphagnum* mire, and ombrotrophic sites.

SAMPLING AND IN SITU MEASUREMENTS

Field sampling was conducted at the sedge, *Sphagnum*, and ombrotrophic sites during the summer thaw period in 2006 (from 12 to 21 June, 1 to 8 August, and 18 to 25 September). The coring sites were located within a 50 m^2 area that represented the three typical vegetation covers of the area: *Eriophorum angustifolium* dominated at the minerotrophic sedge site, *Sphagnum* for the other minerotrophic site, and ericaceous and other woody species for the ombrotrophic bog. Two cores (A and B) were collected at each site using a 60 cm (length) × 15 cm (diameter) cm metal manual peat corer. Water table level and active layer depth were recorded prior to coring using a graduated metal rod. Immediately following core extraction, the temperature of the peat was measured in the soil profile using a Hanna Check Temperature probe (resolution = 0.1 °C; accuracy = ± 0.3 °C), and soil moisture was measured using a delta T HH2 Theta Probe (accuracy = 1 to 5%). Once collected, cores were wrapped in pre-combusted (450 °C for 4.5 h) aluminum foil.

Core Subsampling and Analysis

Cores A and B from each site were subsampled at six depths. The subsampling interval depended on the core length, which was between 22 to 50 cm. Each core section was ~10 cm in diameter and 4 cm long.

Core A was retained for analysis in Abisko and was subsampled in the laboratory within a few hours of collection for (a) pore water nutrient analysis, (b) pH measurement, (c) dissolved CH_4 concentration, and (d) subsequent CH_4 production rate incubations. Pore water pH was measured in the laboratory on core subsample slurries using an Orion 250 A pH meter (resolution: 0.01/0.1 pH; accuracy: ±0.02). A ~2 cm diameter core was removed from each section using a metal mini-corer. Each mini-core (including 3 replicate samples for each depth) was placed in a 35 mL serum vial for CH_4 concentration and production analyses. Our aim was to minimally disturb the peat to avoid outgassing of CH_4 or entry of O_2 that might impact methanogen populations. We did not attempt to remove living roots that were present in the mini-cores, with the exception of the largest ones that could be eliminated

without damage to the peat structure. The presence of severed roots in the peat may have provided labile carbon to support methanogenesis; however, under *in situ* conditions these roots also would have been releasing exudates that are readily metabolized by methanogens. Consequently, minimizing CH_4 outgassing and entry of O_2 were given priority because their impact on the incubation results was deemed to be potentially more detrimental.

Pore water was extracted from soil subsamples by centrifugation (2000 rpm) using ~75 cm^3 of peat in Fisher Vectaspin 20 centrifuge tubes. The water supernatant was filtered immediately through Whatman glass microfibre GF/F filters (pore size = 0.7 μm). The filtrate was subsequently frozen until analysis in the U.K.

Each core B was wrapped in combusted Al foil and stored at −15 °C immediately after collection. Samples were transported to the U.K. encased in plastic pipes and then stored at −20 °C prior to analysis.

Analytical Laboratory Methods

Elemental Analysis. The elemental compositions (C, H, and N) of freeze-dried subsamples from core B were measured using a Carlo Erba EA1108 Elemental Analyser (accuracy ±0.3%). Each analysis was conducted in triplicate.

Pore Water Chemistry Analyses. Pore water filtrate was thawed at room temperature and nutrients (NH_4^+, NO_3^-, NO_2^-, and Soluble Reactive Phosphorus [SRP]) and Si were determined colorimetrically using a Bran and Luebbe AutoAnalyser 3. Detection limits were 0.6 g L^{-1} for NH_4^+, 0.2 g L^{-1} for NO_3^-, 0.04 g L^{-1} for NO_2^-, 0.5 g L^{-1} for SRP, and 0.8 g L^{-1} for Si. Non-Purgeable Organic Carbon (NPOC) and Total Dissolved Nitrogen (TDN) in the samples were determined using a Shimadzu TOC-VCSN/TNM-1 analyzer. NPOC was measured as the carbon remaining after acidification with 2M HCl and sparging with He for 2 min. Six replicate injections were made per sample. Acidified and sparged deionized water samples were used as blanks. Detection limits were 1.2 mg L^{-1} for DOC and 0.1 mg L^{-1} for TDN. Dissolved Organic Nitrogen (DON) was calculated as [TDN] − [DIN], where [DIN] = [NH_4^+] + [NO_3^-] + [NO_2^-]. Data are not available for June samples due to vial breakage during transport.

Dissolved CH_4 Concentrations and CH_4 Production

Dissolved CH_4 Concentrations. Core subsamples, including fragments of small plant roots, collected from 6 depths (3 replicates each) from the three sites were placed in 35 mL serum vials with 20 mL of a 10% KCl solution acidified with HCl to pH 1. Vials were stored at 4 °C at the Abisko research station before departure to the U.K. and were kept cold during transport. The vial headspace gas, representing the dissolved CH_4 in sediment porewater, was analyzed in the U.K. using a CarloErba HRGC 5300 Mega Series Gas-Chromatograph (GC) fitted with a flame ionization detector (FID). The GC was equipped with a 2 m Porapak QS (80/100 mesh) column at oven temperature of 35 °C. The carrier gas was helium (flow rate = 35 mL min^{-1}) and the support gases (H_2 and zero air) were set at flow rates of 35 and 350 mL min^{-1}, respectively.

Methane Production. Core subsamples were placed in 35 mL serum vials within a few hours of core collection and flushed with oxygen-free nitrogen. Large root fragments were removed during the subsampling. Vials were stored in the dark at 4 °C in Abisko for a few days and kept refrigerated with ice during transportation to the U.K. Once in Bristol the samples were stored in an incubator at 4 °C. Samples from the 3 different sites (6 depths each) were subsequently incubated sequentially at 4, 14, and 24 °C. In the choice of this specific methodology we assume that the effect of the incubation sequence does not affect the reliability of CH_4 production rates because the predominant substrate for methanogenesis should be the labile fraction of organic matter. It has been shown elsewhere that in short duration sequential incubations of peat, the age of respired carbon does not change with time and temperature (Dioumaeva et al., 2002).

The headspace gas was sampled (50 μL) by syringe after 1, 2, and 3 days, respectively, for the three different temperatures. CH_4 concentration was determined by gas chromatography as described already. June samples were incubated only at 4 °C due to instrumentation problems.

Data Analysis: Q_{10} Values and Other Biological Coefficients

Methane production data were corrected for peat moisture content after having calculated the natural water content of the samples. Values are reported as μg CH_4 per gram (g^{-1}) of dry peat per day (d^{-1}). Linear regression analyses of the change in CH_4 concentration with time were performed to determine differences in the methanogenic production potential of the peat at different depths.

Biological coefficients were subsequently calculated as follows. The Q_{10} value (Equation 3) is a temperature coefficient that measures the rate of change of a biological or chemical system as a consequence of increasing a temperature change of 10 °C.

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2 - T_1}\right)} \tag{3}$$

where R_1 and R_2 are the rates of methane production (μg g^{-1} d^{-1}) at temperatures T_1 and T_2, respectively, where T is the temperature in °C or Kelvins. An R_0 value is the extrapolated production rate at 0 °C ($R_0 = R/Q_{10}^{T/10}$) and does not take into account the possibility of 'on' vs. 'off' in the metabolism of microorganisms. Calculation of the parameter assumes a gradual decrease in metabolic rate at low temperature.

The apparent Activation Energy (E_a; kJ mol^{-1}) is the minimum energy necessary for a specific chemical reaction to occur (Equation 4) and is calculated as:

$$E_a = [1n(Q_{10}) \circ R \circ T_1 \circ T_2] \circ 10^{-1} \quad \text{(Chapman and Thurlow, 1998),} \tag{4}$$

where Q_{10} is the temperature coefficient (described above), R is the production rate (μg g^{-1} d^{-1}), and T_1 and T_2 are the temperatures in °C.

Results

FIELD MEASUREMENTS

During the three-month study period both the minerotrophic sites were waterlogged, and the water table level in each was close

TABLE 1

pH and temperature values for the three different sites and months.

	Sedge site			*Sphagnum site*			*Ombrotrophic bog*		
	Depth	*Temp*	*pH*	*Depth*	*Temp*	*pH*	*Depth*	*Temp*	*pH*
	0	5	5.98	**0**	4.8	4.41	**0**	5.2	4.02
	5	4.2	5.85	**5**	3.4	4.30	**5**	5.5	4.23
June	**10**	2.5	5.72	**10**	2.8	4.40	**10**	4.2	4.11
	15	2.3	5.54	**15**	2.8	4.16	**15**	3.0	4.17
	20	1.8	5.76	**20**	2.5	3.95	**20**	0.8	4.12
	0	17.4	5.60	**0**	16.2	4.28	**0**	14.5	4.23
	5	17.3		**5**	13.7		**5**	13.2	
	10	13.7	5.63	**10**	13.5	4.17	**10**	11.3	4.19
	15	12.9		**15**	13.1		**15**	8.5	3.94
	20	12.2	5.51	**20**	11.4	4.13	**20**	6.4	
August	**25**	12.5	5.50	**25**	12.3		**25**	6.1	3.85
	30	10.4		**30**	11.8	4.05	**30**	4.8	3.95
	35	11.5	5.64	**35**	10.9	4.12	**33**	4.0	4.18
	40	10.4		**40**	9.6		**40**	6.1	
	45	13.6	5.76	**45**	9.2	4.19			
	0	9.2	5.58	**0**	6.8	4.14	**0**	3.7	4.02
	5	8.8		**5**	6.3		**5**	3.5	
	10	8.7	5.39	**10**	6.4	4.11	**10**	3.2	4.15
	15	8.7		**15**	5.9	4.08	**15**	3.1	4.19
September	**20**	8.4	5.62	**20**	6.7		**20**	1.8	
	25	8.2	5.49	**25**	6.2	4.05	**25**	1.0	3.81
	30	8.0		**30**	6.1	4.13	**30**	1.3	4.09
	35	8.2	5.84	**35**	5.6		**33**	1.3	
	40	8.5	5.47	**40**		4.31	**40**	1.2	4.79
	45	8.2		**45**					

to the surface (~2 cm depth). In contrast, the ombrotrophic bog was relatively dry [moisture = 20 (top 20 cm) to 50 (40–50 cm)%] with no obvious water table within the upper 50 cm. In June, only the upper 20 cm of soil was thawed at all three sites. In August and September, the sedge and *Sphagnum* sites were permafrost free and the ombrotrophic bog active layer depths were 32 and 53 cm, respectively. Mean soil temperatures along the soil profile for all sites on the days of core collection were 3.4 ± 1.4 °C, 11.3 ± 3.2 °C, and 5.7 ± 2.8 °C in June, August, and September, respectively (Table 1). The difference between the surface and deeper temperatures was more evident in August where the variation was ~7 °C over 45 cm depth range (e.g. *Sphagnum* site). Pore water pH was relatively constant (within 0.2 units) with depth at each site (Table 1). The pH of pore water at the minerotrophic *Sphagnum* mire (mean 4.2 ± 0.1) and ombrotrophic bog (mean pH = 4.1 ± 0.2) were lower than that of the sedge mire (mean pH = 5.6 ± 0.2).

ELEMENTAL ANALYSIS AND NUTRIENT CHARACTERIZATION

Soil Samples

The sedge (Fig. 2, part a) and *Sphagnum* mires (Fig. 2, part b) displayed relatively constant soil Total Organic Carbon (TOC) contents with depth (240 ± 14 to 590 ± 22 mg g^{-1}) and exhibited little variation between sampling periods. The ombrotrophic bog displayed similar values for TOC concentration in the upper soil profile (<25 cm) for June and August but below 25 cm there was a decrease in percent TOC with depth (Fig. 2, part c). The September samples showed a sharp decrease in percent TOC at 15 cm of depth. Total Nitrogen (TN) concentrations at all sites ranged from 9 ± 4 to 25 ± 4 mg g^{-1}. There are few well-defined trends in TN, but soil TN concentrations in the *Sphagnum* and *Eriophorum* mires tended to be higher in June and September. In the ombrotrophic bog (Fig. 2, part c), TN generally increased in concentration with depth and through the thaw season.

Pore Water Samples

Non-Purgeable Organic Carbon (NPOC), Total Nitrogen (TN), and Total Organic Nitrogen (TON) exhibited high down-profile variability in the sedge and *Sphagnum* spp. sites (Fig. 2, parts a and b). Concentrations of TN and NPOC were generally higher in June (1.2 ± 0.2 to 3.7 ± 0.2 mg L^{-1} for TN and 21 ± 3 to 200 ± 13 mg L^{-1} for NPOC) than in August (1.0 ± 0.1 to 2.5 ± 0.1 mg L^{-1} for TN and 19 ± 3 to 164 ± 13 mg L^{-1} for NPOC) and September (1.0 ± 0.2 to 2.6 ± 0.1 mg L^{-1} for TN and 23 ± 12 to 122 ± 14 mg L^{-1} for NPOC).

There was comparatively little variation in dissolved species with depth and between sampling periods in the ombrotrophic bog (Fig. 2, part c) other than an increase in NPOC in the upper 10 cm of the core in all three sampling periods (mean NPOC at 5 cm = 137 ± 24 mg L^{-1}).

METHANE CONCENTRATIONS

The highest concentrations of CH_4 were recorded in the sedge (Fig. 3, part a) and *Sphagnum* sites (Fig. 3, part b) with mean values ranging from 13 ± 5 to 153 ± 69 μmol L^{-1} and 13 ± 16 to 160 ± 103 μmol L^{-1}, respectively. The pore water concentrations of CH_4 decreased from June to August and then increased in September. Methane concentrations generally increased with depth (Fig. 3, parts a and b) during each sampling period, and the position of the CH_4 concentration maxima tended to shift down the soil profile as the size of the active layer increased at both these sites.

The ombrotrophic bog (Fig. 3, part c) displayed much lower CH_4 concentrations (<6 μmol L^{-1}) during all sampling periods and at all depths. The deepest sample (30–35 cm) contained a slightly higher CH_4 concentration (~14 μmol L^{-1}) in August and September.

METHANE PRODUCTION

The temperature sensitivities of CH_4 production at the three main sites and at different depths in the soil profile are shown in Figures 4 and 5. Incubation of peat subsamples in the absence of oxygen demonstrated that CH_4 production rates vary with temperature, peatland type, and soil depth. In general, the response of CH_4 production to an increase in temperature was strongest in the sedge mire, followed by the *Sphagnum* site. In the former, the average CH_4 production rate at 14 °C was 27 ± 22 μg d^{-1} g^{-1} compared with 48 ± 44 μg d^{-1} g^{-1} at 24 °C (Fig. 5, parts a and b). Incubations of ombrotrophic bog samples produced only a few μg d^{-1} g^{-1} of CH_4 and there was no significant change in CH_4 production rate with an increase in temperature (Fig. 5, parts e and f).

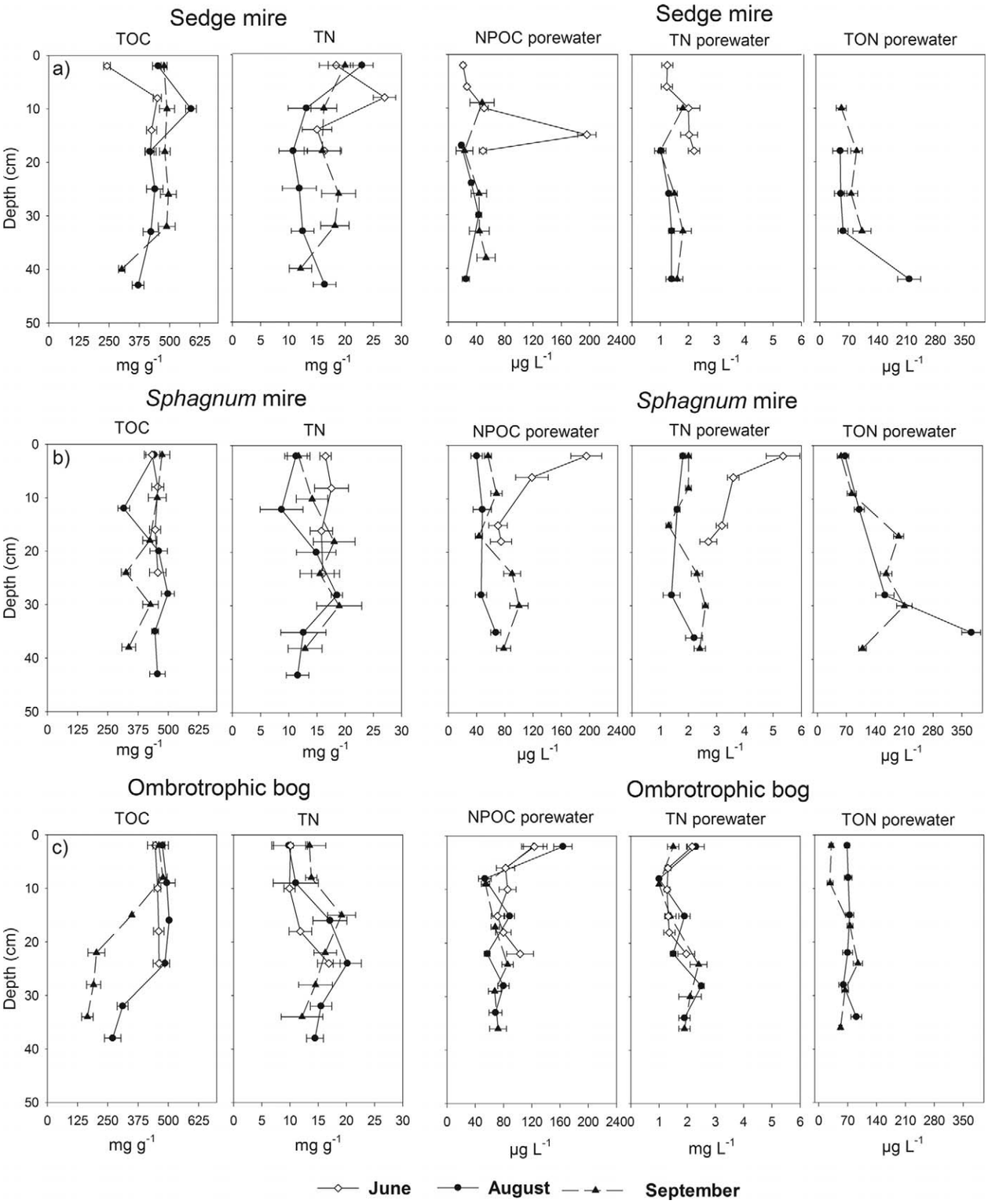

FIGURE 2. (a) Sedge mire, (b) *Sphagnum* mire, and (c) ombrotrophic bog: concentrations of total organic carbon (TOC), non-purgeable organic carbon (NPOC), and total nitrogen (TN) (both in peat and pore water), total organic nitrogen (TON) along the soil profile for the sampling months.

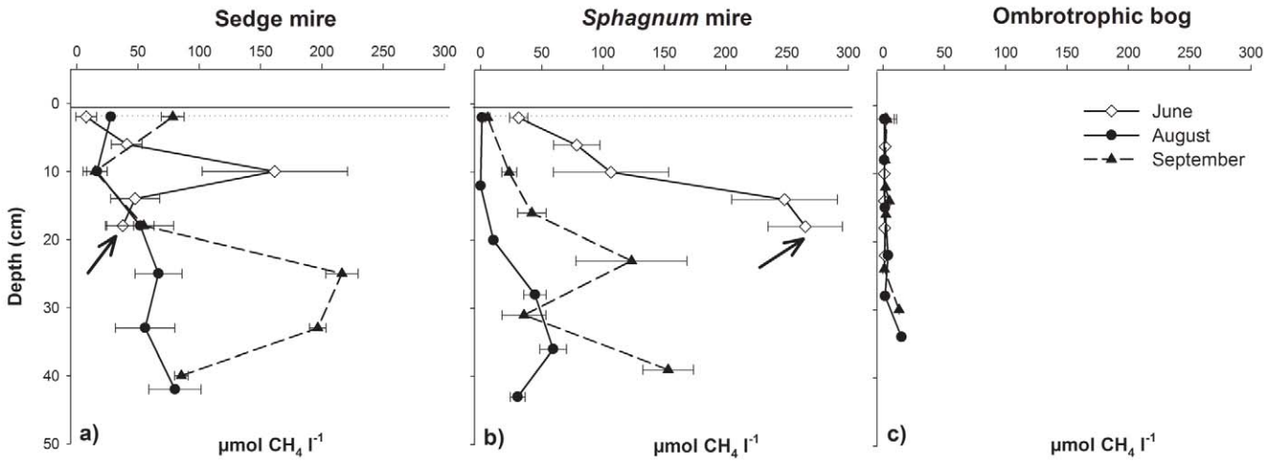

FIGURE 3. Methane concentration profiles for the three sampling months in the (a) sedge mire, (b) *Sphagnum* mire, and (c) ombrotrophic bog. The horizontal lines in (a) and (b) represent the position of the water table at the different sampling times. The black arrows indicate the active layer depth in June. Error bars represent the standard deviation of analyses conducted in triplicate.

These site-dependant temperature responses of CH_4 production varied with soil profile depth and time of sampling. For example, rates of CH_4 production in the sedge site, with their high temperature sensitivity, decreased with increasing soil depth for all sampling months and at the three temperatures (Fig. 4, except June; Fig. 5, parts a and b). By comparison, the *Sphagnum* site displayed much smaller variations in rate with depth (Fig. 5, parts c and d). Comparison of CH_4 production rates in the two minerotrophic sites at a single temperature (4 °C) but for different sampling times show highest rates of methane production for the September soil samples (Fig. 4, parts a and b). In the *Sphagnum* mire, rates of CH_4 production in June and August samples were negligible at 4 °C compared to September samples incubated at the same temperature. Sedge site rates of CH_4 production showed a progressive increase from June to September in the top 20 cm of the active layer when incubated at 4 °C.

BIOLOGICAL COEFFICIENTS

In order to better understand the CH_4 production trends described above and therefore how the consortium of microorganisms responsible for soil methanogenesis responds to temperature change, we calculated R_0 and Q_{10} values (Table 2; Fig. 6). A true Q_{10} response should fit the relationship $R = R_0 Q_{10}^{(T/10)}$ and most of the data sets exhibit a high R^2 value (Table 2) albeit it is based upon CH_4 production rates determined at three temperatures (4, 14 and 24 °C; Fig. 6). In general, Q_{10} values in the sedge site are within the same range for the two sampling months (2.4 to 3.5 and 1.9 to 2.8, in August and September, respectively; Table 2). Q_{10} values are higher in the *Sphagnum* site (3.2–5.8 and 2.5–4.2, in August and September, respectively) relative to the sedge mire (2.4–3.5 and 1.9–2.8, in August and September, respectively). The difference in the means of the Q_{10} values for the two sites is significant at the 95% confidence interval using a 2-tailed Student's *t*-test ($p = 0.012$). Q_{10} values also vary by depth with deeper samples exhibiting slightly higher values.

Extrapolated production rates at 0 °C (R_0) also are shown in Table 2. The sedge mire displayed higher values (e.g., August mean = 5.6 ± 6.3) than the *Sphagnum* site (e.g., August mean = 0.5 ± 0.3) at all depths and during August and September. R_0 values in the sedge mire also tended to decrease with depth, exhibiting

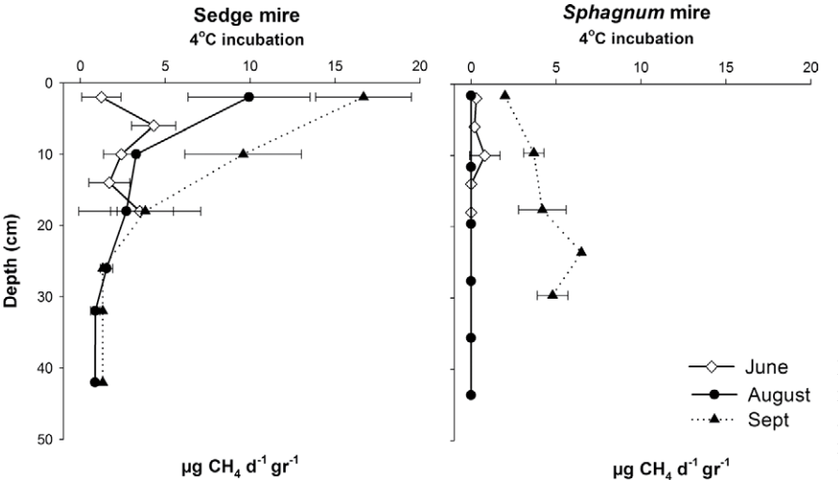

FIGURE 4. The 4 °C CH_4 production response in peat from different depths of (a) sedge mire and (b) *Sphagnum* mire for the three sampling months. Error bars represent the standard deviation of analyses conducted in triplicate.

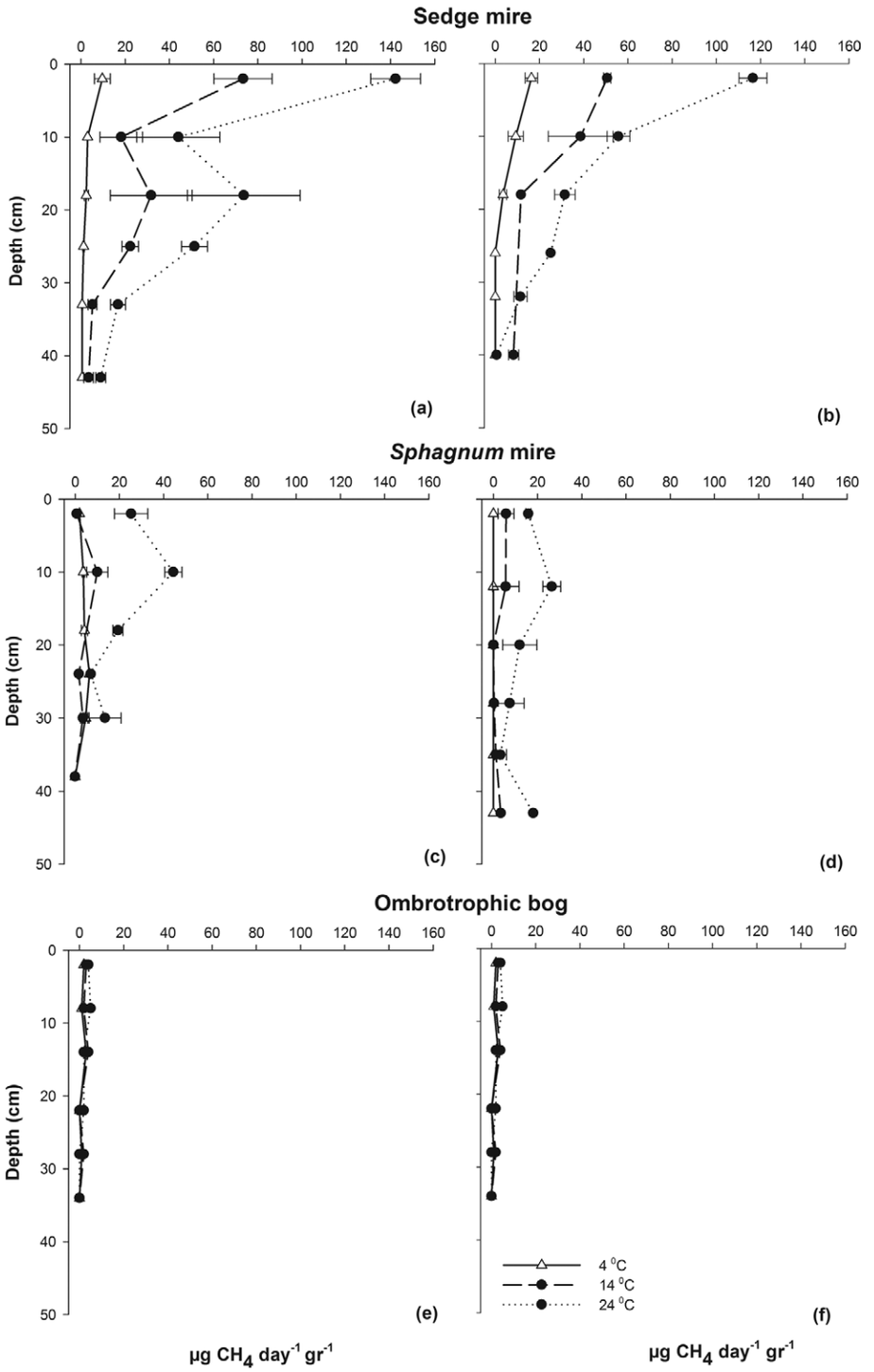

FIGURE 5. Methane production rates in incubated peat from different depths in the sedge mire [(a) August, (b) September], *Sphagnum* mire [(c) August, (d) September], and ombrotrophic bog [(e) August, (f) September]. Error bars represent the standard deviation of analyses conducted in triplicate.

TABLE 2

Main biological coefficients for the sedge and *Sphagnum* mire in August and September (the numbers in parentheses indicate the standard deviation).

Sedge site							
August							
Depth (cm)	**2**	**10**	**18**	**25**	**33**	**43**	***Mean***
R_o (μg CH_4 d gr^{-1})	17.7 (11.2)	3.9 (1.7)	6.3 (4.1)	4.3 (3.1)	0.8 (0.3)	0.7 (0.3)	5.6 (6.3)
Q10 (4–24 ^{0}C)	2.4 (0.7)	2.8 (0.5)	2.8 (0.8)	2.8 (0.9)	3.5 (0.6)	2.9 (0.6)	2.9 (0.4)
R^2	0.95	0.99	0.97	0.97	0.99	0.99	0.98 (0.02)
Ea (Activation Energy)	70.0	81.0	82.2	82.6	100.3	84.7	83.5 (9.8)
September							
Depth (cm)	**2**	**10**	**18**	***Mean***			
R_o (μg CH_4 d gr^{-1})	13.8 (2.3)	12.8 (7.5)	2.7 (0.3)	9.8 (6.2)			
Q10 (4–24 ^{0}C)	2.4 (0.2)	1.9 (0.5)	2.8 (0.2)	2.4 (0.5)			
R^2	1.00	0.90	1.00	0.96 (0.06)			
Ea (Activation Energy)	71.2	50.0	81.9	67.7 (16.2)			
***Sphagnum* site**							
August							
Depth (cm)	**2**	**12**	**35**	**43**	***Mean***		
R_o (μg CH_4 d gr^{-1})	0.9 (0.7)	0.5 (0.2)	0.2 (0.1)	0.3 (0.1)	0.5 (0.3)		
Q10 (4–24 ^{0}C)	3.3 (1.1)	5.1 (1.0)	3.2 (1.1)	5.8 (1.0)	4.4 (1.3)		
R^2	0.98	1.00	0.97	1.00	0.99 (0.01)		
Ea (Activation Energy)	95.5	129.8	93.2	140.1	114.6 (23.9)		
September							
Depth (cm)	**10**	**30**	***Mean***				
R^0 (μg CH_4 d gr^{-1})	1.4 (0.4)	1.7 (1.8)	1.5 (0.2)				
Q10 (4–24 ^{0}C)	4.2 (0.5)	5.4 (1.1)	4.8 (0.6)				
R^2	1.00	0.82	0.91 (0.09)				
Ea (Activation Energy)	114.5	68.0	91.3 (23.2)				

particularly high values ($R_0 = 18$) in the upper 2 cm of soil. The apparent Activation Energy (E_a) showed slightly higher values in the *Sphagnum* site with a mean of 115 and 91 kJ mol^{-1} in August and September, respectively. In the same months, the sedge site had values of 83 and 68 kJ mol^{-1}. This difference between the E_a at the two minerotrophic sites was statistically significant at the 95% confidence level ($p = 0.003$; 2-tailed *t*-test).

Discussion

ENVIRONMENTAL CONTROLS ON CH_4 CONCENTRATIONS AND PRODUCTION

Methane concentration profiles reflect the interaction of several processes (e.g., CH_4 production and oxidation rates, transport of CH_4 by plants), while the CH_4 production rates termed via incubation of peat indicate the potential for methanogenesis over short-time intervals under anoxic conditions and with a fixed organic carbon pool. Plant-mediated effects on CH_4 production (e.g., gas transport and root exudation) are absent in the production potentials.

The highest CH_4 production potentials and extrapolated production rates at 0 °C (R_0; Table 1) always occurred in surface peat and declined with depth (for both mire sites and months). High CH_4 production potentials in surface soil have been reported elsewhere (Segers, 1998; Valentine et al., 1994; Sundh et al., 1994; Yavitt et al., 1987) and reflect the accumulation of above-ground litter inputs, in addition to inputs of fresh organic matter from root turnover and exudation in these layers (Joabsson and Christensen, 2001). The low CH_4 concentrations and production rates in the ombrotrophic bog reflect the unsuitable conditions of this environment for methanogenesis. The absence of a high water table and, consequently, the presence of a deep oxic zone coupled with low temperature during a large part of the year (annual mean $= -0.7$ °C), and the dominance of recalcitrant organic matter (due to a dominance of feather mosses, ericaceous and other woody species), are not conducive to the development of a significant and active community of anaerobic microorganisms (Valentine et al., 1994). Despite the common conception that ombrotrophic bogs have a low nutrient status, our results indicate solid phase and dissolved nutrient and organic carbon levels that are comparable to the sedge and *Sphagnum* sites (Fig. 2), suggesting that the lower CH_4 production potentials arise primarily from the presence of a deep oxic zone. These findings are consistent with the low total hydrocarbon emissions [CH_4 + non-methane volatile organic compounds (NMVOCs)] from these sites in Stordalen of 2.2 ± 0.3 mg C m^{-2} d^{-1} (mean 2003 to 2006) as reported in Bäckstrand et al. (2008).

The high water tables in the sedge and *Sphagnum* sites throughout the summer promote anoxic conditions and high con-

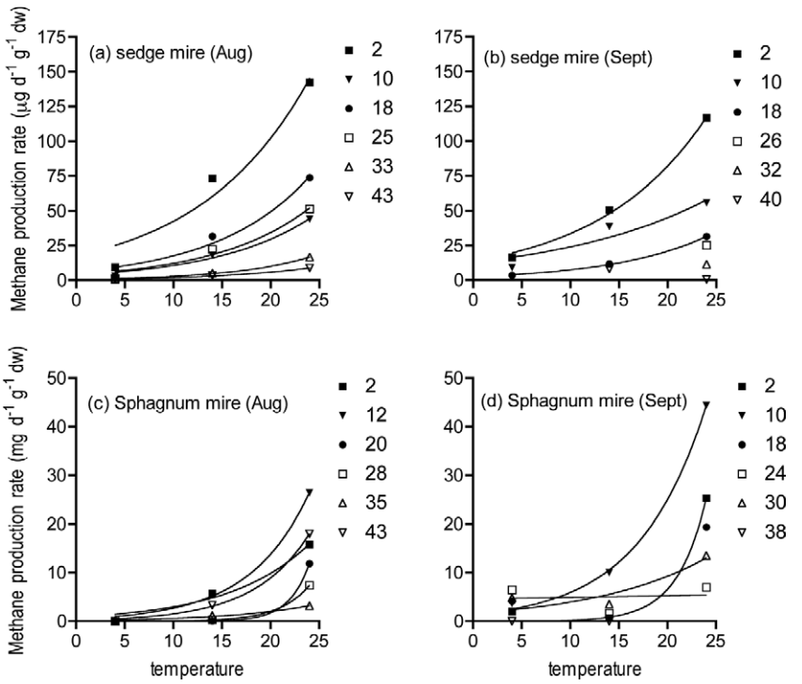

FIGURE 6. Methane production rate versus temperature showing Q_{10} relationships for incubated peat from the sedge (a–b) and Sphagnum (c–d) sites in August and September 2006. Peat depths corresponding to the different symbols are provided in the inset legends.

centrations of CH_4 and potential rates of CH_4 production (Figs. 3 and 5). The slightly higher concentrations of CH_4 in the sedge mire relative to the *Sphagnum*-dominated mire during August and September are supported by the CH_4 production experiments (discussed below), which show higher potential rates of CH_4 production in the sedge soil compared to the *Sphagnum* peat (Fig. 5). Total hydrocarbon emission data are consistent with this observation and show higher average rates of CH_4 flux from the sedge site (120 $\pm$ 1.4 mg C m^{-2} d^{-1}) compared to 28 $\pm$ 0.3 mg C m^{-2} d^{-1} for the *Sphagnum* site during 2003–2006 (Bäckstrand et al., 2008).

These data can be explained by the different hydrological conditions and associated contrasts in plant species composition between the two sites. The sedge site is dominated by *Eriophorum angustifolium* and the other minerotrophic mire by *Sphagnum* spp. Plant species composition determines the quality of peat that develops at the respective sites and several studies have recognized the importance of vegetation as a predicator of CH_4 production and emission because it integrates several ecological variables (Bubier et al., 1995). In the *Sphagnum*-dominated mire, the lack of a well-developed rhizoid system results in little labile organic carbon being released to anaerobic peat layers (Galand et al., 2005). The presence of recalcitrant carbon compounds leads to slow bacterial decomposition rates beneath the *Sphagnum* spp. groundcover (Karunen and Ekman, 1982; Chapin et al., 1986; Johnson and Damman, 1991).

Pore water CH_4 concentrations are similar in the sedge and Sphagnum mires, but CH_4 production rates are as much as 40-fold greater in the former site. This difference likely reflects the greater potential for methanogenesis in the sedge peat resulting from the release of root exudates but also the higher capacity for plant-mediated export of CH_4 through *Eriophorum angustifolium*. Moreover, the high concentrations of CH_4 in soil at the sedge site in June may also reflect lower rates of loss via plant-mediated transport early in the thaw season. This observation is consistent with the low CH_4 fluxes measured from the sedge site at Stordalen in early summer by Bäckstrand et al. (2010) and Jackowicz-Korczynski et al. (2010). It is also supported by the findings of Heyer et al. (2002) who reported low early summer CH_4 emissions from peatlands in Siberia.

By August at Stordalen, the soil had been thawed for ~2 months, soil temperatures were higher (9 to 17 °C), and vegetation growth was well established. Lower pore water concentrations of CH_4 in August and September in the sedge-dominated mire compared with June likely reflect a more highly developed plant root system in the later summer months (Shaver and Billings, 1975), resulting in higher rates of plant-mediated gas transport to the atmosphere (Fig. 5) (Joabsson and Christensen, 2001; King et al., 1998; Frenzel and Karofeld, 2000) and less CH_4 in soil pore water.

SENSITIVITY OF CH_4 PRODUCTION TO TEMPERATURE

Our results suggest that temperature has a variable influence on CH_4 production rates in sedge and *Sphagnum* mires as indicated by Q_{10} values, ranging from 1.9 to 5.8 (overall mean = 3.2). The reported values compare well with published Q_{10} values for temperate peatlands (Bridgham and Richardson, 1992; Frenzel and Karofeld, 2000; Priemé, 1994; Updegraff et al., 1995) and other anoxic habitats (e.g. paddy soils, lake sediment, or swamp) reported in Segers et al. (1998) and Dunfield et al. (1993). The apparent activation energies determined in this study (50–140 kJ mol^{-1}, mean

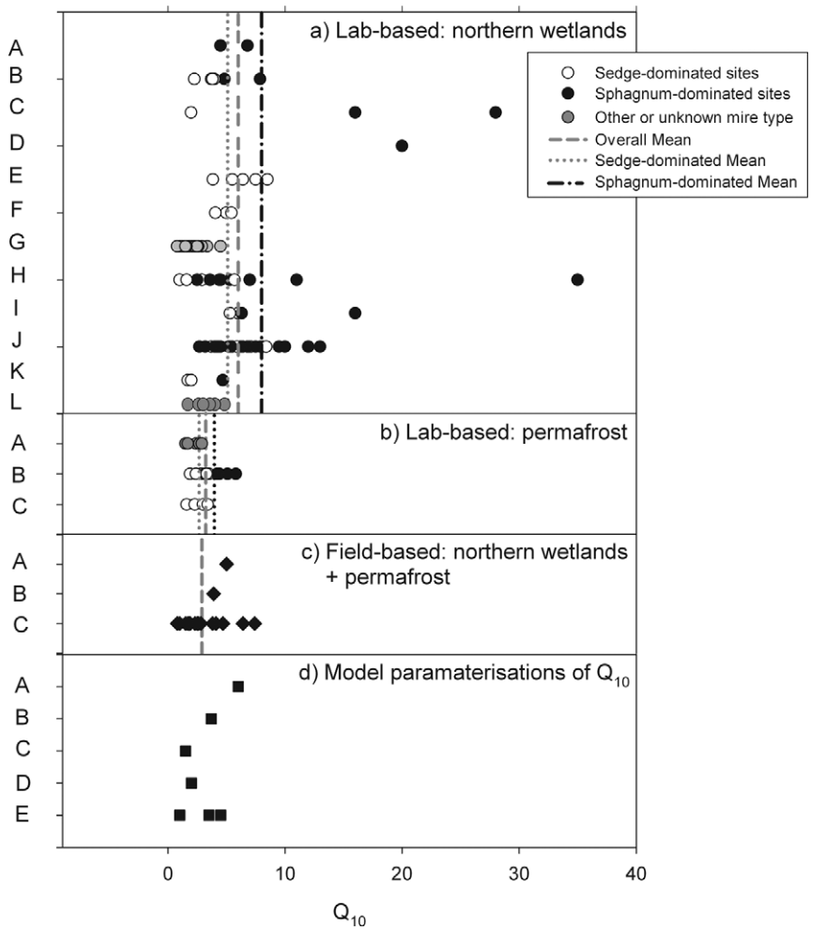

FIGURE 7. A comparison of Q_{10} values determined from laboratory incubations of soil (<50 cm depth) from (a) northern wetlands (non-Arctic), (b) Arctic wetlands where permafrost is present, (c) field-based studies in northern and Arctic wetlands, and (d) Q_{10} values used in numerical models of global or wetland carbon cycling. Key: (a) A—Frenzel and Karofeld (2000), B—McKenzie et al. (1998), C—Updegraff et al. (1995), D—Nedwell and Watson (1995), E—Westermann (1993), F—Westermann and Ahring (1987), G—Yavitt et al. (2000), H—Bergman et al. (1998), I—Dunfield et al. (1993), J—Bergman et al. (2000), K—Valentine et al. (1994), L—Juottonen et al. (2008). (b) A—Dutta et al. (2006), B—this study, C—Heyer et al. (2002). (c) A—Christensen et al. (2003), B—Worthy et al. (2000), C—Pelletier et al. (2007). (d) A—Walter and Heimann (2000), B—Frolking et al. (2001), C—Gedney et al. (2004), D—Hein et al. (1997), E—Fung et al. (1991).

90 kJ mol^{-1}) are slightly lower than those for northern peatlands (123–271 kJ mol^{-1}, Dunfield et al., 1993) but within the range reported for other anoxic environments such as paddy soils (53–132 kJ mol^{-1}, Shültz et al., 1990; 68–91 kJ mol^{-1}, Conrad et al., 1987) and alder swamp (92–117 kJ mol^{-1}, Westermann and Ahring, 1987), suggesting that the energy necessary for methanogenesis in permafrost areas is broadly similar to that in other anoxic freshwater wetlands.

Figure 7 compares Q_{10} values measured in this study with published values for northern (non-permafrost sites) (Fig. 7, parts a and c) and permafrost wetlands (Fig. 7, parts b and c) that have been determined using laboratory-based incubations and field-based relationships between soil or air temperatures and CH_4 fluxes. Our results (1.9–5.8) are similar to those of Heyer et al. (2002) who reported Q_{10} values ranging from 1.3 to 5.6 for a permafrost site in northern Siberia. In general, the Q_{10} values determined for peatlands at Stordalen lie at the low end of the range of published values for northern wetlands and do not display any unusually high values, which have been reported in other studies. Those high values typically are derived from *Sphagnum*-dominated peatlands, for example the values reported by Bergman et al. (1998) (Q_{10} = 2.5 to 35), Bergman et al. (2000) (Q_{10} = 4.4 to 13), and Dunfield et al. (1993) (Q_{10} = 6 to 16). Field-based determinations of Q_{10} for northern wetlands (including permafrost peatlands) as a whole do not yield dramatically different average Q_{10} values compared to laboratory studies (Fig. 7, parts a–c).

Differences in Q_{10} values reported in Table 2 and CH_4 production rates at different temperatures (Fig. 5; 4–14 °C and 14–24 °C; 95% confidence interval, $p < 0.001$, for the sedge site and 95% confidence interval, $p < 0.0012$ for the *Sphagnum* site using a *t*-test) between the two minerotrophic sites likely also reflect differences in temperature sensitivity of microbial processes that generate CH_4-precursors in the anaerobic chain of decay.

The higher mean Q_{10} values and apparent activation energy (Ea) in the *Sphagnum* mire (Q_{10} = 4.5; Ea = 110 kJ mol^{-1}) versus the sedge site (Q_{10} = 2.7; Ea = 78 kJ mol^{-1}) at Stordalen are consistent with the presence of more recalcitrant organic matter, possibly due to a greater predominance of *Sphagnum* spp. in the former mire (Verhoeven and Toth, 1995). Such a difference is consistent with fundamental principles of enzyme kinetics associated with the Arrehenius equation, and the carbon quality temperature (CQT) hypothesis (Davidson and Janssens, 2006; Bosatta and Ågren, 1999) predicts that the temperature sensitivity of microbial decomposition should increase with increasing Ea of a reaction. A similar pattern is evident in Figure 7 based upon published data in which the highest Q_{10} values (>8) derive primarily from *Sphagnum*-dominated mires and the lower values from sedge-rich mires. Notably the mean Q_{10} values for these two peatland types differ

significantly ($Q_{10} = 7$ for *Sphagnum* mires and 4.2 for sedge mire; 99% confidence interval using a 2-tailed Student's *t*-test, $p = 0.002$).

The intra-site differences in Q_{10} values suggest subtle contrasts in the temperature response of methanogenesis between peatland types. In general, areas containing more recalcitrant organic matter typically are characterized by lower rates of organic carbon decomposition (Craine et al., 2010; Davidson and Janssens, 2006) and hence, contribute less to total CH_4 emissions than sites where vascular plants are present. However, in most northern peatlands recalcitrant compounds are more abundant than labile compounds, with *Sphagnum*-dominated mires globally covering a greater area than sedge-dominated peatlands (Charman, 2002), in particular in the Arctic where mesic (with a moderate supply of moisture) and drier ecosystems cover 44 to 58% of ice-free areas (Bliss and Matveyeva, 1992). At Stordalen, *Sphagnum* mires account for 36% of the total area of the 16.5 ha mire complex (versus 49% ombrotrophic bog and 12% sedge mire) (Johansson et al., 2006). Hence, differences in temperature sensitivity between these two peatland types may be significant for the future response of northern wetlands to climate change. While CH_4 emissions are significantly less from the *Sphagnum* mire than the wetter sedge-dominated areas at Stordalen (Bäckstrand et al., 2008) and other Arctic sites, the significantly higher Q_{10} values for methanogenesis in the *Sphagnum*-rich areas could yield proportionally larger changes in CH_4 flux for changes in temperature. Whether such an effect would be sustained will depend upon the longer term ecosystem response to climate forcing, and how other factors that impact methanogenesis (e.g., changes in hydrology) are altered (e.g., Oechel et al., 2000; Christensen et al., 2004). At Stordalen, the ombrotrophic palsa area has already decreased in size yielding larger areas of wetter minerotrophic peatland during the period 1970 to 2000 and an associated increase in CH_4 emissions from the new sedge-dominated mires (Christensen et al., 2004, Johansson et al., 2006). However, a future shift towards drier conditions would deepen the oxic zone and most likely lower CH_4 production potentials and enhance methanotrophy, limiting the flux of CH_4 from these areas of former *Sphagnum* mire.

Our findings have implications for the parameterization of methanogenesis in numerical models of the global and regional carbon cycles as discussed recently by Craine et al. (2010). Some models rely on a single Q_{10} function to determine the potential impact of climate warming on CH_4 fluxes from wetlands (e.g., Frolking et al., 2001; Gedney et al., 2004). The assumed Q_{10} values typically are similar to the median of published values summarized in Figure 7, indicating a generally good parameterization given the uncertainty and potential range of Q_{10} values. There is considerable variability in the temperature sensitivity of methanogenesis in northern and Arctic wetlands (Fig. 7, parts a–c), in particular, within mesic bogs versus minerotrophic mires. Hence, employing a single parameterization of Q_{10} may lead to inaccurate prediction of future CH_4 flux from these environments, especially in models that are able to incorporate changes in ecosystem type and organic matter decomposition as a function of climate (e.g., where surface hydrology, and hence the spatial extent of mire type changes with climate). Recent soil carbon models that employ spatially variable values for Q_{10} to predict response to climate change support this viewpoint (e.g., Zhuang et al., 2003). In this context, Craine et al. (2010) suggested that in order to predict how the present-day soil organic carbon pool will respond to climate change we need to determine the generality of the carbon quality–temperature correlation and hence, the use of a single value of Q_{10} to describe decomposition response to temperature is likely to be inadequate. Craine et al. (2010) implied that the kinetic theory underlying temperature sensitivity of decomposition at a molecular level could also be employed at the soil scale, suggesting that large-scale models using temperature sensitivity of organic matter decomposition within their parameters might be based accurately on soil incubations or possibly through the creation of a global system of soil-incubation experiments (Janssens and Vicca, 2010).

Conclusions

Investigation of the temperature sensitivity of methanogenesis in peatland soil from Stordalen, northern Sweden, indicates that CH_4 production is controlled by a complex suite of interrelated factors, including water table level, plant composition, and temperature. Temperature has a clear and direct effect on CH_4 production rates, although its influence is moderated by the site-specific factors of vegetation composition and hence, organic matter quality. The Q_{10} values determined for sedge and *Sphagnum* mires are similar to published values for northern peatlands. Permafrost wetlands, including Stordalen, do not display a significantly different response of CH_4 production to temperature forcing in comparison to northern, non-permafrost wetlands. However, our results from Stordalen exhibit intra-sites differences that demonstrate stronger temperature sensitivity of methanogenesis based upon presumably more recalcitrant soil organic matter in the *Sphagnum* mire versus the sedge-dominated site. This contrasting response in CH_4 production has been reported in other studies of northern wetlands and in general, methanogenesis in *Sphagnum*-dominated wetlands responds more strongly to temperature forcing than within wetter, sedge-rich peatlands. This finding is significant given that *Sphagnum* sites constitute a significant proportion of the northern peatland area. Our results provide potentially useful data to inform parameterization of Q_{10} values in models of carbon cycling in northern wetlands, in particular, for anaerobic decomposition in the active layer of permafrost peatlands. The data indicate the importance of using spatially variable Q_{10} values in such models to reflect differences in temperature response of CH_4 production in key biotypes in high-resolution, coupled climate-ecosystem models.

Acknowledgments

This work was supported by a Marie Curie PhD Fellowship to M. Lupascu via the EU Early Stage Training Programme ''Biotransformations of trace elements in aquatic systems.'' We thank Professor Torben Christensen for his input in relation to sampling at Abisko and for providing access to the field site. We thank the staff at the Abisko Research Station and at the University of Bristol for assistance during fieldwork and laboratory analysis. The UK Joint Higher Education Funding Council for England and Office of Science and Technology Science Research Investment Fund (SRIF) are thanked for infrastructure funding. Work was conducted

in the Low Temperature Experimental and BIOGAS Facilities in Bristol.

References Cited

Anderson, J. M., 1992: Responses of soils to climate change. *Advanced in Ecological Research,* 22: 163–210.

Bäckstrand, K., Crill, P. M., Mastepanov, M., Christensen, T. R., and Bastviken, D., 2008: Total hydrocarbon flux dynamics at a subarctic mire in northern Sweden. *Journal of Geophysical Research*, 113: 16 pp., http://dx.doi.org/10.1029/2008JG000703.

Bäckstrand, K., Crill, P. M., Jackowicz-Korczynski, M., Mastepanov, M., Christensen, T. R., and Bastviken, D., 2010: Annual carbon gas budget for a subarctic peatland, northern Sweden. *Biogeosciences*, 7(1): 95–108.

Bellisario, L. M., Bubier, J. L., and Moore, T. R., 1999: Controls on CH_4 emissions from a northern peatland. *Global Biogeochemical Cycles*, 13(1): 81–91.

Bergman, I., Svensson, B. H., and Nilsson, M., 1998: Regulation of methane production in a Swedish acid mire by pH, temperature and substrate. *Soil Biology & Biochemistry*, 30(6): 729–741.

Bergman, I., Klarqvist, M., and Nilsson, M., 2000: Seasonal variation in rates of methane production from peat of various botanical origins: effects of temperature and substrate quality. *FEMS Microbial Ecology*, 33(3): 181–189.

Bliss, L. C., and Matveyeva, N. V., 1992: Circumpolar Arctic vegetation. In Chapin, F. S., III, Jeffries, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate. An Ecological Perspective*. San Diego: Academic Press Inc., 59–89.

Bosatta, E., and Ågren, G. I., 1999: Soil organic matter quality interpreted thermodynamically. *Soil Biology and Biochemistry*, 31: 1889–1991.

Bouwman, A. F., 1990: *Soils and the Greenhouse Effect*. Chichester, U.K.: Wiley.

Bridgham, S. D., and Richardson, C. J., 1992: Mechanism controlling soil respiration (CO_2 and CH_4) in southern peatlands. *Soil Biology & Biochemistry*, 24: 1089–1099.

Brouchkov, A., and Fukuda, M., 2000: Preliminary measurements on methane content in permafrost, central Yakutia, and some experimental data. *Permafrost & Periglacial Processes*, 13(3): 187–197.

Bubier, J. L., Moore, L. T., Bellisario, R. M., and Comer, N. T., 1995: Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. *Global Biogeochemical Cycles*, 9(4): 455–470.

Callaghan, T. V., Björn, L. O., Chapin, F. S., III, et al., 2005: Arctic tundra and polar ecosystem. *In* Symon, C., Arris, L., Heal, B., et al. (eds.), *Arctic Climate Impact Assessment ACIA*. Cambridge: Cambridge University Press, 243–351.

Chapin, F. S., Vitousek, P. M., and Van Cleve, K., 1986: The nature of nutrient limitation in plant communities. *American Naturalist*, 127(1): 48–58.

Chapin, F. S., III, Sturm, M., Serreze, M. C., McFadden, J. P., Key, J. R., Lloyd, A. H., McGuire, A. D., Rupp, T. S., Lynch, A. H., Schimel, J. P., Beringer, J., Chapman, W. L., Epstein, H. E., Euskirchen, E. S., Hinzman, L. D., Jia, G., Ping, C. L., Tape, K. D., Thompson, C. D. C., Walker, D. A., and Welker, J. M., 2005: Role of land surface change in Arctic summer warming. *Science* 310: 657–660.

Chapman, S. J., and Thurlow, M., 1998: Peat respiration at low temperatures. *Soil Biology & Biochemistry*, 30(8-9): 1013–1021.

Charman, D., 2002: *Peatlands and Environmental Change*. Chichester, U.K.: Wiley.

Christensen, T., 1991: Arctic and sub-Arctic soil emissions: possible implications for global climate change. *Polar Record*, 27: 205–210.

Christensen, T., Ekberg, A., Strom, L., Mastepanov, M., Panikov, N., Oquist, M., Svenson, B. H., Nykanen, H., Martikainen, P. J., and Oskarsson, H., 2003: Factors controlling large scale variations in methane emissions from wetlands. *Geophysical Research Letters*, 30: 7 pp., http://dx.doi.org/10.1029/2002GL016848.

Christensen, T. R., Johansson, T. R., Akerman, H. J., Mastepanov, M., Malmer, N., Friborg, T., Crill, P., and Svensson, B. H., 2004. Thawing sub-arctic permafrost: effects on vegetation and methane emissions. *Geophysical Research Letters*, 31: L04501, http://dx.doi.org/10.1029/2003GL018680.

Conrad, R., 1989. Controls on methane production in terrestrial ecosystems. *In* Andrea, M. O., and Schimel, D. S. (eds.), *Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere*. New York: Wiley, 39–58.

Conrad, R., 1999: Contribution of hydrogen to methane production and control of hydrogen concentrations in methanogenic soils and sediments. *FEMS Microbiology Ecology*, 28: 193–202.

Conrad, R., Shültz, H., and Babbel, M., 1987: Temperature limitation of hydrogen turnover and methanogenesis in anoxic paddy soil. *FEMS Microbial Ecology*, 45: 281–289.

Craine, J. M., Fierer, N., and McLauchlan, K. K., 2010: Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nature GeoScience*, 3: 854–857.

Davidson, E. A., and Janssens, I. A., 2006: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440: 165–173.

Dioumaeva, I. S., Trumbore, S., Schuur, E. A. G., Goulden, M. L., Litvak, M., and Hirsch, A. I., 2002: Decomposition of peat from upland boreal forest: temperature dependence and sources of respired carbon. *Journal of Geophysical Research: Atmospheres*, 108(D3): http://dx.doi.org/10.1029/2001JD000848.

Dunfield, P., Knowles, R., Dumont, R., and Moore, T. R., 1993: Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. *Soil Biology & Biochemistry*, 25(3): 321–326.

Dutta, K., Schuur, E. A. G., Neff, J. C., and Zimov, S. A., 2006: Potential carbon release from permafrost soils of northeastern Siberia. *Global Change Biology*, 12: 2336–2351.

Frenzel, P., and Karofeld, E., 2000: CH_4 emission from a hollow-ridge complex in a raised bog: the role of CH_4 production and oxidation. *Biogeochemistry*, 51: 91–112.

Frolking, S., Roulet, N. T., and Moore, T. R., 2001: Modeling northern peatland decomposition and peat accumulation. *Ecosystems*, 4(5): 479–498.

Fung, I., John, J., Lerner, J., Matthews, E., Prather, M., Steele, L., and Fraser, P., 1991: Global budget of atmospheric methane: results from a three-dimensional global model synthesis. *Journal of Geophysical Research*, 96: 13033–13065.

Galand, P. E., Fritze, H., Conrad, R., and Yrjala, K., 2005: Pathways for methanogenesis and diversity of methanogenic archaea in three peatland ecosystems. *Applied & Environmental Microbiology*, 71(4): 2195–2198.

Gedney, N., Cox, P. M., and Huntingford, C., 2004: Climate feedback from wetland emissions. *Geophysical Research Letters*, 31: http://dx.doi.org/10.1029/2004GL020919.

Gorham, E., 1991: Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecology Applied*, 1: 182–195.

Hargreaves, K. J., and Fowler, D., 1998: Quantifying the effects of water table and soil temperature on the emission of methane from peat wetland at the field scale. *Atmospheric Environment*, 32(19): 3275–3282.

Harriss, R. C., Sebacher, D. I., and Day, F. P., Jr., 1982: Methane flux in the Great Dismal Swamp. *Nature*, 297: 673–674.

Hein, R., Crutzen, P. J., and Heimann, M., 1997: An inverse modelling approach to investigate the global atmospheric methane cycle. *Global Biogeochemical Cycles*, 11: 43–76.

Heyer, J., Berger, U., Kuzin, I. L., and Yakovlev, O. N., 2002: Methane emission from different ecosystem structures of the subarctic tundra in western Siberia during midsummer and during the thawing period. *Tellus*, 54B: 231–249.

Hogan, K. B., 1993: *Current and Future Methane Emission from Natural Sources*. Washington, D.C.: U.S. Environmental Protection Agency, Office of Air and Radiation.

IPCC, 2007: Summary for policy makers. *In* Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L. (eds.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press, 1–18.

Jackowicz-Korczynski, M., Christensen, T. R., Backstrand, K., Crill, P., Friborg, T., Mastepanov, M., and Strom, L., 2010: Annual cycle of methane emission from a subarctic peatland. *Journal of Geophysical Research*, 115: http://dx.doi.org/10.1029/2008JG000913.

Janssens, I. A., and Vicca, S., 2010: Biogeochemistry: soil carbon breakdown. *Nature GeoScience*, 3: 823–824.

Joabsson, A., and Christensen, T. R., 2001: Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. *Global Change Biology*, 7: 919–932.

Johansson, T., Malmer, N., Crill, P. M., Friborgs, T., Akerman, J. H., Mastepanov, M., and Christensen, T. R., 2006: Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing. *Global Change Biology*, 12(12): 2352–2369.

Johnson, L. C., and Damman, A. W. H., 1991: Species-controlled *Sphagnum* decay on a south Swedish raised bog. *Oikos*, 61(2): 234–242.

Juottonen, H., Tuittila, E., Juutinen, S., Fritze, H., and Yrjälä, K., 2008. Seasonality of rDNA and rRNA derived archaeal communities and methanogenic potential in a boreal mire. *The ISME Journal*, 2: 1157–1168.

Karunen, P., and Ekman, R., 1982: Age-dependent content of polymerized lipids in *Sphagnum fuscum*. *Physiologia Plantarum*, 54(2): 162–166.

King, J. Y., Reeburgh, W. S., and Regli, S. K., 1998: Methane emission and transport by arctic sedges in Alaska: results of a vegetation removal experiment. *Journal of Geophysical Research*, 103: 29089–29092.

Le Mer, J., and Roger, P., 2001: Production, oxidation, emission and consumption of methane by soils: a review. *European Journal of Soil Biology,* 37: 25–50.

McKenzie, C., Schiff, S., and Aravena, R., 1998: Effect of temperature on production of CH_4 and CO_2 from peat in a natural and flooded boreal forest wetland. *Climatic Change*, 40: 247–266.

Metje, M., and Frenzel, P., 2005: Effects of temperature on anaerobic ethanol oxidation and methanogenesis in acidic peat from a northern wetlands. *Applied and Environmental Microbiology*, 71(12): 8191–8200.

Metje, M., and Frenzel, P., 2007: Methanogenesis and methanogenic pathways in a peat from subarctic permafrost. *Environmental Microbiology*, 9(4): 954–964.

Nedwell, D. B., and Watson, A., 1995: CH_4 production, oxidation and emission in a UK ombrotrophic peat bog: influence of SO_4 from acid rain. *Soil Biology & Biochemistry*, 27: 893–903.

Oechel, W. C., Vourlitis, G. L., Hastings, S. J., Zulueta, R. C., Hinzman, L., and Kane, D., 2000: Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, 406: 978–981.

Pelletier, L., Moore, T. R., Roulet, N. T., Garneau, M., and Beaulieu-Audy, V., 2007: Methane fluxes from three peatlands in the La Grande River watershed, James Bay lowland, Canada. *Journal of Geophysical Research Biogeoscience*, 112: http://dx.doi.org/10.1029/2006JG000216.

Petrescu, A. M. R., van Beek, L. P. H., van Huissteden, J., Prigent, C., Sachs, T., Corradi, C. A. R., Parmentier, F. J. W., and Dolman, A. J., 2010: Modeling regional to global CH_4 emissions of boreal and arctic wetlands. *Global Biogeochemical Cycles*, 24: http://dx.doi.org/10.1029/2009GB003610.

Priemé, A., 1994: Production and emission of methane in a brackish and a freshwater wetland. *Soil Biology & Biochemistry*, 26: 7–18.

Rivkina, E., Shcherbakova, V., Laurinavichius, K., Petrovskaya, L., Krivushin, K., Kraev, G., Pecheritsina, S., and Gilichinsky, D. A., 2007: Biogeochemistry of methane and methanogenic archaea in permafrost. *FEMS Microbial Ecology*, 61: 1–15.

Rosswall, T., Flower-Ellis, J. G. K., Johansson, L. G., et al., 1975: Stördalen (Abisko), Sweden. *In* Rosswall, T., and Heal, O. W. (eds.), *Structure and Function of Tundra Ecosystems*. Stockholm: Swedish Natural Science Research Council, *Ecological Bulletins*, 20: 265–294.

Schimel, J. P., Holland, E. A., and Valentine, D., 1993: Controls on methane flux from terrestrial ecosystems. *In* Harper, L. A., Mosier, A. R., Duxbury, J. M., and Rolston, D. E. (eds.), *Agricultural Ecosystems Effects on Trace Gases and Global Climate Change*. Madison, Wisconsin: American Society of Agronomy, 167–182.

Segers, R., 1998: Methane production and methane consumption: a review of processes underlying wetland methane fluxes. *Biogeochemistry*, 41(1): 23–51.

Shaver, G. R., and Billings, W. D., 1975: Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. *Ecology*, 56: 401–409.

Shültz, H., Seiler, W., and Conrad, R., 1990: Influence of soil temperature on methane emission from rice paddy fields. *Biogeochemistry*, 11: 77–95.

Sonesson, M., 1969: Studies on mire vegetation in the Torneträsk area, northern Sweden II; winter conditions of the poor mires. *Botaniska Notiser*, 122: 481–511.

Sundh, I., Nilsson, M., Granberg, G., and Svensson, B. H., 1994: Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. *Microbial Ecology*, 27: 253–265.

Svensson, B. H., 1984: Different temperature optima for methane formation when enrichments from acid peat are supplemented with acetate or hydrogen. *Applied & Environmental Microbiology*, 48(2): 389–394.

Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., and Zimov, S., 2009: Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles,* 23: GB2023, http://dx.doi.org/10.1029/2008GB003327.

Updegraff, K., Pastor, J., Bridgham, S. D., and Johnston, C. A., 1995: Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. *Ecology Applied*, 5(1): 151–163.

Valentine, D. W., Holland, E. A., and Schimel, D. S., 1994: Ecosystem and physiological controls over methane production in northern wetlands. *Journal of Geophysical Research*, 99: 1563–1571.

Verhoeven, J. T. A., and Toth, E., 1995: Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition of living tissue homogenates. *Soil Biology & Biochemistry*, 27: 271–275.

Waddington, J. M., Roulet, N. T., and Swanson, R. V., 1996: Water table control of CH_4 emission enhancement by vascular plants in boreal peatlands. *Journal of Geophysical Research*, 101(D17): 22775–22785.

Wagner, D., Kobabe, S., Pfeiffer, E. M., and Hubberten, H. W., 2003: Microbial controls on methane fluxes from a polygonal tundra of the Lena Delta, Siberia. *Permafrost and Periglacial Processes*, 14: 173–185.

Wagner, D., Lipski, A., Embacher, A., and Gattinger, A., 2005: Methane fluxes in permafrost habitats of the Lena Delta: effects of microbial community structure and organic matter quality. *Environmental Microbiology*, 7(10): 1582–1592.

Wagner, D., Gattinger, A., Embacher, A., Pfeiffer, E., Schloter, M., and Lipski, A., 2007: Methanogenic activity and biomass in Holocene permafrost deposits of the Lena Delta, Siberian Arctic and its implication for the global methane budget. *Global Change Biology*, 13: 1089–1099.

Walter, B. P., and Heimann, M., 2000: A process-based, climate-sensitive model to derive methane emissions from natural wetlands: applications to five wetlands sites, sensitivity to model parameters and climate. *Global Biogeochemical Cycles*, 14(3): 745–765.

Wang, Z. P., Zeng, D., and Patrick, W. H., 1996: Methane emissions from natural wetlands. *Environmental & Monitoring Assessment*, 42: 143–161.

Wania, R., Ross, I., and Prentice, I. C., 2010: Implementation and evaluation of a new methane model within a dynamic global vegetation model: LPJWHyMe v1.3. *Geoscience Model Development Discuss*, 3: 1–59.

Westermann, P., 1993: Temperature regulation of methanogenesis in wetlands. *Chemosphere*, 26(1–4): 321–328.

Westermann, P., and Ahring, B. K., 1987: Dynamics of methane production, sulfate reduction and denitrification in a permanently waterlogged alder swamp. *Environmental Microbiology*, 55: 2554–2559.

Worthy, D. E. J., Levin, I., Hopper, F., Ernst, M. K., and Trivett, N. B. A., 2000: Evidence for a link between climate and northern wetlands methane emissions. *Journal of Geophysical Research*, 105(D3): 4031–4038.

Yavitt, J. B., Lang, G. E., and Wieder, R. K., 1987: Control of carbon mineralization to CH_4 and CO_2 in anaerobic, *Sphagnum*-derived peat from Big Run Bog, West Virginia. *Biogeochemistry*, 4: 141–157.

Yavitt, J. B., Williams, C. J., and Wieder, R. K., 2000: Controls on microbial production of methane and carbon dioxide in three *Sphagnum*-dominated peatland ecosystems as revealed by a reciprocal field peat transplant experiment. *Geomicrobiology Journal*, 17: 61–88.

Zhuang, Q., Melillo, J. M., Kicklighter, D. W., Prinnn, R. G., McGuire, A. D., Steudler, P. A., Felzer, B. S., and Hu, S., 2003: A process-based modeling analysis of methane exchanges between Alaskan terrestrial ecosystems and the atmosphere. *Global Biogeochemical Cycles*, 18: http://dx.doi.org/10.1029/2004GB002239.

MS accepted May 2012