

Methane flux dynamics in an Irish lowland blanket bog

Anna Laine · David Wilson · Gerard Kiely ·
Kenneth A. Byrne

Received: 25 October 2006 / Accepted: 30 July 2007 / Published online: 22 September 2007
© Springer Science + Business Media B.V. 2007

Abstract Pristine peatlands are a significant source of atmospheric methane (CH₄). Large spatio-temporal variation has been observed in flux rates within and between peatlands. Variation is commonly associated with water level, vegetation structure, soil chemistry and climatic variability. We measured spatial and temporal variation in CH₄ fluxes in a blanket bog during the period 2003–2005. The surface of the bog was composed of different vegetation communities (hummocks, lawns and hollows) along a water level gradient. CH₄ fluxes were measured in each community using a chamber method. Regression modelling was used to relate the fluxes with environmental variables and to integrate fluxes over the study period. Water level was the strongest controller of spatial variation; the average flux rate was lowest in hummocks and highest in hollows, ranging from 3 to 53 mg CH₄ m⁻² day⁻¹. In vegetation communities with a permanently high water level, the amount and species composition of vegetation was also a good indicator of flux rate. We observed a clear seasonal variation in flux

that was chiefly controlled by temperature. The annual average flux (6.2 g CH₄ m⁻² year⁻¹) was similar to previous estimates from blanket bogs and continental raised bogs. No interannual variation was observed.

Keywords Peatland · Vegetation composition · Spatial variation · Water table

Introduction

Pristine peatlands are a significant source of methane (CH₄) (Huttunen et al. 2003), that is one of the most important greenhouse gases (IPCC 2001). Much of the research on CH₄ fluxes has focused on peatlands in the boreal and continental climatic zones (e.g. Bubier et al. 1993; Huttunen et al. 2003). In contrast, CH₄ fluxes in blanket bogs of the temperate zone have received relatively little attention (e.g. Fowler et al. 1995; MacDonald et al. 1998). Blanket bogs are ombrotrophic peatlands and occur in maritime areas with high and regular rainfall (in Ireland the requirement is at least 1,250 mm distributed over more than 250 rain days per year (Hammond 1981)). Blanket bogs differ from continental bogs in terms of water level, which remains close to the surface throughout the year due to the regular rain events (Sparling 1967). In addition, the concentrations of maritime salts (Cl, Na, SO₄²⁺) are high compared to the main nutrients (Adamson et al. 2001). Consequently, the pH in blanket bogs is relatively high, 4.4–4.9 (Shotyk 1997) compared to other ombrotrophic bogs. These

Responsible Editor: Hans Lambers

A. Laine (✉) · G. Kiely · K. A. Byrne
Department of Civil and Environmental Engineering,
University College Cork,
Cork, Ireland
e-mail: anna.m.laine@helsinki.fi

D. Wilson
School of Biology and Environmental Science,
University College Dublin, Belfield,
Dublin 4, Ireland

abiotic differences are reflected in the vegetation composition, which is a combination of species common in continental bogs and fens (O'Connor and Skeffington 1997; Osvald 1949).

The CH₄ flux depends on the height of the water level (Dise et al. 1993), vegetation structure (Bubier 1995), pH (Williams and Crawford 1984) and the presence of sulphate reducing bacteria (Granberg et al. 2001b). The vegetation affects the flux rate through substrate quality and quantity (Ström et al. 2003) and by offering a fast transport pathway for the gas (Conway 1937; Garnet et al. 2005). These properties vary between plant species; deep rooting sedges with aerenchymatic cell structure are generally associated with high CH₄ flux rates (Bubier et al. 1995). The controlling factors vary not only between but also within peatlands since the surface of bogs is often a mosaic of vegetation communities characterized by different water levels (Daulat and Clymo 1998). The small scale differences in species composition and water level has caused large spatial variation in CH₄ fluxes in raised and blanket bogs (Bubier et al. 1993; MacDonald et al. 1998).

In addition to spatial variation the CH₄ efflux has been shown to vary diurnally (Käki et al. 2001), seasonally (Saarnio et al. 1997) and inter annually (Granberg et al. 2001a). This temporal variation is dependent on temperature, in addition to water level and vegetation properties (Granberg et al. 2001a).

To date, studies of CH₄ fluxes in blanket bogs have been based on short or irregular measurement campaigns (Chapman and Thurlow 1996; Fowler et al. 1995; MacDonald et al. 1998) and no long-term studies exist. We measured CH₄ fluxes from different vegetation communities in an Irish lowland blanket bog over a 29-month period using a closed chamber method (Saarnio et al. 1997). The aims of this study are (1) to quantify the CH₄ flux of different vegetation communities, (2) to define the environmental controls on the spatial variation in CH₄ flux and (3) to investigate the seasonal variation in CH₄ flux.

Materials and methods

Site description

The study site was located in an extensive lowland blanket bog in Glencar, Co Kerry, Ireland (51°55' N,

9°55' W). The surface of the bog is composed of different vegetation communities ranging from dry hummocks (HU) to permanently inundated hollows (HO). HU had a cover of mosses such as *Racomitrium lanuginosum*, *Sphagnum rubellum* and *Sphagnum papillosum* and vascular plants *Calluna vulgaris*, *Erica tetralix* and *Molinia caerulea*. Hollows supported a sparse cover of species such as *Sphagnum cuspidatum*, *Sphagnum auriculatum*, *Menyanthes trifoliata*, *Schoenus nigricans*, *Carex limosa* and *Eriophorum angustifolium*. The flat surfaces between HU and HO were covered by lawn level vegetation, which were divided into two groups according to water level and the abundance of the vegetation. High lawns (HL) had a vigorous cover of *S. nigricans*, *M. caerulea*, *E. tetralix* and *Rhynchospora alba*. Low lawns (LL) had water level closer to the surface than HL and were dominated by *R. alba*. The peat depth in the study site was 2–3 m.

Permanent sample plots were established by inserting six stainless steel collars (0.6 m×0.6 m×0.15 m) into the peat in HU, HL and LL, respectively in June 2003. To cover the entire vegetation community continuum, three sample plots were established in hollows in March 2004. Each collar had a water channel at the top to enable air sealing during gas sampling. Boardwalks were constructed around the sample plots to minimize disturbance. For the purposes of analysis, within the vegetation community groups, the sample plots were coded according to their water level (WT) using numbers from 1 to 6. Consequently, HU1 was the driest and HO3 the wettest sample plot.

CH₄ flux measurements

CH₄ measurements began in August 2003 and were carried out at biweekly to monthly intervals until September 2004 when a water level manipulation experiment was started in 12 sample plots (data not shown). After this date measurements were continued until September 2005 in those plots that were not part of the water level manipulation experiment (i.e. HU1, HU2, HL2, HL4, LL4, LL5, HO1, HO2 and HO3). The closed chamber method was used (Saarnio et al. 1997). Each chamber (0.6 m×0.6 m×0.25 m) had a vent to ensure pressure equilibration, which was closed only after the chamber had been placed on the collar. A fan ensured the circulation of air inside

the chamber and the water filled channel enabled air sealing during gas sampling. Four 40 ml air samples were taken into plastic syringes equipped with three way stopcocks, at 5 min intervals. A 10-min interval was used in wintertime when low flux rates were a norm due to cold temperatures and low vascular plant cover. Samples were analysed within 48 h on a Shimadzu GC-14-B gas chromatograph equipped with a flame ionisation detector (FID). Column, injector and detector temperatures were set to 40, 100 and 330°C, respectively and nitrogen was used as the carrier gas. The GC was regularly calibrated using a CH₄ standard (4 ppm; BOC Gases Ireland Ltd.). In order to remove moisture, samples and standards were injected through a 12 cm long Tygon tube (6 mm diameter) filled with drierite (10/20 mesh) prior to entering the 2 ml sample loop. The CH₄ concentration in the chamber headspace increased linearly with time and the flux rates were calculated as the linear rate of change in gas concentration over time (mg CH₄ m⁻² day⁻¹).

To relate fluxes to environmental conditions, the temperatures inside the chamber and in the peat at 5, 10, 20 and 30 (T_5 , T_{10} , T_{20} , T_{30}) cm depths were measured during CH₄ measurements. The water level (WT) was measured from perforated PVC pipes inserted into the peat adjacent to each sample plot.

The vascular green leaf area of CH₄ transporting species (*C. limosa*, *E. angustifolium*, *Eriophorum vaginatum*, *M. trifoliata*, *M. caerulea*, *R. alba*, *S. nigricans*, *Trichophorum caespitosum*) (VGA_{AER}) was used to relate the CH₄ flux to the sample plot vegetation. VGA_{AER} was estimated by summing up the green leaf area (GA) of each species. Green leaf area was measured at biweekly to monthly intervals and regression models were used to describe the seasonal dynamics in GA. For a description of the measurement method and regression models see Laine et al. (2006). The percentage cover of each moss species was estimated for each sample plot in August 2004. The nomenclature of the vascular plants, mosses and liverworts follows Stace (1997), Smith (2004) and Smith (1990), respectively.

Modelling of CH₄ fluxes

Nonlinear regression modelling was used to reconstruct CH₄ fluxes over the study period from August 2003 to September 2005 by establishing relationships

between CH₄ fluxes and environmental variables. To facilitate statistical analysis, we reconstructed the annual CH₄ flux for each sample plot individually and thus the model was parameterised for each sample plot. As has been shown previously (Kettunen et al. 2000) the performance of the models increased when data from different vegetation communities was treated separately. We used a multiplicative model format in which the sub-models, representing the responses of fluxes to different environmental variables, were multiplied by each other. We examined the distribution of residuals of the individual response functions and models to validate the model formats and to choose the necessary terms and parameters for the models. Temperature had the highest explanatory power. Air temperature and soil temperatures at different depths from 5 to 30 cm below surface were tested and showed little differences in response to CH₄ fluxes. Soil temperature at 20 cm depth (T_{20}) was used in modelling, partly for practical reasons, since the continuous time series at the onsite weather station between 2003 and 2005 was most complete for that temperature depth. CH₄ fluxes had an exponential relationship with temperature. In most sample plots the linear WT function increased the goodness of fit of the models; in sample plots HU2, HU3, HU4, HU5, HU6, LL1, LL3 and LL4 where it did not increase the explanatory power, it was replaced with a parameter a . VGA_{AER} was strongly correlated with temperature and therefore it was not included in the model. The models took the form:

$$CH_4 = (c + dWT)(\exp(bT_{20})) \quad (1)$$

where b , c and d are parameters, WT is water level and T_{20} is soil temperature at 20 cm depth. The model parameters and R^2 for each plot are given in Table 1.

CH₄ flux integration

An hourly time series of T_{20} were obtained from a weather station located ~250 m from the study site (Sottocornola and Kiely 2005) and linear interpolation between the measurement campaigns was used to reconstruct the daily WT for each sample plot. Using these environmental data and sample plot specific models, the CH₄ flux was estimated for each hour of the study period. The annual CH₄ flux was integrated for each sample plot from October 2003 to September

Table 1 Model parameters and R^2 for each sample plot

SP	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	R^2
HU1		0.106 (0.043)	0.167 (0.099)	0.003 (0.003)	0.24
HU2	0.084 (0.064)	0.143 (0.053)			0.29
HU3	0.055 (0.041)	0.073 (0.054)			0.17
HU4	0.001 (0.002)	0.458 (0.104)			0.73
HU5	0.013 (0.023)	0.270 (0.117)			0.40
HU6	0.002 (0.002)	0.431 (0.083)			0.73
HL1		0.3210 (0.0856)	0.0159 (0.0197)	0.0002 (0.0005)	0.73
HL2		0.299 (0.060)	0.018 (0.016)	0.0004 (0.0004)	0.71
HL3		0.418 (0.096)	0.004 (0.006)	0.0001 (0.0001)	0.81
HL4		0.521 (0.125)	0.0002 (0.001)	0.00001 (0.00002)	0.65
HL5		0.475 (0.096)	0.002 (0.003)	-0.00001 (0.0001)	0.84
HL6		0.243 (0.074)	0.028 (0.030)	0.001 (0.001)	0.57
LL1	0.003 (0.004)	0.446 (0.097)			0.72
LL2		1.155 (0.286)	2.8E-08 (1.2E-07)	-4.6E-09 (2.0E-08)	0.83
LL3	0.011 (0.017)	0.360 (0.108)			0.68
LL4	0.004 (0.006)	0.336 (0.097)			0.50
LL5		0.177 (0.073)	0.150 (0.154)	0.008 (0.009)	0.33
LL6		0.375 (0.066)	0.003 (0.003)	-0.0006 (0.001)	0.87
HO1		0.241 (0.056)	0.024 (0.019)	-0.001 (0.001)	0.69
HO2		0.177 (0.075)	0.295 (0.336)	-0.035 (0.043)	0.55
HO3		0.136 (0.055)	0.768 (0.649)	-0.066 (0.058)	0.66

2004 and from April 2004 to May 2005 for the hollow sample plots. Fluxes were averaged for each of the vegetation community groups: HU, HL and LL. Due to the differences in vegetation properties and in flux rates, HO1 was treated separately, while fluxes of HO2 and HO3 were averaged and presented as HO2-3.

In addition, we performed a sensitivity analysis for the temperature dependency of the modelled CH_4 flux of each sample plot by changing the environmental input of T_{20} by $\pm 10\%$.

Water chemistry analysis

Soil water chemistry samples were collected from the bog area in December 2005, (Unpublished data, M. Sottocornola). Sampling wells of 4.5 cm diameter PVC pipes pierced with 4 mm diameter holes on opposite sides every 2.5 cm were inserted into the peat prior to sampling. Water samples were collected using an electric water pump. Samples were taken from HU ($n=20$), HL ($n=41$), LL ($n=15$) and HO ($n=9$), respectively. Samples were not taken from the gas flux sample plots. Samples were analysed for Ca, Na, Cl and SO_4^{2+} using flow injection analysis and ion chromatography (QuikChem IC+FIA 8000 series, Lachat Instruments, Milwaukee, USA), while pH

was determined on site (WTW pH 320 model, Geotech Environmental Equipment, Inc, Colorado, USA).

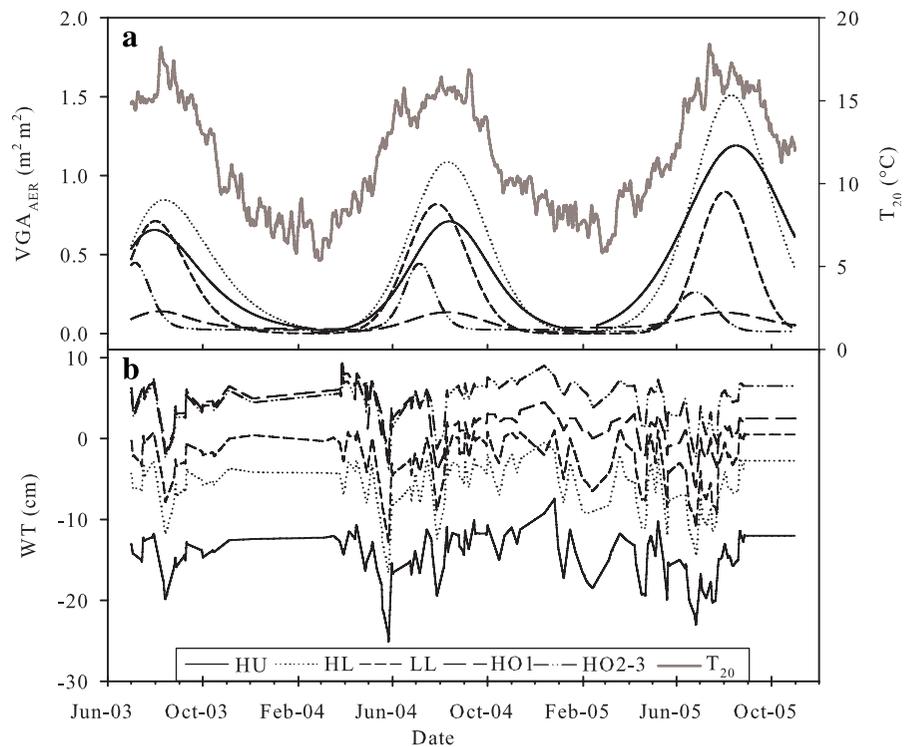
Results

Environmental conditions

Environmental conditions were relatively similar during the 3 years of the study. During 2003, 2004 and 2005 the annual rainfall in the study site was 2510, 2356 and 2459 mm yr^{-1} , respectively. The average air temperature for the warmest month of July and the coldest month of February was 14.6 and 6.1°C, respectively, during the 3-year study period. The annual average air temperature varied from 10.3 to 10.7°C between the years. The variation in average daily soil temperature at 20 cm depth (T_{20}) was modest (from 5.3 to 18°C) over the 29-month study period (Fig. 1a).

The vascular green leaf area of CH_4 transporting species (VGA_{AER}) followed the seasonal trend in temperature but peaked more distinctively than temperature during summers (Fig. 1a). VGA_{AER} varied between vegetation communities (ANOVA,

Fig. 1 Environmental conditions during the study period. **a** Vascular green leaf area of CH₄ transporting plants (VGA_{AER}) in vegetation communities hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO3, HO2-3) and average daily soil temperature at 20 cm depth (*T*₂₀). **b** Average daily water level (WT) in different vegetation communities



$p < 0.05$), being highest in high lawn and lowest in hollow communities. The peak in VGA_{AER} of high lawns was higher in the summer of 2005 than in the summer of 2003 (Tukey, $p < 0.05$) (Fig. 1a). The VGA_{AER} of hollows was somewhat lower in the summer of 2005 compared to the two previous summers. The different vegetation communities were characterized by different water levels (WT). Hummocks had the deepest WT, while hollows were regularly inundated (Fig. 1b). The WT varied moderately during the study period (Fig. 1b). The deepest WT was measured at the end of May 2004 when the WT in hummocks was 25 cm below the soil surface.

Soil water chemistry (pH, Na, Ca, Cl, SO₄²⁻) within the bog area varied little between vegetation communities (Table 2). However, the pH of hollows (4.7) was somewhat higher than that of other communities (4.5–4.6) (Tukey, $p < 0.05$) and SO₄²⁻ concentration was higher in high lawns compared to low lawns and hollows (Tukey, $p < 0.05$) (Table 2).

Spatial variation in CH₄ flux

The measured mean CH₄ flux varied between vegetation communities from 3 to 53 mg m⁻² day⁻¹ (Fig. 2). Fluxes were lowest in hummock plots that

Table 2 Soil water chemistry in vegetation communities: hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO)

Vegetation communities	pH	Na (mg l ⁻¹)	Ca (mg l ⁻¹)	Cl (mg l ⁻¹)	SO ₄ ²⁺ (mg l ⁻¹)
HU	4.5 (0.1)	6.4 (0.9)	0.9 (0.6)	8.6 (1.2)	1.8 (0.5)
HL	4.5 (0.1)	6.8 (1.4)	0.8 (0.4)	9.0 (1.2)	2.0 (0.5)
LL	4.6 (0.2)	6.3 (0.5)	0.8 (0.5)	8.8 (1.2)	1.6 (0.5)
HO	4.7 (0.2)	6.3 (0.5)	0.7 (0.4)	8.7 (0.7)	1.5 (0.5)

Standard errors are presented in parenthesis.

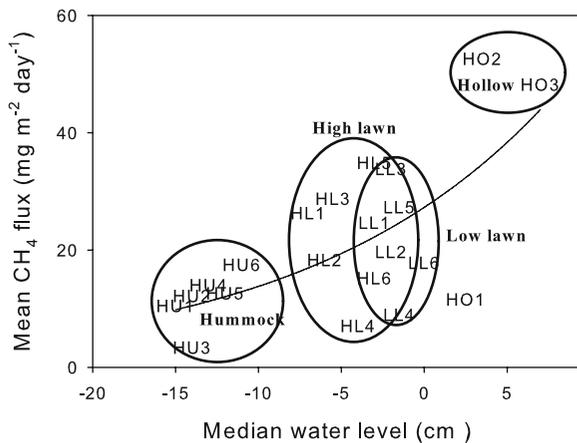


Fig. 2 Relationship between mean CH_4 flux and median water level of each sample plot. The R^2 is 0.43 and $p < 0.05$ for the exponential regression. Sample plots are grouped into vegetation communities: hummocks, high lawns, low lawns and hollows

had a median WT more than 10 cm below the surface (Fig. 2). The variation within the hummock plots was small compared to other vegetation communities (Fig. 2). Fluxes in lawns (HL, LL) were higher than in hummocks and had greater variation between the sample plots. The mean fluxes in high lawn and low lawn communities were of similar magnitude (Table 3) ranging from 7.1 to $34.9 \text{ mg m}^{-2} \text{ day}^{-1}$ between sample plots (Fig. 2). The variation (SD) and the maximum flux were higher in low lawn than in high lawn (Table 3). One hollow measured (HO1) had a low VGA_{AER} and lacked *Menyanthes trifoliata*, and therefore had low CH_4 flux compared to other vegetation communities, while the other hollows (HO2-3) had the highest fluxes (Table 3). Statistically the differences in annual flux estimates between the four vegetation communities (HU, HL, LL, HO) were insignificant (ANOVA, $p = 0.06$); however, the post

hoc test showed that hummocks and hollows had significantly different fluxes (Tukey, $p < 0.05$).

Seasonal patterns in CH_4 fluxes

Seasonality was evident in all vegetation communities (Fig. 3). The measured fluxes were low from December until May (Fig. 3) with an average of $7.9 \text{ mg m}^{-2} \text{ day}^{-1}$ ($\text{SE} = 0.94$, $n = 132$). The cumulative wintertime fluxes (November–April) at $0.7 \text{ g CH}_4 \text{ m}^{-2}$ were identical in hummock, high lawn and low lawn communities and were 26, 13 and 15 % of the annual flux, respectively. Winter fluxes in hollow plots HO1 and HO2-3 were 0.5 and $1.4 \text{ g CH}_4 \text{ m}^{-2}$ and represented 31 and 10 % of the annual flux, respectively. Flux rates started to increase in early summer and peaked during August (Fig. 3). The study period included three summers (2003, 2004 and 2005) that showed no significant differences in cumulative peak season (July–September) CH_4 fluxes (one-way ANOVA, $p > 0.05$). Therefore, interannual variation was not observed.

Annual CH_4 flux

The annual CH_4 flux estimates were reconstructed for each sample plot using regression models. The average annual fluxes varied between vegetation communities: HO1 and hummocks had low fluxes; fluxes in high lawns were slightly higher than in low lawns; while HO2-3 were the hotspots of CH_4 (Table 3). The standard errors (SE) of the average annual fluxes of vegetation communities ranged from 0.1 to 1.3 (Table 3).

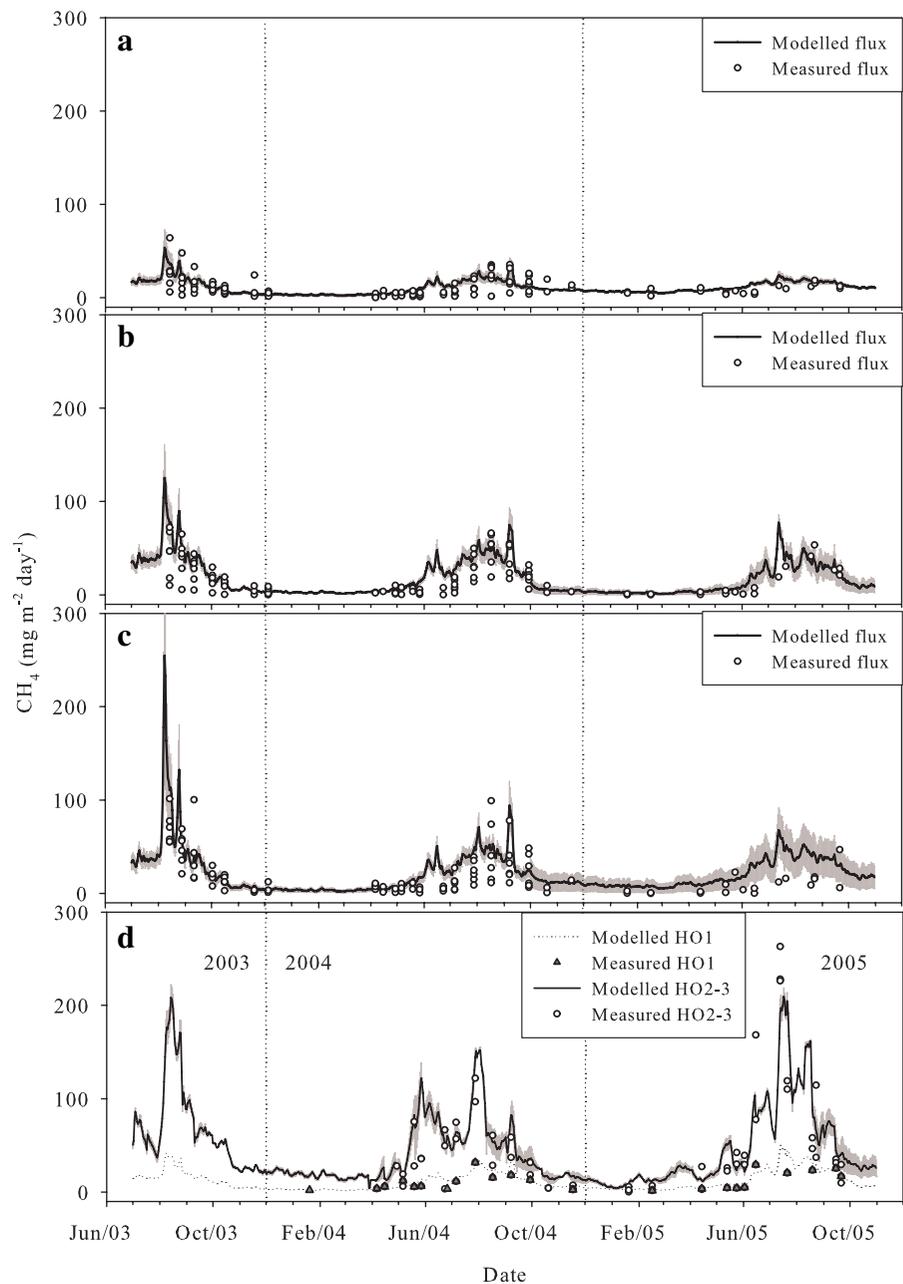
Laine et al. (2006) surveyed the distribution of vegetation communities within an area of $\sim 28 \text{ ha}$ in

Table 3 Methane flux statistics and median water level for vegetation groups (VG) hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO1, HO2-3)

VG	Annual ($\text{g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$)	CH_4 flux ($\text{mg m}^{-2} \text{ day}^{-1}$)					Water level (cm)
		Mean	SD	Min	Max	<i>N</i>	
HU	3.3 (0.5)	11.8	10.9	0.1	64.1	112	-13
HL	5.8 (1.1)	19.2	19.1	0.0	72.2	109	-5
LL	6.1 (1.4)	20.9	23.3	0.1	101.4	111	-1
HO1	3.5	11.6	9.4	1.7	31.8	23	3
HO2-3	13.0 (0.1)	50.4	54.6	0.3	263.0	50	5

The annual fluxes for HU, HL and LL are calculated for the time period 1st October 2003–30th September 2004. Annual fluxes for HO are calculated for the time period 1st April 2004–31st March 2005. Standard error of the annual flux is given in parenthesis.

Fig. 3 Measured (circles) and modelled (line) CH_4 flux in vegetation communities: **a** hummocks, **b** high lawns, **c** low lawns and **d** hollows from July 2003 to October 2005. Grey shadow is the standard error of the modelled mean CH_4 flux of the sample plots. Starting from September 2004, only fluxes from sample plots HU1, HU2, HL2, HL4, LL4, LL5, HO1, HO2 and HO3 are shown. HO1 (grey triangles) is treated separately from the other two HO sample plots due to different plant species composition



the bog and we used the same distribution (6, 62, 21 and 11 % for hummocks, high lawns, low lawns and hollows respectively) to estimate the areal CH_4 flux. Since Laine et al. (2006) did not classify the hollow communities according to the occurrence of *Menyanthes trifoliata* we used an average flux of the three hollow plots ($9.8 \text{ g CH}_4 \text{ m}^{-2} \text{ year}^{-1}$) in the weighting procedure. The areal annual flux was $6.2 \text{ g CH}_4 \text{ m}^{-2} \text{ year}^{-1}$.

Factors controlling CH_4 flux

The spatial variation was most strongly related to WT. The relationship between median WT and mean CH_4 fluxes of sample plots was exponential (Fig. 2). Variation between hummocks was small but followed the WT gradient, except in HU3 that had a very low flux (Fig. 2). The variation of fluxes in high lawn and low lawn sample plots was independent of WT. The

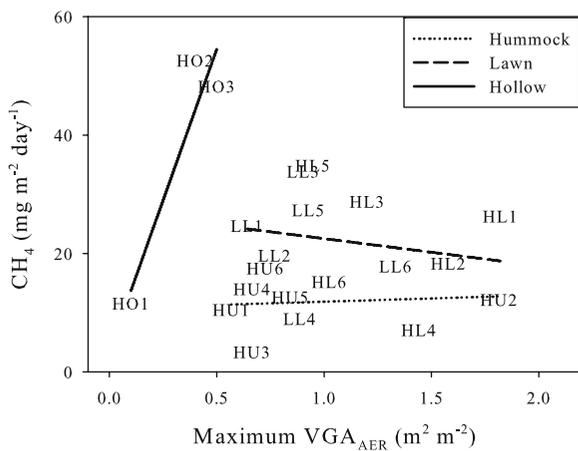


Fig. 4 Relationship between mean CH₄ flux and maximum leaf area of CH₄ transporting species (VGA_{AER}) of each sample plot. Separate relationships are defined for each vegetation community i.e. hummocks, lawns (high and low lawns) and hollows

small flux in HO1 could not be explained by WT (Fig. 2).

No clear relationship was found between VGA_{AER} and CH₄ flux (Fig. 4) with VGA_{AER} having little effect on the spatial variation in CH₄ fluxes, except in hollow communities where it was positively correlat-

ed with CH₄ flux (Fig. 4). The R² of the correlations were 0.89, 0.03 and 0.01 for hollows, lawns and hummocks, respectively, *p* values for all regressions were >0.05 and therefore regressions were statistically insignificant.

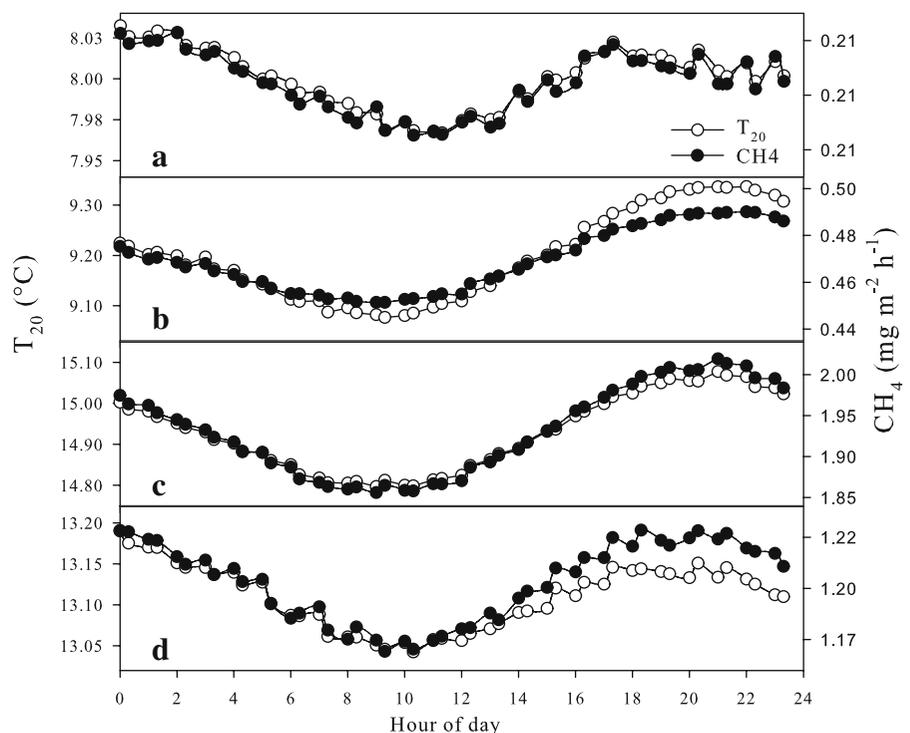
In the CH₄ flux model the seasonal variation in fluxes was explained by soil temperature at 20 cm depth (*T*₂₀) and WT. In all sample plots *T*₂₀ explained most of the variation in CH₄ flux, with an average R² of 0.54 (SD=0.21), while the effect of oscillating WT was less clear, with an average R² of 0.11 (SD=0.15). The CH₄ flux was highly dependent on *T*₂₀, since a 10 % increase in *T*₂₀ data caused on average 77% increase in the annual CH₄ flux (SE=23) and 10% decrease in *T*₂₀ data caused on average 35% decrease in the annual CH₄ flux (SE=4). The diurnal pattern in CH₄ flux followed the *T*₂₀ during all seasons (Fig. 5).

Discussion

Spatial variation in CH₄ flux

In general methane fluxes followed the WT gradient being lowest in hummocks and highest in hollows. In

Fig. 5 Diurnal cycle of average hourly soil temperature at 20 cm depth (*T*₂₀) and CH₄ flux (in sample plot HL1) during **a** winter (November–February), **b** spring (March–May), **c** summer (June–August), and **d** autumn (September–October)



hollows the presence of *Menyanthes trifoliata* seemed to determine the flux level; however due to limited sampling this observation requires further investigation. A similar pattern in CH₄ flux has been detected in many peatland ecosystems (e.g. Bubier et al. 1993; MacDonald et al. 1998). Compared to similar vegetation communities in a Scottish blanket bog (Fowler et al. 1995; MacDonald et al. 1998) our mean CH₄ fluxes were similar in hollows, but were 270% higher in hummocks and 47% lower in lawns (Table 3). Compared to continental raised bogs the mean fluxes in different vegetation communities were in the same range as those measured in a Swedish bog by Granberg et al. (1997). However, Bubier et al. (1993) measured lower fluxes in hummocks (2.3 mg m⁻² day⁻¹) and lawns (15.6 mg m⁻² day⁻¹) in Canada than was observed in this study. The most likely reason for the lower fluxes in the Canadian site is the lower WT that ranged from -15 cm in hollows to -46 cm in hummocks.

Although high and low lawns had different WT and VGA_{AER}, they had similar CH₄ fluxes. This is in contrast to the marked difference in net ecosystem CO₂ exchange (NEE) between the two communities (Laine et al. 2006). Low lawn plots had negative annual NEE (i.e. were sources of CO₂), while high lawn plots had positive annual NEE. This suggests that the spatial variation in CH₄ and CO₂ fluxes is controlled by different mechanisms. The low lawns were dominated by almost pure stands of *Rhynchospora alba*. Although this community had low productivity, it appears that the plants were as effective at producing substrate for methanogens and in transporting CH₄ through the shallow aerobic peat layer as the more diverse and higher productivity high lawn vegetation, where the CH₄ oxidation in the thicker aerobic layer may have been higher (Frenzel and Karofeld 2000).

Seasonal variation in CH₄ flux

The seasonal dynamics in CH₄ fluxes were similar in all vegetation communities and followed the changes in temperature and leaf area, being highest in late summer. Similar seasonality has been observed in a blanket bog (Chapman and Thurlow 1996) and other peatlands (e.g. Saarnio et al. 1997).

The summertime fluxes were at the same level in all 3 years and no interannual variation was observed.

This reflects the similarity in environmental conditions during the three years of the study. Most of the interannual variation is caused by differences in hydrological condition and temperature (Granberg et al. 2001a). In our study the difference in precipitation between the driest and wettest year was only 150 mm (c. 5%) and the annual average temperature varied by only 0.3°C. The interannual differences in weather conditions are generally small in Ireland compared to continental areas; during the past 20 years the average annual temperature has varied within 2°C and rainfall within 300 mm year⁻¹ (Sweeney et al. 2002). As an example, in Finland during the same time period the variation in average annual temperature was ~4°C and in rainfall ~500 mm year⁻¹ (http://www.fmi.fi/saa/tilastot_99.html#1).

The contribution of wintertime flux (November–April) to the annual flux was similar to that measured in bogs in Finland (Alm et al. 1999). The contribution of wintertime was highest in HO1 with low annual flux and little temporal variation and lowest in HO2-3, which had a distinctive growing season peak flux resulting from the growth pattern of *Menyanthes trifoliata*. The spatial variation between vegetation communities was less pronounced during winter, when hummocks, high lawns and low lawns in particular had nearly identical fluxes.

Annual CH₄ flux

Our estimate of the average annual flux for the blanket bog is 6.2 g CH₄ m⁻² year⁻¹. This is similar to the few existing estimates for blanket bogs that are 4.9 g CH₄ m⁻² year⁻¹ (Chapman and Thurlow 1996) and 6.9 g CH₄ m⁻² year⁻¹ (Hargreaves and Fowler 1998). Overall, the estimates (3.3 to 13.0 g CH₄ m⁻² year⁻¹) for the different vegetation communities are in the low end of the range measured in different wetlands. The CH₄ flux estimates vary largely ranging from 3.6 g CH₄ m⁻² year⁻¹ in a non-forested bog to 80 g CH₄ m⁻² year⁻¹ in a temperate marsh (e.g. Cao et al. 1996; Granberg et al. 2001a; Huttunen et al. 2003; Kim et al. 1998).

Due to the maritime impact, blanket bog vegetation shares some characteristics with fens (O'Connor and Skeffington 1997; Osvald 1949); in the study site this is indicated by the high proportion of sedges compared to continental bogs where the major part of biomass and leaf area are composed of mosses and

shrubs (Moore et al. 2002). For the same reason blanket bogs have higher pH than continental bogs (Shotyk 1997). The pH in ombrotrophic bogs is usually <4 (Laine and Vasander 1996), while in the study site the pH ranged from 4.2 to 5.1. pH is one of the factors affecting CH₄ flux (Crill et al. 1988), with most methanogens having an optimum at pH 6 (Williams and Crawford 1984). Even though the vegetation in the study site was dominated by aerenchymatous species and the pH was high compared to continental bogs, the CH₄ fluxes were still at a lower range of those measured in continental fens (Huttunen et al. 2003; Saarnio et al. 1997). High sulphate (SO₄²⁺) concentrations are known to suppress CH₄ flux due to competition of sulphate reducing bacteria. SO₄²⁺ concentrations are, however, seldom expressed together with CH₄ fluxes, and they also vary considerably throughout the year. The SO₄²⁺ concentration in the studied bog was low (0.52–3.81 mg l⁻¹) compared to other measurements in blanket bogs in Ireland and the UK (3.5–4.7 mg l⁻¹) (Adamson et al. 2001; Proctor 2006; Shotyk 1997) but higher than in peatlands in Ontario (Vitt and Bayley 1984).

The CH₄ fluxes might be underestimated, since the estimate does not consider ebullition that may be abundant in the mud bottom hollows. Estimating the amount and importance of episodic ebullition is difficult (Chanton 2005). Yet, Christensen et al. (2003) estimated that ebullition may account for 18 to 50% of the CH₄ flux in wetland monoliths, depending on vegetation properties and temperature. We did not encounter ebullition during the chamber measurements since the measured increase in CH₄ concentration with time was always linear; however some ebullition is likely to occur. Using chamber method to estimate temporal (seasonal, annual) CH₄ fluxes has been criticized due to the discontinuous measurements. However, chamber CH₄ measurements can result in similar and equally reliable seasonal flux estimates as continuous eddy covariance measurements, this was shown by Riutta et al. (2007) in a Finnish fen, which has comparable vegetation to the site of this study.

The diurnal variation was not considered, as its importance is likely to be insignificant as was detected by Rinne et al. (2007) in a Finnish oligotrophic fen using continuous eddy covariance measurements. Fowler et al. (1995), also using eddy

covariance method, found that the diurnal variation correlated with temperature variation in a Scottish blanket bog. Similarly, we observed a high temperature dependency on the fluxes. In addition, the study site did not include plant species that are known to have a pronounced effect on diurnal dynamics of CH₄ flux e.g. *Phragmites australis* and *Typha latifolia* (Armstrong et al. 1996; Whiting and Chanton 1996).

Environmental controls on CH₄ flux

The correlation between sample plot WT and CH₄ flux is evident. Within the WT range experienced in this study (from -15 to 7 cm) the CH₄ flux increased exponentially. A similar relationship has been observed, for example, by Moore and Roulet (1993) and Saarnio et al. (1997). A high WT induces the anaerobic conditions required for CH₄ production and therefore controls the size of the microbial population (Dise et al. 1993). A high WT also affects the oxidation capacity of methanotrophs (Frenzel and Karofeld 2000) and through vegetation, the substrate quality and quantity (Moore and Dalva 1993).

The effect of WT on seasonal CH₄ flux dynamics was more complex. Throughout the study period the variation in WT was less than 20 cm, with more oscillation during the summer and remaining high during the winter. The high winter WT did not cause high CH₄ fluxes due to the contrasting effect of low temperature and low substrate input for methanogens during the nongrowing season. In addition, the regression models were unable to capture the effect of the oscillating WT especially in June/July of 2004. Moore and Roulet (1993) also found it difficult to explain the temporal pattern between WT and CH₄ flux. This may be due to hysteresis (Lloyd et al. 1998; Moore and Dalva 1993), where there is a considerable lag between changes in WT and CH₄ flux.

Bowes and Hornibrook (2006) measured significantly higher flux rates in plots with dense vascular plant cover and concluded that passive plant-mediated transport was responsible for the majority of CH₄ flux in a blanket bog. In our study the effect of vegetation was unclear and connected to WT. The leaf area of vascular plants and moss cover were highest in hummocks and high lawns, which also had the highest net ecosystem CO₂ exchange (NEE) (Laine et al. 2006). The deep WT was a more important regulator than vegetation in these communities and

CH₄ fluxes were low. Therefore, no relationship was found between VGA_{AER} and CH₄ flux in lawn and hummock communities.

The importance of vascular plants is obvious in the inundated vegetation communities. The presence of *Menyanthes trifoliata* in HO2-3 is likely to be responsible for the substantially higher flux rates than in HO1. This observation is based on only three sample plots and the quantification of the effect of *M. trifoliata* would require further sampling. However, the importance of *M. trifoliata* for CH₄ fluxes was observed also in a Scottish blanket bog (MacDonald et al. 1998). *M. trifoliata* is an efficient transporter of CH₄ and the emission occurs through the stems (MacDonald et al. 1998). Frenzel and Karofeld (2000) found large differences in CH₄ dynamics between different types of hollows and pools and considered vascular plants to indicate hotspots for CH₄ emissions, while in *Sphagnum* covered and mud-bottom hollows oxidation decreased flux rates significantly since CH₄ transport through vascular plants did not occur.

Temperature was the driver of seasonal variation in CH₄ fluxes. It affects the metabolic rate of the microbial communities (Dise et al. 1993) and since methanogens are more sensitive to temperature than methanotrophs (Dunfield et al. 1993), the seasonality is accentuated. The seasonal development of VGA_{AER} is closely coupled with temperature and even if VGA_{AER} was not included in the CH₄ flux model it is likely to affect the seasonal flux dynamics.

Within the bog the variation in soil water chemistry between the vegetation communities was small and unable to explain the spatial variation in flux levels. The high variation in CH₄ fluxes in lawn communities was not connected with WT, vegetation or water chemistry but may be linked with possible spatial variation in microbial communities.

CH₄ flux in relation to net ecosystem CO₂ exchange (NEE)

The areal annual CH₄ flux was 5.8 % of the areal NEE (Laine et al. 2006). Despite the small CH₄ flux rate, this is more than was estimated by Cao et al. (1996) (4.2 %) for temperate wetlands. For each vegetation community the CH₄ flux was 1.9, 3.7 and 30 % of NEE in hummocks, high lawns and hollows, respectively. For low lawns, which are a net source of

CO₂, the CH₄ flux increased the C source strength by 47% from 9.8 to 14.3 g C m⁻². This result highlights the importance of CH₄ fluxes in the wet and low productivity communities of the bog.

Conclusions

In this study, the CH₄ fluxes in a blanket bog are at a similar level to those in raised bogs, even if the consistently high WT, the large proportion of sedges in vegetation and the higher pH than in most bogs would suggest higher fluxes. Seasonal variation is strong and winter fluxes are similar to those of boreal bogs, although the temperature is significantly milder due to the maritime climate in Ireland.

The CH₄ flux is ~70 % lower in hummocks than in hollows. The controls on the spatial variation in CH₄ fluxes in maritime blanket bog are similar to those in continental raised bogs. Water level is the most important controller, while in inundated communities also vegetation composition, particularly the presence of *Menyanthes trifoliata* has an impact on the flux rate. The hollows with this species are hotspots for CH₄ emission.

CH₄ flux has modest importance for the carbon gas budget in dry, high productivity communities (hummocks, high lawns), while the impact is significant in the low productive communities with high water level (low lawns and hollows). In the studied blanket bog the average areal annual CH₄ flux was 5.8 % of the average annual NEE.

Acknowledgements This study was funded by the Environmental ERTDI Programme 2000-2006, financed by the Irish Government under the National Development Plan and administered on behalf of the Department of Environment and Local Government by the Environmental Protection Agency (CEL-TICFLUX 2001-CC-C2-M1). AL is funded by an Environmental Protection Agency PhD fellowship (Grant code 2002_PhD2_46). Thanks to Anna Nokso-Koivisto and Matteo Sottocornola for assistance with the field measurements and Adrian Birky for management of the weather station. We also appreciate valuable comments made by Sari Juutinen.

References

- Adamson JK, Scott WA, Rowland AP, Beard GR (2001) Ionic concentration in a blanket peat bog in northern England and correlations with deposition and climate variables. *Eur J Soil Sci* 52:69–79

- Alm J, Saarnio S, Nykänen H, Silvola J, Martikainen PJ (1999) Winter CO₂, CH₄ and N₂O fluxes on some natural and drained boreal peatlands. *Biogeochemistry* 44:163–186
- Armstrong J, Armstrong W, Beckett PM, Halder JE, Lythe S, Holt R, Sinclair A (1996) Pathways of aeration and the mechanisms and beneficial effects of humidity- and Venturi-induced convections in *Phragmites australis* (Cav.) Trin. ex Steud. *Aquat Bot* 54:177–197
- Bowes HL, Hornibrook ERC (2006) Emission of highly ¹³C-depleted methane from an upland blanket mire. *Geophys Res Lett* 33:DOI 10.1029/2005GL025209
- Bubier JL (1995) The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *J Ecol* 83:403–420
- Bubier JL, Costello A, Moore TR, Roulet NT, Savage K (1993) Microtopography and methane flux in boreal peatlands, northern Ontario, Canada. *Can J Bot* 71:1056–1063
- Bubier JL, Moore TR, Bellisario L, Comer NT (1995) Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. *Global Biochem Cycles* 9:455–470
- Cao M, Marshall S, Gregson K (1996) Global carbon exchange and methane emissions from natural wetlands: application of a process-based model. *J Geophys Res* 101(14):14399–14414
- Chanton JP (2005) The effect of gas transport on the isotope signature of methane in wetlands. *Org Geochem* 36:753–768
- Chapman SJ, Thurlow M (1996) The influence of climate on CO₂ and CH₄ emissions from organic soils. *Agric For Meteorol* 79:205–217
- Christensen TR, Panicov N, Masterpanov M, Joabsson A, Stewart A, Öquist M, Sommerkorn M, Reynaud S, Svensson B (2003) Biotic control on CO₂ and CH₄ exchange in wetlands—a closed ecosystem study. *Biogeochemistry* 64:337–354
- Conway V (1937) Studies in the autoecology of *Cladium mariscus* R.Br. III The aeration of the subterranean parts of the plant. *New Phytol* 36:64–96
- Crill PM, Bartlett KB, Harriss RC, Gorham E, Verry ES, Sebacher DI, Madzar L, Sanner W (1988) Methane flux from Minnesota peatlands. *Glob Biogeochem Cycles* 2:371–384
- Daulat WE, Clymo RS (1998) Effects of temperature and watertable on the efflux of methane from peatland surface cores. *Atmos Environ* 32:3207–3218
- Dise NB, Gorham E, Verry ES (1993) Environmental factors controlling methane emission from Peatlands in Northern Minnesota. *J Geophys Res* 98:10583–10594
- Dunfield P, Knowles R, Dumont R, Moore TR (1993) Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. *Soil Biol Biochem* 25:321–326
- Fowler D, Hargreaves KJ, Macdonald JA, Gardiner B (1995) Methane and CO₂ exchange over peatland and the effects of afforestation. *Forestry* 68:327–334
- Frenzel P, Karofeld E (2000) CH₄ emission from a hollow-ridge complex in a raised bog: the role of CH₄ production and oxidation. *Biogeochemistry* 51:91–112
- Garnet KN, Megonigal JP, Litchfield C, Taylor GE Jr (2005) Physiological control of leaf methane emission from wetland plants. *Aquat Bot* 81:141–155
- Granberg G, Mikkilä C, Sundh I, Svensson B H, Nilsson M (1997) Sources of spatial variation in methane emission from mires in northern Sweden: a mechanistic approach in statistical modeling. *Glob Biogeochem Cycles* 11:135–150
- Granberg G, Ottosson-Löfvenius M, Grip H, Sundh I, Nilsson M (2001a) Effect of climatic variability from 1980 to 1997 on simulated methane emission from a boreal mixed mire in northern Sweden. *Glob Biogeochem Cycles* 15:977–991
- Granberg G, Sundh I, Svensson BH, Nilsson M (2001b) Effects of temperature, and nitrogen and sulfur deposition, on methane emission from a boreal mire. *Ecology* 82:1982–1998
- Hammond RF (1981) The Peatlands of Ireland. An Foras Talúntais, Dublin, p 60
- Hargreaves KJ, Fowler D (1998) Quantifying the effects of water table and soil temperature on the emission of methane from peat wetland at the field scale. *Atmos Environ* 32:3275–3282
- Huttunen JT, Nykänen H, Turunen J, Martikainen PJ (2003) Methane emissions from natural peatlands in the northern boreal zone in Finland, Fennoscandia. *Atmos Environ* 37:147–151
- IPCC (2001) Climate change 2001. The scientific basis. Contribution of working group 1 to the third assessment report of the inter-governmental panel on climate change
- Käki T, Ojala A, Kankaala P (2001) Diel variation in methane emissions from stands of *Phragmites australis* (Cav.) Trin. ex Steud. and *Typha latifolia* L. in a boreal lake. *Aquat Bot* 71:259–271
- Kettunen A, Kaitala V, Alm J, Silvola J, Nykänen H, Martikainen PJ (2000) Predicting variations in methane emissions from boreal peatlands through regression models. *Boreal Environ Res* 5:115–131
- Kim J, Verma SB, Billesbach DP (1998) Seasonal variation in methane emission from a temperate *Phragmites*-dominated marsh: effect of growth stage and plant-mediated transport. *Glob Chang Biol* 5:433–440
- Laine J, Vasander H (1996) Ecology and vegetation gradients of peatlands. In Vasander H (ed) Peatlands in Finland, Finnish Peatland Society pp 10–19
- Laine A, Sottocornola M, Kiely G, Byrne KA, Wilson D, Tuittila E-S (2006) Estimating net ecosystem exchange in a patterned ecosystem: example from blanket bog. *Agric For Meteorol* 138:231–243
- Lloyd D, Thomas KL, Benstead J, Davies KL, Lloyd SH, Arah JRM, Stephen KD (1998) Methanogenesis and CO₂ exchange in an ombrotrophic peat bog. *Atmos Environ* 32:3229–3238
- MacDonald JA, Fowler D, Hargreaves KJ, Skiba U, Leith ID, Murray MB (1998) Methane emission rates from a northern wetland; response to temperature, water table and transport. *Atmos Environ* 32:3219–3227
- Moore TR, Dalva M (1993) The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. *J Soil Sci* 44:651–664
- Moore TR, Roulet NT (1993) Methane flux: water table relation in northern wetlands. *Geophys Res Lett* 20:587–590
- Moore TR, Bubier JL, Frolking S, Lafleur PM, Roulet NT (2002) Plant biomass and production and CO₂ exchange in an ombrotrophic bog. *J Ecol* 90:25–36

- O'Connor M, Skeffington MS (1997) Roundstone bog, conemara: the challenges for conservation. In: Tallis JH, Meade R, Hulme PD (ed) Blanket mire degradation, causes, consequences and challenges. The Macaulay Land Use Research Institute, Aberdeen, pp 189–202
- Osvald H (1949) Notes on the vegetation of British and Irish mosses. Acta Phytogeogr Sueic 26:1–62
- Proctor MCF (2006) Temporal variation in the surface-water chemistry of a blanket bog on Dartmoor, southwest England: analysis of 5 years' data. Eur J Soil Sci 57:167–178
- Rinne J, Riutta T, Pihlatie M, Aurela M, Haapanala S, Tuovinen J-P, Tuittila E-S, Vesala T (2007) Annual cycle of methane emission from a boreal fen measured by the eddy covariance technique. Tellus B 9:449–457
- Riutta T, Laine J, Aurela M, Rinne J, Vesala T, Laurila T, Haapanala S, Pihlatie M, Tuittila E-S (2007) Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem. Tellus B (in press)
- Saarnio S, Alm J, Silvola J, Lohila A, Nykänen H, Martikainen PJ (1997) Seasonal variation in CH₄ emissions and production and oxidation potentials at microsites on an oligotrophic pine fen. Oecologia 110:414–422
- Shotyk W (1997) Atmospheric deposition and mass balance of major and trace elements in two oceanic peat bog profiles, northern Scotland and the Shetland Islands. Chem Geol 138:55–72
- Smith AJE (1990) The liverworts of Britain and Ireland. Cambridge University Press, Cambridge
- Smith AJE (2004) The moss flora of Britain and Ireland. Cambridge University Press, Cambridge, p 1012
- Sottocornola M, Kiely G (2005) An Atlantic blanket bog is a modest CO₂ sink. Geophys Res Lett 32, L23804 DOI 23810.21029/22005GLO24731
- Sparling JH (1967) The occurrence of *Schoenus nigricans* L. in Blanket Bogs: I. environmental conditions affecting the growth of *S. nigricans* in Blanket Bog. J Ecol 55:1–13
- Stace C (1997) New Flora of the British Isles. Cambridge University press, Cambridge, p 1130
- Ström L, Ekberg A, Mastepanov M, Rojle Christensen T (2003) The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Glob Chang Biol 9:1185–1192
- Sweeney J, Donnelly A, McElwain L, Jones M (2002) Climate change. Indicators for Ireland. Environmental Protection Agency, Wexford, p 54
- Vitt DH, Bayley SE (1984) The vegetation and water chemistry of four oligotrophic basin mires in northwestern Ontario. Can J Bot 62:1485–1500
- Whiting GJ, Chanton JP (1996) Control of the diurnal pattern of methane emission from emergent aquatic macrophytes by gas transport mechanisms. Aquat Bot 54:237–253
- Williams RT, Crawford RL (1984) Methane production in Minnesota Peatlands. Appl Environ Microbiol 47:1266–1271