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METHANE EMISSION RATES FROM A NORTHERN WETLAND; RESPONSE TO TEMPERATURE, WATER TABLE AND TRANSPORT

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Abstract—Static chamber measurements of CH_4 flux were made from a range of micro-environments in an area of blanket bog in Northern Scotland. CH_4 flux covered a wide range, the largest rate of CH_4 emission, at 175.6 μmol m^{-2} h^{-1}, was observed in pool areas through the vascular plant *Menyanthes trifoliata*. Investigations into the response of net CH_4 emission rates to temperature and water table were carried out under semi-natural conditions on 45 large peat monoliths, maintained in open-top chambers, over a three-year period. The mean rate of CH_4 emission at 10°C was an order of magnitude larger from pool monoliths (surface water table) at 78.0 μmol m^{-2} h^{-1}, than from hummock monoliths (water table 15 cm below surface) at 8.4 μmol m^{-2} h^{-1}. Rates of CH_4 emission showed a positive linear response to increasing temperature from pool and lawn monoliths with activation energies of 74.3 and 79.5 kJ mol^{-1} and Q_{10} values of 3.0 and 3.3, respectively. When conditions of temperature, water table, light and humidity were controlled pool cores showed an exponential increase in CH_4 emission rates between 5 and 30°C.
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Key word index: Methanogenesis, vascular, oxidation, peat, stomata.

INTRODUCTION

Wetlands are the largest source for tropospheric CH_4 and estimates cover a wide range currently between 55 and 150 Tg yr^{-1} (IPCC, 1994). CH_4 emission from wetlands is characterised by high spatial and temporal variability (Roulet *et al*., 1993, Dise *et al*., 1993) and is affected by a wide variety of environmental variables. The primary controlling factor has been shown to be water table height (Moore and Dalva, 1993; Dise *et al*., 1993), which affects the degree of anaerobicity of the peat, an essential requirement for methanogenesis, and also affects the depth of the aerobic layer and hence the oxidising capacity of the peat. Soil temperature also strongly affects the rate of methanogenesis and can significantly affect annual variations in flux (Williams and Crawford, 1984; Crill *et al*., 1988). The transport of CH_4 from zones of production, through vascular plants (macrophytes), to the atmosphere can affect the net flux of CH_4 by bypassing oxic zones where the CH_4 would otherwise be oxidised. Using a specific inhibitor Oremland and Culbertson (1992) estimated that up to 90% of CH_4 produced could be consumed by methanotrophs at some sites. Plant-dependent transport of CH_4 is therefore an important pathway and has been estimated to account for up to 90% of the emission from a *Carex* dominated fen in Quebec, Canada and in an ombrotrophic peat in Michigan, USA (Whiting and Chanton, 1992; Shannon *et al*., 1996). Other factors found to affect rates of CH_4 emission include the presence of alternate electron acceptors such as sulphate or nitrate (Kristjansson *et al*., 1982; Fowler *et al*., this issue). Substrate quality and the botanical composition of the peat can also influence CH_4 production (Nilsson and Bohlin, 1993; Martikainen *et al*., 1995).

In order to investigate the environmental parameters affecting rates of CH_4 emission from wetland environments, measurements of CH_4 flux were made in the blanket bogs of Caithness, Northern Scotland. Processes affecting CH_4 flux were then investigated under controlled conditions at ITE Edinburgh. The effects of temperature and water table were investigated using peat monoliths in open top chambers (OTC's) (Fowler *et al*., 1989) and controlled environment cabinets (CONVIRONS). The transport of CH_4 through *Menyanthes trifoliata* (bog bean) was investigated in the field and in controlled conditions.

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MATERIALS AND METHODS

Site description

Field measurements were made at Loch More (ND 065453), 135 m asl, an area of blanket bog in The Flow Country, Caithness, Scotland in May 1994. The area of study represented a broad range of micro-environments ranging from a relatively dry area of bog heather moor to an open pool area, where pools represented up to 30% of the land cover. The total rainfall for 1994 was 1129 mm and the average temperature was 6.8°C (K. Hargreaves, personal communication). The vegetation and water table height from the sites studied are shown in Table 1.

Process-based investigations were carried out on intact peat monoliths (30 cm in diameter, 40 cm deep), which were collected using large cylindrical aluminium coring devices in 1992, from an area of blanket bog near Loch Caluim (ND 023511) in Caithness, an area similar in vegetation type and topography to Loch More. Three peat monolith types were cored and consisted of pools (or hollows) which had a surface water table and vegetation dominated by *Menyanthes trifoliata* and *Eriophorum* spp., lawn monoliths which had a water table 5 cm below the surface and vegetation dominated by *Sphagnum* spp., *Eriophorum* spp. and *Menyanthes trifoliata*, and hummock monoliths which had a water table 15 cm below the surface and vegetation which consisted primarily of *Eriophorum* spp., *Nardus stricta* and *Calluna vulgaris*. The use of these large monoliths allowed a close approximation of field conditions to be made, with the monoliths being large enough to maintain the peat structure and vegetation while allowing experiments under controlled conditions to be carried out.

Flux measurement methods

Measurements of CH_4 flux were made in the field, from peat monoliths under controlled conditions and from individual plants using the chamber techniques described below.

In the field CH_4 flux measurements were made using a static chamber method (MacDonald *et al*., 1996). Briefly, polypropylene chambers, volume 25 ℓ, (Clayton *et al*., 1994), were inserted into the ground to a depth of about 5 cm with as little disturbance as possible. Chambers were enclosed and ambient samples were taken at time zero and after periods of up to 20 min. Samples were collected into 1 ℓ tedlar bags and analysed using tunable diode laser spectroscopy (TDL), (Aerodyne Reasearch, MA), within 24 h of collection. Standard gas mixtures containing 2110 ppb CH_4 remained stable in the tedlar bags for at least two weeks. The flux was calculated from the change in concentration over a known time period, the headspace volume and the area of peat enclosed. Three peat samples (top 10 cm), were taken and bulked every time fluxes were measured. A subsample (2×10 g) was analysed for moisture content (% weight loss on drying). Soil temperature at 5 cm depth was routinely measured during flux measurements.

The long-term seasonal temperature response was carried out on the peat monoliths which were maintained in plastic buckets and were stored, sunk into the ground, in OTC's. Rainfall was kept out and water table heights were maintained at field levels with deionised water according to whether they were pool, lawn or hummock type (surface, 5 and 15 cm below the surface of the peat, respectively). Flux measurements from the pool, lawn and hummock cores were made over three sampling periods encompassing a wide range of environmental conditions. The sampling periods were October and November 1992, May–July 1993, and August and September 1995. The number of flux measurements made is shown in Table 2. In total 45 peat monoliths were sampled; 15 pools, 16 lawns and 14 hummocks. In 1992 and 1993 flux measurements were made using a dynamic chamber technique, whereby chambers (25 ℓ) were sealed to the peat monoliths. Headspace air samples and alternate ambient samples were withdrawn at a rate of $\sim 1\ \ell\ min^{-1}$ and analysed by flame ionisation detection gas chromatography (GC). In 1995 measurements were made using a static chamber technique similar to that used in the field with analysis by GC. In order to confirm the assumption that the change in headspace concentration was linear replicate samples were withdrawn at regular intervals using gas tight syringes (Hamilton, UK) and analysed by GC. The temperature profile within the peat was continuously recorded throughout each measurement.

A water table manipulation experiment on hummock monoliths was carried out during the August and September 1995 sampling period. In 3 monoliths the water table was raised from about 28 cm below the surface, to the surface over an 18 d period. Another 3 monoliths were allowed to dry out over the same measurement period. The flux of CH_4 was determined using a static chamber technique similar to the field technique described above.

A temperature response investigation was carried out on pool monoliths ($n = 3$) which were maintained in CONVIRONS under constant conditions of humidity (70%) and light ($300\ \mu E\ m^{-2}\ 12\ h^{-1}\ d^{-1}$). Flux measurements were made ($n = 4\ d^{-1}$) using a static chamber technique similar to the field technique described above, and were made in the dark, in order to avoid heating effects by the lights. A temperature response was carried out by maintaining the monoliths at 5, 10, 15, 20, 25 and 30°C, the temperature being stepped up every 24 h. Peat temperature was monitored using a temperature probe at 4 depths (0, 5, 10, 20 cm) which showed it took approximately 15 h for the whole core to equilibrate at each temperature. Following this investigation the monoliths were maintained at 15°C.

The vascular transport of CH_4 was investigated using peat monoliths in the OTC and CONVIRON. An infra-red gas

Table 1. CH_4 flux and site characteristics from the sites studied at Loch More, Caithness between 31 May and 20 June 1994

Site	Dominant vegetation	Water table (cm below surface)	Mean CH_4 flux (std. dev.) ($\mu mol\ m^{-2}\ h^{-1}$)	*n*
Bog heather moor	*Calluna vulgaris*	> 100[a]	1.5 (3.1)	40
Hummock	*Eriophorum* spp., *Sphagnum* spp. *Calluna vulgaris*	> 10	17.5 (8.0)	5
Hollow	*Sphagnum* spp., *Menyanthes trifoliata*	surface	128.8 (114.0)	6
Pool-open water	—	surface[b]	14.5 (6.6)	4
Pool-bog bean	*Menyanthes trifoliata*	surface[b]	175.6 (16.5)	5

[a]Peat depth was greater than 100 cm and water table was below subsoil.
[b]Depths of standing water estimated to be between 20 and 100 cm.

Table 2(a). Temperature response characteristics of the peat monoliths maintained in the OTC which showed a positive response to temperature. Flux measurements were made throughout October and November 1992, May–July 1993, and August and September 1995, and (b) Temperature response characteristics of the peat monoliths maintained in the OTC which showed a negative response to temperature during the August and September 1995 sampling period

Peat monolith	n	Slope (μmol m^{-2} h^{-1} °C^{-1})	E_a (kJ mol^{-4})	Q_{10} (5–15°C)	Mean CH_4 flux at 10°C (μmol m^{-2} h^{-1})
(a) Pool	100	11.4	74.3	3.0	78.0
Lawn	69	13.7	79.5	3.3	98.5
Hummock[a]	33	2.5	104.1	4.8	8.4
(b) Lawn	68	− 6.9	—[b]	—[b]	81.0
Hummock	81	− 1.1	—[b]	—[b]	11.3

[a]Not significant at 95%.
[b]E_a and Q_{10} were not applicable as a result of more than one process occuring.

analyser (Li-Cor, Lincoln, NE, USA) was used to measure stomatal conductance and CH_4 emission rates from individual leaves of *Menyanthes trifoliata*. Leaves (or stems or whole plants) were enclosed within a cuvette through which ambient air was circulated around a closed loop with a total volume of 1 ℓ. Stomatal conductance readings were made within one minute of closing the cuvette, the cuvette was then flushed with ambient air, and then closed again to allow the CH_4 measurement to be made. Samples were withdrawn using 5 ml gas-tight syringes (Hamilton) at time 0 and after 5 min. Enclosure time was minimised to avoid varying CO_2 concentrations and stomatal conductance. Relative humidity was kept constant by adjusting the flow of the gas through a dessicant. CH_4 samples were analysed by GC. CH_4 emission rates were measured from a range of plants in peat monoliths in OTCs. The effect of light was investigated by measuring CH_4 emission and stomatal conductance from plants in peat monoliths in CONVIRONS at 10°C and 20°C under light and dark conditions. The physiology of *Menyanthes trifoliata* was investigated by examining thin films and cross sections of leaves and stems under a compound microscope.

RESULTS

Field measurements of CH_4 *flux at Loch More*

The microtopography of the bog was split according to vegetation type and water table depth into the classes shown in Table 1. Peat temperature (5 cm) ranged from 7.8 to 12.5°C, however, this change was not linear over the measurement period and no significant effect on the CH_4 flux was observed. The flux of CH_4 spanned two orders of magnitude, from a small CH_4 source on the moorland of 1.5 μmol m^{-2} h^{-1} to greater than 150 μmol m^{-2} h^{-1} from open pool areas vegetated with *Menyanthes trifoliata*. Intra-site CH_4 flux also spanned a large range, particularly from the hollows where temperatures tended to be higher and ebullition could periodically be observed. In the open-water pool areas vascular transport of CH_4 through *Menyanthes trifoliata* was found to be the largest CH_4 source and emitted most of the CH_4 from the open water pool areas. CH_4 emission averaged 175.6 μmol m^{-2} h^{-1} from chambers containing *Menyanthes trifoliata*, compared to 14.5 μmol m^{-2} h^{-1} from open water.

The response of CH_4 *flux to water table height and temperature in the OTC*

Rates of CH_4 emission from the peat monoliths maintained in the OTCs were strongly affected by water table height. CH_4 emission rates were an order of magnitude smaller from the hummock monoliths with a mean emission rate at 10°C of 8.4 μmol m^{-2} h^{-1}, compared to 78.0 and 97.9 μmol m^{-2} h^{-1} from the pool and lawn monoliths, respectively (Table 2). Rates of CH_4 emission were not significantly different between pool and lawn monoliths. The distribution of CH_4 flux at 10°C measured from the three peat monolith types over the three measurement years with a constant water table height is shown in Fig. 1. The water table manipulation experiment on the hummock monoliths showed a significant positive response between increasing water table height and CH_4 emission rates. The response was log-linear and is shown in Fig. 2. However, the hummock monoliths which were allowed to dry out naturally showed no significant response, although the water table (which was already low) only dropped by about 3 cm over the measurement period.

Temperature also strongly influenced CH_4 flux on an annual basis. Of the pool monoliths (surface water table) in the OTC measured over the three years, 12 out of the 15 showed a positive linear response to increasing temperature. The mean temperature response of the monoliths is shown in Fig. 3a. The CH_4 emission rate increased at a rate of 11.4 μmol m^{-2} h^{-1} °C^{-1}. An Arrhenius plot of the data gave an activation energy of 74.3 kJ mol^{-1}, equivalent to a Q_{10} of 3.0 (Table 2). The lawn monoliths showed both positive and negative temperature responses. Eight out of the 16 monoliths showed a positive response to increasing temperature with an activation energy of 79.5 kJ mol^{-1} and a Q_{10} value of 3.3 (Table 2). The CH_4 emission rate increased at a rate of 13.7 μmol m^{-2} h^{-1} °C^{-1}. However, six of the monoliths, which were all measured during the late summer sampling period in 1995, showed a negative response

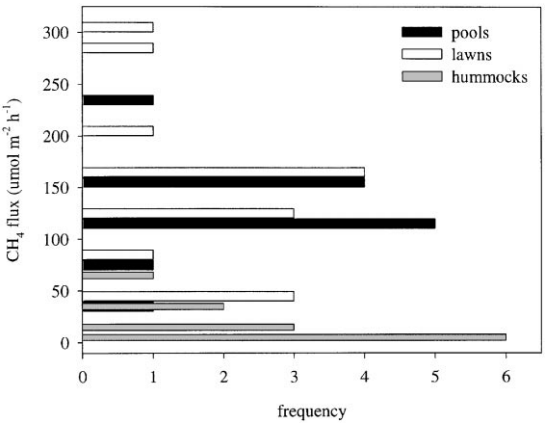

Fig. 1. The frequency distribution of CH_4 flux from the pool, lawn and hummock monoliths maintained in the OTC and measured October and November 1993, May–July 1993 and August and September 1995.

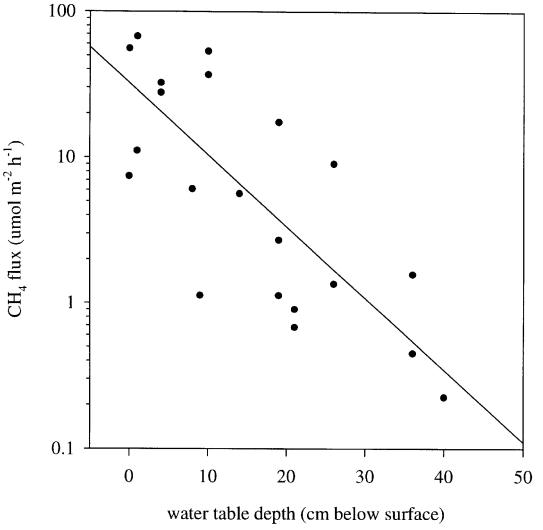

Fig. 2. The relationship between water table height and CH_4 flux ($r^2 = 0.621$, $p < 0.01$) from 3 hummock monoliths measured throughout September 1995.

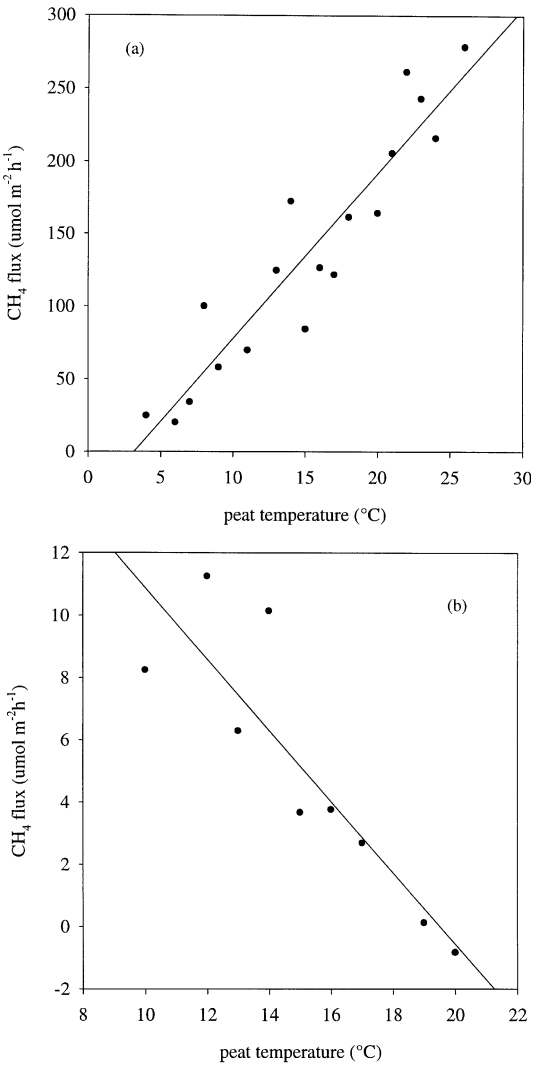

Fig. 3. (a) The correlation between temperature and CH_4 emission rates from the pool monoliths maintained in the OTC under semi-natural conditions measured ($n = 100$) throughout the period October and November 1993, May–July 1993 and August and September 1995. The regression equation was CH_4 flux = 11.4 × temperature − 36.0 ($r^2 = 0.877$, $p < 0.001$). (b) The negative correlation between CH_4 flux and soil temperature from 7 hummock monoliths measured during August and September 1995. The regression equation was CH_4 flux = − 1.14 × temperature + 22.3 ($r^2 = 0.773$, $p < 0.05$).

to temperature (Table 2). The hummock monoliths also showed both positive and negative responses to increasing temperature. Five out of the 14 monoliths showed a positive, although not statistically significant, response to increasing temperature. Only one monolith showed a net oxidation of CH_4 at 10°C. CH_4 emission rates from all seven of the monoliths measured during the late summer 1995 sampling period showed a negative response to increasing temperature (Fig. 3b). The temperature and water table response of CH_4 emission rates from all the pool, lawn and hummock monliths maintained in the OTC, which showed a positive response to increasing temperature, is shown in Fig. 4.

Response of CH_4 *flux to temperature in CONVIRONS*

Rates of CH_4 emission from each pool monolith in the CONVIRON increased exponentially with increasing temperature between 5 and 30°C. The response from Core 3 is shown in Fig. 5a. Arrhenius plots of each of the three temperature responses gave activation energies ranging between 51.8 and 73.2 kJ mol^{-1} and Q_{10} values between 2.2 and 3.0 (Table 3). Following the temperature response the monoliths were maintained at 15°C, however, depite an initial decrease (in monoliths 1 and 2), following

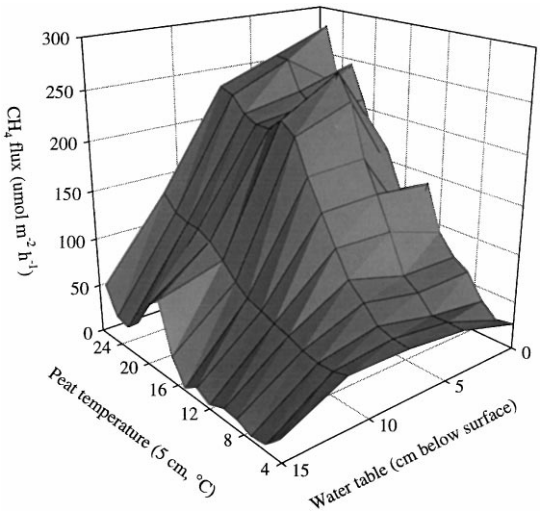

Fig. 4. The temperature and water table response of the pool (0 cm below the surface), lawn (5 cm below the surface) and hummock (15 cm below the surface) monoliths, maintained in the OTC and measured throughout the period October and November 1993, May–July 1993 and August and September 1995 for the pool monoliths and October and November 1993 and May–July 1993 for the lawn and hummock monoliths.

the temperature drop from 30 to 15°C, the CH_4 emission rate continued to increase (Fig. 5b). The rate of CH_4 emission from monolith 2 was greater after 9 d at 15°C ($\sim$260 μmol $m^{-2} h^{-1}$), than it had been at 30°C ($\sim$160 μmol $m^{-2} h^{-1}$).

CH_4 *emission through Menyanthes trifoliata*

Methane emission was observed to occur through the stems of *Menyanthes trifoliata* in a range of plants in peat monoliths in the OTC. It was found that the emission was occurring through the stems of the plants and no detectable flux was observed through the leaves alone. No significant correlation was observed between stomatal conductance and CH_4 emission rates. Peat temperature affected rates of CH_4 emission through the plants with significantly ($p < 0.05$) larger fluxes at 20°C than at 10°C. CH_4 fluxes ranged from 0.8 to 272.5 μmol $m^{-2} h^{-1}$. The internal structure of the *Menyanthes trifoliata* root and stem is shown in Plates 1a and b.

DISCUSSION

Field measurements of CH_4 *flux at Loch More*

The wide range of CH_4 emission rates observed in this study is typical of most wetland environments (Crill *et al*., 1988; Moore *et al*., 1990; Dise *et al*., 1993; Martikainen *et al*., 1995). Variations in the microtopography, on a scale of less than 1 m^2, creates a range of conditions, such as redox potential, water table depth, presence or absence of vascular plants, which strongly affect CH_4 production. Water table depth and plant transport appeared to be the most important factors affecting the CH_4 flux from the range of sites studied. However, temperature would presumably also have been important had

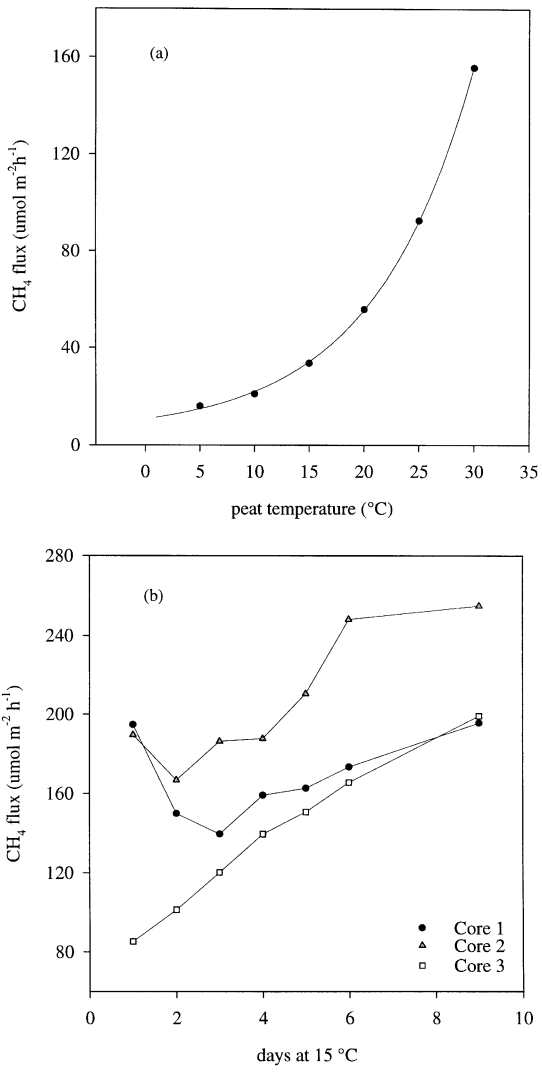

Fig. 5 (a) The temperature response of CH_4 emission from a pool core under controlled conditions. The regression equation was CH_4 flux $= 25.86 \times \exp(0.12 \times \text{temp.}) + 137.13$, and (b) Rates of CH_4 emission from the pool-type peat monoliths maintained at 15°C following the temperature response investigation.

Table 3. The temperature response characteristics of the peat monoliths maintained under controlled conditions in the CONVIRONS

Pool core	Mean CH_4 emission at 10°C (μmol $m^{-2} h^{-1}$)	Activation energy (kJ mol^{-1})	Q_{10} (5–15°C)
1	55.1	73.2	3.0
2	21.9	65.5	2.7
3	50.2	51.8	2.2

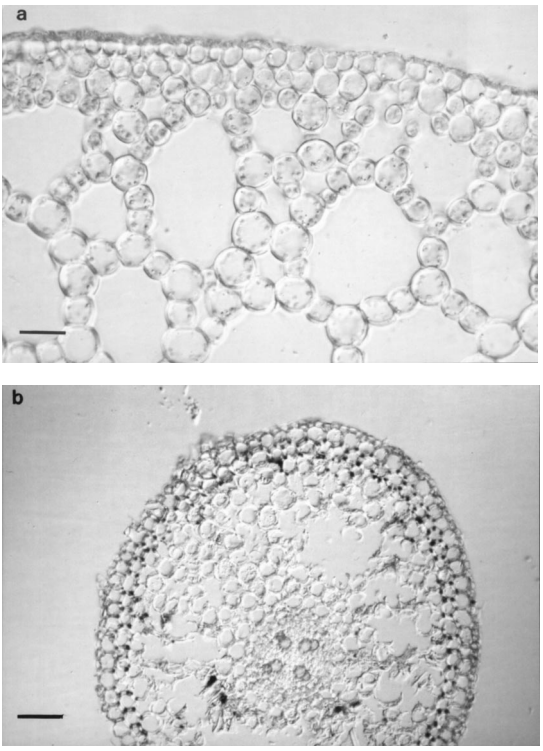

Plate 1. The internal structure of (a) the stem and (b) the root of the vascular plant *Menyanthes trifoliata*.. Scale bar = 75 μm.

measurements been made over a longer time period. Small rates of both CH_4 emission and oxidation were observed from areas where the water table was >100 cm below the surface, compared to rates of CH_4 emission two orders of magnitude larger observed when the water table was at or above the surface of the bog. However, the largest rates of CH_4 emission from the pool areas were almost entirely dependent on transport through *Menyanthes trifoliata.*

The response of CH_4 *flux to temperature and water table height*

Rates of CH_4 emission from the peat monoliths were in a similar range to those observed in the field, both as described above and by micrometeorological methods at the same site (Fowler *et al.*, 1995; Hargreaves *et al.*, this issue), and were well within the extremely large range of 2.5–5625 μmol $m^{-2} h^{-1}$ reported in a review by Bartlett and Harriss (1993).

The pool and lawn monoliths maintained in the OTC showed a highly significant positive response to increasing temperature. This temperature response, from a population of monoliths spanning a wide range of net CH_4 emission rates (Fig. 1), and experiencing natural variations in environmental conditions over 3 yr, is believed to be highly representative of natural conditions. A comparable temperature response, when the mosaic of pools, lawns, and hummocks is taken into account, has been observed at the field scale by micrometeorological methods (Hargreaves *et al.*, this issue). Under the controlled conditions of the CONVIRON the temperature response was exponential with CH_4 emission rates responding strongly to increasing temperatures between 5 and 30°C. Q_{10} values and activation energies were in a similar range to those observed from the OTC monoliths and to other studies (Conrad *et al.*, 1987; Dise *et al.*, 1993). The strong positive relationship between CH_4 production and temperature has been well characterised under laboratory conditions (Williams and Crawford, 1984; Svensson, 1984), with Q_{10}'s between 2.5 and 3.5 and E_a ranging from 60 to 90 kJ mol^{-1} (Conrad, 1989). However, under field conditions the relationship is less straightforward (Whalen and Reeburgh, 1988; Moore and Knowles, 1990) and can span a wide range of activation energies and Q_{10} values compared to laboratory values. For example, Crill *et al.* (1988) observed E_a values between 116 and 177 kJ mol^{-1} and Q_{10}'s between 5.4 and 13 from Minnesota peatlands, and Dise *et al.* (1993), also from Minnesota peatlands, observed Q_{10} values between 2.7 and 7.9. Temperature may affect a range of parameters, apart from the metabolic activities of the methanogens themselves, which will alter the net CH_4 flux. For instance, net CH_4 emission may be influenced by the different temperature responses of the CH_4-oxidising and CH_4-producing microbial communities (Dunfield *et al.*, 1993), by hysteresis effects due to falling and rising water table (Moore and Dalva, 1993), or by the growth stages of vascular plants. CH_4 production may be affected by the rate of population growth of methanogens, or by the concentration and availability of methanogenic substrates. Because methanogenic bacteria depend on a suite of other microorganisms for provision of substrates, a range of temperature responses are involved. Conrad *et al.* (1987) showed that temperature limited hydrogen turnover, and hence availability of substrate, to a greater extent than methanogenic activity, and that E_a's were larger in the presence of substrate additions. Svensson (1984) observed the presence of two methanogenic populations with different temperature optima, an acetogenic population with an optimum of 20°C, and a hydrogen-oxidising population with an optimum of 28°C. Therefore, Q_{10} and E_a's may not just be representative of the process under investigation, but may be any combination of the above, which could explain the large variability in these parameters observed in the field.

The negative response to temperature of CH_4 emission rates from several hummock and lawn monoliths indicates the complexity of the response to temperature throughout the year. The negative response was observed when the peat temperature was decreasing in late summer, and in monoliths where the water table was below the surface of the peat. The change in temperature affecting the CH_4-producing microorganisms, 15 cm below the surface of the peat, may have been damped relative to the CH_4-oxidising

microrganisms in the surface peat. As the peat surface temperature decreased and the activity of the CH_4-oxidising microrganisms subsequently decreased, the net emission of CH_4 to the atmosphere could have increased. However, other factors, such as the release of labile carbon fron senescing plants, may also have influenced the flux. Fowler *et al.* (1995) recently made micrometeorolgical measurements of CH_4 flux over an area of blanket bog in Caithness and estimated that 30% of the fetch was dominated by pool areas. If this estimate is representative and 70% of the blanket bog in late summer shows a negative response to temperature then this effect may significantly influence annual CH_4 budgets.

The continuing increase in CH_4 emission rates, after the temperature response investigation had been carried out and the cores were returned to 15°C, demonstrates the role of factors other than metabolic effects influencing CH_4 emission rates. Microbial populations may have continued to rise in response to increased substrate supply, as a result of the effect of temperature on decomposition and mineralisation processes. Higher temperatures would almost certainly have stimulated plant growth resulting in the increased production of root exudates. These easily decomposable substances are known to stimulate CH_4 production (Conrad, 1989). However, it should be noted that the outcome of long-term increases in temperature may have a different result as the balance between substrates and microbial populations reaches equilibrium and possible changes in vegetation cover take place, and therefore care should be taken when using the results of short-term laboratory experiments to predict the effects of likely changes in climate.

The importance of water table depth in determining CH_4 flux was demonstrated by the large difference observed between pool and lawn, and hummock monoliths, and the positive response raising the water table had on rates of CH_4 emission from hummock monoliths. Water table depth has been found to be the major controlling factor affecting CH_4 emission rates from several wetlands. For example, Dise *et al.* (1993) observed that water table position controlled 62% of the variance from a range of peatland ecosystems in northern Minnesota, and Moore and Dalva (1993) observed strong relationships between water table height and CH_4 emission in peat cores.

The influence of water table height and temperature on the CH_4 flux, shown in Fig. 4, demonstrates the relative effects of the two variables. At low water tables temperature had only a weak influence relative to the response observed when the water table was at the surface of the peat. However, Fig. 4 does not fully represent the annual variations in CH_4 flux. As discussed above, a negative response to increasing temperature may be observed at certain yimes of year, and other factors, such as the growth stages of vascular plants may also be important, as discussed below.

Transport of CH_4 *through plants*

The largest source of CH_4 observed in the sites studied at Loch More was through *Menyanthes trifoliata*. CH_4 flux increased by an order of magnitude when flux measurements included plants as opposed to just open water. The transport of CH_4 through vascular plants has been subject to several recent investigations, and it has been estimated that plant-dependent emission can account for up to 90% of CH_4 flux from wetlands (Whiting and Chanton, 1992; Shannon *et al.*, 1996). Many wetland plants have adapted to anoxic conditions by developing large intercellular spaces and arenchyma which allow the movement of oxygen into the roots (Armstrong, 1979), and also allow the diffusion of CH_4 from anoxic layers to the atmosphere (Sebacher *et al.*, 1985). Plates 1a and b show the aerenchyma present in the root and stem of *Menyanthes trifoliata* for gaseous exchange. Wetland plants also affect the net CH_4 flux by providing root exudates which stimulate CH_4 production (Schhtz *et al.*, 1991 and references therein), and by the transport of oxygen into the rhizosphere which supports a methanotrophic community, which has been estimated to oxidise up to 80% of the CH_4 produced (Holzapfel-Pschorn *et al.*, 1985; Schipper and Reddy, 1996). What controls CH_4 emission from the plant to the atmosphere has been investigated in several studies and results show that the means of transport and emission to the atmosphere differs among species. Stomatal control has been observed to be important only in a few studies, with clear diurnal patterns in CH_4 emission being observed (Yavitt and Knapp, 1995; Thomas *et al.*, 1996). Morrissey *et al.* (1993) observed a positive correlation between CH_4 emission and stomatal conductance but significant CH_4 flux was observed even when stomata were closed. Many studies have found no stomatal control on CH_4 emission rates (Seiler *et al.*, 1984; Holzapfel-Pschorn *et al.*, 1986; Whiting and Chanton, 1996) and Nouchi *et al.* (1993) found that the main source of CH_4 emission from rice plants was from micropores located on the abaxial epidermis of the leaf sheath. In this study presence or absence of light had no effect on CH_4 emission, however, the discovery that most of the CH_4 was escaping from the stem before it reached the leaves implies that that it is unlikely that stomatal control would have any effect. An examination of leaves and stems showed virtually no stomata on the stem compared to the leaves. The mode of CH_4 release from these stems is unknown, it is possible that micropores exist as observed by Nouchi *et al.* (1993). *Menyanthes trifoliata* are widespread throughout the peatlands of Caithness and Sutherland (Ratcliffe and Oswald, 1988) and will play a significant role in the net CH_4 flux. A large degree of seasonality due to the growth stages of the plant is likely, as is seen in rice paddies (Holzapfel-Pschorn *et al.*, 1985). During the winter anabiosis occurs and in spring when the first shoots appear a large pulse of CH_4 is likely, as a result

of the restricted transport of CH_4 over the winter period causing CH_4 concentration in the sediments to build up.

CONCLUSIONS

In the field, rates of CH_4 emission spanned a wide range (1.5–175 μmol m^{-2} h^{-1}), with the largest rate of CH_4 emission through the vascular plant *Menyanthes trifoliata*. A laboratory investigation showed that the majority of the CH_4 was emitted through the stem and stomatal conductance had no effect on CH_4 emission rates. CH_4 flux in the field, using static chambers and micrometeorological techniques, and CH_4 flux from the peat monoliths were comparable. Typical rates of CH_4 emission at 10°C were 78, 98 and 8 μmol m^{-2} h^{-1} from pool, lawn and hummock monoliths, respectively. The importance of water table was demonstrated with net fluxes an order of magnitude lower from hummock than from pool or lawn monoliths. Temperature had a strong effect on rates of CH_4 emission from the pool and lawn monoliths, with Q_{10} values between 3.0 and 3.3, but had a less significant effect on CH_4 flux from hummock monoliths. During the late summer a negative temperature response was observed from hummocks and lawns possibly as a result of the temperature response of the CH_4-oxidising community. These results corroborate other studies demonstrating the sensitivity of CH_4 emission rates from peatlands to climate change.

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