



EFFECTS OF TEMPERATURE AND WATERTABLE ON THE EFFLUX OF METHANE FROM PEATLAND SURFACE CORES

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(First received 10 April 1997 and in final form 4 February 1998. Published July 1998)

Abstract—(1) Cylindrical cores, 30 cm diameter by 40 cm deep, were cut from the living surface of a raised bog and installed in buckets of the same diameter. The cores were kept outdoors, and their natural water levels maintained with distilled water, until transfer to constant temperature rooms for experiments. Gas fluxes and concentration profiles were measured by quadrupole mass spectrometry. (2) Concentration profiles show that there is an intense source of CH₄ about 15 cm below the watertable, and that peaks in the profile move up and down with the watertable. The source can be turned on and off in a few hours. (3) The efflux of CH₄ depends exponentially on (Celsius) temperature, and is 20% greater in light than it is in the dark, even when the surface vegetation is *Sphagnum* moss without any vascular plants. (4) Efflux from hollow, lawn, and hummock microhabitats depends negatively and linearly on the depth of the watertable. The slope of the relation is almost the same in all three microhabitats. (5) When *Menyanthes trifoliata* (bogbean) is present in hollows the efflux is greater than when only *Sphagnum* is present. The movement of argon shows that the roots and shoots of *Menyanthes* provide a high-conductance route between the peat and the atmosphere. (6) Field temperature, precipitation and watertable were recorded for a hydrological (Oct–Sept) year on a raised bog in southwest Scotland. Expected efflux of CH₄ was calculated using the experimentally determined relations and the measured temperature and watertable. The mean of these calculated values agreed with the mean of measured values, though individual points were scattered.
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Key word index: *Sphagnum*, raised bog, hummocks and hollows, CH₄ oxidation.

1. INTRODUCTION

Northern peatlands cover about 3% of the Earth's land surface (Matthews and Fung, 1987; Gorham, 1991). Many peatlands have grown above the regional watertable and their surface vegetation relies on precipitation to maintain a perched watertable. Others depend on water that has run over or through rocks or soil containing little that is soluble. In both cases the surface vegetation contains a high proportion of the bog-moss, *Sphagnum*, which makes the water around it acid and, together with the small supply of solutes in precipitation, restricts the vascular plant species to a small number of specialists. The way in which these interact is one of the main determinants of fluctuations in the watertable and hence of the anoxic conditions that encourage the methane production that is the subject of several of the articles in this issue. We therefore give a brief description of the salient structural features here.

1.1. Hummocks, lawns, hollows and pools

At the higher levels above the watertable are dwarf shrubs of the family Ericaceae (*Calluna vulgaris*, *Erica*

tetralix are examples) whose woody stems support the *Sphagnum* and interact with it to create low hummocks up to about 50 cm above the watertable (Malmer *et al.*, 1994). These hummocks also provide an unwaterlogged medium for the roots of the dwarf shrubs, which do not tolerate waterlogging.

Lower down are linear-leaved plants such as the cotton grasses (*Eriophorum vaginatum*, *E. angustifolium*) and beaked sedge (*Rhynchospora alba*) which provide little support but whose roots contain intercellular gas spaces and can survive in the waterlogged conditions of the lawns and hollows that interdigitate with the hummocks. The watertable in these hollows is above the surface in winter but a few centimetres below it in summer.

More extreme are pools in which the watertable is above the surface at all times. They usually contain rather sparse vegetation amongst which the bog-bean, *Menyanthes trifoliata*, may be conspicuous.

1.2. Surface processes

The plants of *Sphagnum* form the matrix in which the other species grow. The individual *Sphagnum* plant grows at the apex. The capitula (moss "heads") of densely packed branches absorb incident light so that 2–5 cm below the surface there is barely 1% of that incident on the surface and the branches die and

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begin to decay. The whole mass is highly permeable to water and gases, so decay (mainly by fungi) is aerobic, producing CO_2 as its main product, and water drains down the plants easily though the plants retain 10–40 times their dry mass as capillary water in spaces among the leaves and branches (Hayward and Clymo, 1982). As the apices grow upward so the weight of plants and water increases while decay weakens the structure. Eventually the structure collapses, and dry bulk density increases perhaps 4-fold. Spaces between elements reduce proportionally, and hydraulic resistance increases in proportion (approximately) to the fourth power i.e. by about $4^4 \approx 250$ times. Water can no longer drain away easily vertically so it runs off horizontally. As long as precipitation exceeds losses in runoff, evaporation and downward percolation the deeper peat remains waterlogged. During the summer, if evaporation exceeds precipitation for long periods the watertable may gradually sink by perhaps 30 cm, but it is rapidly restored by autumn rains. The higher the watertable rises the greater the hydraulic conductance becomes and the more rapidly the water runs off. At Ellergower Moss in southwest Scotland (used later in this article), where the precipitation was 3050 mm, the watertable spent about 70% of the time within ± 2 cm of its mean, and sank much further below the mean (-12 cm) than it rose above it ($+4$ cm; Clymo and Pearce, 1995; Fig. 7).

Microorganisms in the few centimetres at the top of the waterlogged zone use up O_2 and do so faster than it is replaced from the air above because O_2 diffuses 10,000 times more slowly in water than it does in air. The peat thus becomes anoxic and further decay, which does continue though much more slowly than before, is anaerobic and mediated mainly by bacteria. The main gaseous products are CH_4 and CO_2 .

The term acrotelm is used to describe the surface layers down to the depth to which the watertable sinks in a dry summer (perhaps 30 cm), while everything below that (perhaps 500–1000 cm of peat) is the catotelm (Ingram, 1978).

1.3. Gas production in peat

The concentration profiles of CH_4 and CO_2 in the catotelm are highest near the base and decrease ever more steeply towards the acrotelm Clymo and Pearce (1995) for Ellergower Moss in Scotland; and Romanowicz *et al.* (1995) for a peatland in Minnesota), but with an increase just below the watertable. From the Ellergower profiles it is possible, using diffusion theory, to calculate the efflux from the catotelm into the acrotelm. This value is barely 2% of the efflux measured from hollows at the same site, implying that most of the CH_4 in the efflux is generated in or close to the acrotelm. Field measurements of gas concentration profiles in the top 50 cm of the bog (Clymo and Pearce, 1995) showed higher values about 10–20 cm below the watertable, wherever it happened to be, than the smooth decline already described would have given. These peaks were greater

in summer than in winter. But because the inferred generation site was so close to the surface the gases could diffuse to the surface relatively rapidly so the peaks never became very large. (Experience in Minnesota is rather different: Romanowicz *et al.*, 1995.)

1.4. Effects of temperature and watertable on gas efflux

There have been several attempts to infer from field measurements the effects of temperature and of watertable on CH_4 effluxes from peatlands (e.g. Moore *et al.*, 1990; Crill *et al.*, 1992; Roulet *et al.*, 1992; Dise 1993; Dise *et al.*, 1993; Bubier and Moore, 1994; Bubier, 1995; Bubier *et al.*, 1995). There has often been a lot of variation in effluxes in nominally identical conditions, and the results have been complex and to some extent conflicting.

1.5. Purposes of this work

We therefore decided to take samples of peatland surface, as little damaged as possible, to the laboratory where methods with much greater spatial resolution and speed could be applied, and where experimental conditions could be controlled. The objective was to acquire the response surface of CH_4 efflux to temperature and watertable, to drive this with measured field microclimate, and to compare these calculations with already existing field measurements of efflux.

The first experiments were to investigate the rate of change in CH_4 concentration profiles when the watertable was displaced up or down, so that we would know how long to run the following experiments for. Then came a series to discover the effects on CH_4 efflux of temperature, of light, and of moving the watertable up or down. Next we examined the effect on CH_4 transport of the presence of rooted plants. We recorded temperatures and watertable in the field for a year and used these measurements to drive a model based on the results of the experiments to calculate expected CH_4 efflux in the field, and to compare the calculated values with measured ones.

We collected the peatland cores in company with a group at the Institute of Terrestrial Ecology, Bush but then worked independently. They describe their results in a companion article in this volume (MacDonald *et al.*, 1998).

2. METHODS

2.1. Terminology and units

We use "height" to refer to a vertical distance relative to the watertable, either the instantaneous position or the mean position, depending on context. Positive heights are above the watertable, negative below it. For example, in summer the watertable might be at a height of -20 cm relative to its mean position. "Depth" is a vertical distance relative to the local peatland surface. For consistency, though slightly confusing in isolation, we use the same sign convention, with negative depth being below the surface.

The CH₄ flux units “mg m⁻² d⁻¹” have been widely used. It is not always clear whether CH₄ or CH₄-C is meant, and comparisons with (for example) CO₂ or conversion to carbon need factors. We therefore use the chemical unit “mol” which avoids these problems. We compromise between the micrometeorologist’s time unit “s” and the ecologist’s “d” with “h” because it gives similar numerical values to those these groups are used to. Our usual unit is thus $\mu\text{mol m}^{-2} \text{h}^{-1}$.

A rough median value for CH₄ efflux in our experiments is $100 \mu\text{mol m}^{-2} \text{h}^{-1}$ which is equivalent to $38.4 \text{ mg m}^{-2} \text{d}^{-1}$ and $444 \text{ ng m}^{-2} \text{s}^{-1}$ ($0.44 \mu\text{g m}^{-2} \text{s}^{-1}$).

2.2. Cores of peatland surface

An open-ended 30 cm diameter, 50 cm long cylindrical corer was made from 1.5 mm stainless-steel sheet welded at the vertical join. The lower end had sinuous 3 cm teeth at 3 cm pitch. With a tommy bar this corer was caused to cut to –45 cm depth into the peatland surface using alternate 30° clockwise and anticlockwise rotations. A 30 cm wide trench was made slanting from the base of the core to the surface. A cut was then made with a spade below the core, the core was slanted at 45° on the trench, and then dragged out up the slope, using the spade across the bottom to stop the peat sliding out. The horizontal core of peat, still in the corer tube, was cut to 40 cm long, and the corer teeth were slid into the top of a near-parallel sided plastic bucket, 30 cm diameter and 40 cm deep, laid horizontal and in line with the corer. Bucket and corer plus core were slowly raised to the vertical and the core then slid into the bucket. After a little practice the whole operation took barely a minute.

Hummock cores contained *Sphagnum capillifolium*, *Erica tetralix*, and some *Calluna vulgaris*; lawn cores were dominated by *S. papillosum* and *S. magellanicum* with some *Eriophorum vaginatum* and *Menyanthes trifoliata*; and hollow cores contained *S. cuspidatum* and, in some cases, *M. trifoliata*.

An initial set of 108 cores (36 each from hollows, lawns and hummocks) was collected in Caithness. Of these, 12 + 12 + 12 were taken to London and the rest to ITE, Bush near Edinburgh. The London cores were each installed in a cylindrical hole (the same size as the bucket) in a 40 cm cube of expanded polystyrene. The cubes, packed together in a square array outdoors on the roof of a building, served to maintain a thermal regime not too different from the natural one, though at a mean temperature about 4°C higher. The cores were placed randomly and were re-randomised every few months. An automatic watering system was built. When the watertable dropped 1 cm below a set point distilled water was supplied until the watertable was 0.5 cm above the set point. When it rained, water drained out between the same limits. Similar cores had already been maintained in this situation for about 15 yr.

For experiments, the cores in their cubes were moved to constant temperature rooms and later returned to the roof.

2.3. Quadrupole mass spectrometry

We needed to make rapid and near-continuous measurements on tiny samples of gas, so we chose to use a VG quadrupole mass spectrometer (QMS) with a membrane inlet to minimise gas consumption, and a triple filter and enclosed ion source to reduce problems with the dominance of water vapour in the samples. Clymo and Pearce (1995) who used a similar machine had to build a carrier gas system to bring samples from up to 15 m away to the QMS inlet. This gave their instrument a response time of about 45 min. We needed a much more rapid response so we chose to take the QMS inlet (the membrane interface between high vacuum and atmospheric pressure) into the core. To reduce gas consumption, and hence local depletion with consequent rapid change in measured concentration, we reduced the exposed diameter of the membrane to 2 mm. To minimise

the frequency of ruptured membranes, as the membrane moved into the peat, we made the membrane rather stouter (12 μm thick) than is usual in these instruments. The sample inlet was mounted at the end of a 5 mm internal diameter 200 cm long stainless steel tube, the other end of which entered the QMS chamber. The tube went horizontally out from the QMS for 130 cm, then turned down on a curve to a 70 cm long vertical section at the end of which was the membrane inlet. The tube was held firmly in position along the horizontal section and at the bend.

A cylindrical “Perspex” chamber with a gas-tight removable lid was fixed to the top of the core with a gas-tight seal. The lid contained inlet and outlet tubes for the supply and removal of gases when required, and a fan to stir the enclosed gas. The core plus chamber assembly was placed on the platform of a hoist driven by a programmable stepper motor. The tip of the QMS inlet passed vertically through a sliding seal placed eccentrically in the lid. While the inlet was in the enclosed gas space it could be used to measure fluxes, calculated from the slope of the temporal change in concentrations (the inlet consumed only a few pmol s^{-1}). When the hoist was started it raised the core around the fixed inlet and recorded a profile of concentration in the peat. We routinely measured N₂, Ar, O₂, CH₄ and CO₂ virtually simultaneously using mass/charge (m/z) quotients of 28 or 29, 20 or 40, 32, 15, and 44, respectively. A 35 cm profile could be made in 10–60 min.

Some precautions were necessary. If the inlet was left in the same place for 30 min or more the recorded concentration began to decline because the QMS removed gases faster than they were replaced by diffusion. The conductance of the membrane itself was temperature sensitive and all measurements were corrected to standard temperature. In O₂-free water-saturated N₂ there was a repeatable residual m/z 32 signal which we routinely subtracted.

A Pt resistance thermometer element was attached to the QMS inlet after it had been pushed through the sliding seal and moved in the peat as the inlet did.

3. RESULTS

The experiments were made to answer the following questions: what are the effects on CH₄ concentration profiles of moving the watertable up or down (Section 3.1); what are the effects on CH₄ efflux of temperature (Section 3.2), of light (Section 3.3), and of moving the watertable up or down (Section 3.4); and what is the effect on CH₄ transport of the presence of rooted plants (Section 3.5)? We also measured temperatures and watertable in the field for a year (Section 3.6) and used these results and those from the experiments to calculate CH₄ efflux in the field and compare it with that measured (Section 3.7).

3.1. CH₄ concentration profiles and watertable change

In Fig. 1 is shown the result of an experiment in which a ‘lawn’ core with *Sphagnum papillosum* and little else was kept at 10°C. The watertable began at the surface and a profile of CH₄ concentration was measured. There was a conspicuous peak in concentration at a height of about –15 cm. The watertable was then dropped to a depth of –14 cm by siphoning water out from the top and 24 h later the profile was re-measured. The peak had re-formed still at a height (relative to the new watertable) of about –15 cm. A similar result was recorded at a higher temperature

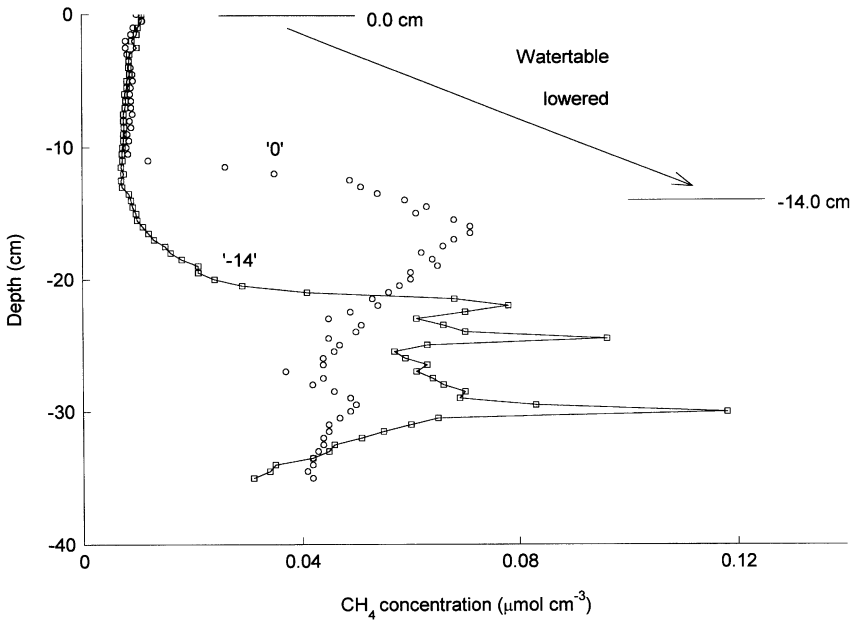


Fig. 1. Profile of CH_4 concentration in the same *Sphagnum papillosum* lawn core at two times. The watertable began at the surface (depth -0.0) at temperature 10°C and the "0" profile was recorded. The watertable was then lowered, by removing water from the top, to -14 cm and 24 h later the second (" -14 ") profile was recorded.

by Benstead and Lloyd (1993). This rapid response is important because it makes possible calculations that assume rapid microbiological response, though it does not exclude longer-term effects consequent on microbial population growth or substrate exhaustion. Given that, in these experiments, CH_4 is probably moving by diffusion it seems that the active CH_4 -producing layer may be no more than 2–3 cm thick at any one time.

3.2. Effect of temperature on CH_4 efflux

Three "lawn" cores were chosen which were dominated by *S. papillosum* and which had only three small (<7 cm) rooted plants of *Eriophorum vaginatum* in them. The watertable was fixed at a depth of -3 cm. The cores were moved in a random design among rooms at four nominal temperatures. (The actual temperatures of the rooms were changed several times during the experiment because the rooms were being calibrated, but the changes were made only at the times we moved the cores.) This random movement was important. It avoided the systematic bias associated with regular movement up or down the temperature range: a defect of many similar experiments. We recorded the temperature at a height of -5 cm. Each core visited each nominal temperature four times. On each occasion 8–10 flux measurements were made and from these the mean and standard error were calculated. These standard errors are thus measurement errors alone. Each core was left at a fixed temperature in dim ("room") light for 3–4 d before effluxes were

measured at the same temperature in the same dim light. These conditions are labelled "dark" in Fig. 2 where the results are shown. An exponential curve gives as good a fit as might be sought given the variability. In the same figure are mean values of measurements made at ITE, Bush (Edinburgh) by different methods and different people on a different subset of the same collection of cores. The shape of the curve is very similar to ours though displaced upward by $10\text{--}20 \mu\text{mol m}^{-2} \text{h}^{-1}$.

3.3. Effect of light

As part of the temperature experiment the same cores with the same watertable were kept, alternately with the dark treatments but at a different randomly chosen nominal temperature, in bright light supplied by a halide lamp at $200 \mu\text{mol m}^{-2} \text{s}^{-1}$. This raised the temperature inside the Perspex chamber. We recorded the temperature at a height of -5 cm and this is the temperature used in Fig. 2 where the results are recorded at the right hand side. The temperature at -15 cm, which the results in Section 3.1 suggest is the position of the main source of CH_4 , were always a degree or so lower than those at -5 cm. This would move the light curve to the left and thus increase the light effect. As with the "dark" part of the experiment, an exponential gives as good a fit as might be sought. This curve is consistently above the "dark" one by about $10\text{--}20 \mu\text{mol m}^{-2} \text{h}^{-1}$. The cores in this experiment contained *Sphagnum* only and lacked significant rooted plants.

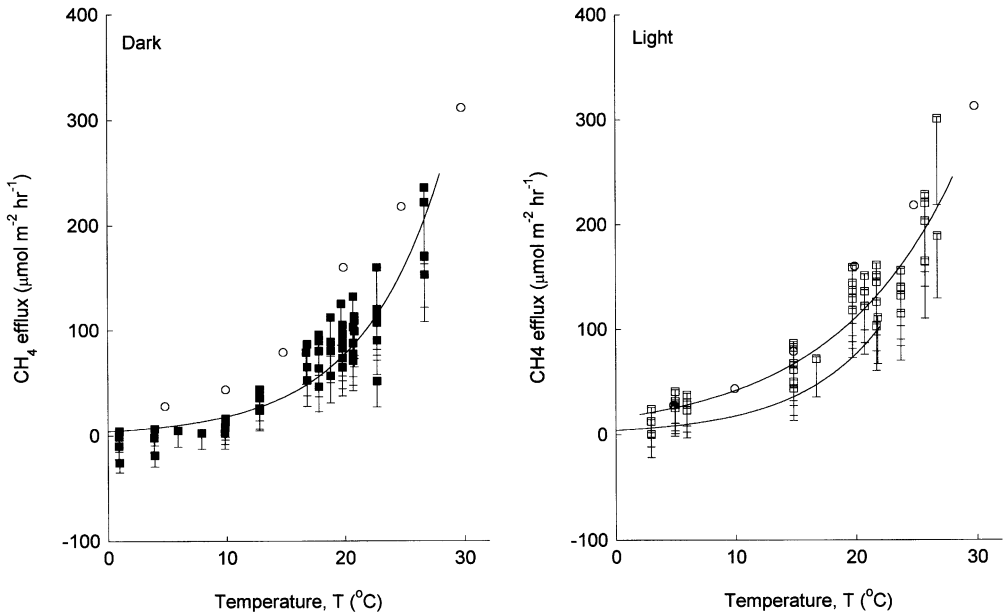


Fig. 2. Effects of temperature and light on mean efflux of CH_4 from 30 cm diameter *Sphagnum papillosum* lawn cores. The cores had been kept at constant temperature and with watertable at -3 cm depth for 3–4 d before the measurements. Bars show ± 1 S.E. for 8–10 replicate measurements on the same core. Filled squares, left hand graph, are for pretreatment and measurements made in “dark” (dim room light); open squares, right-hand graph, are for pretreatment and measurements made in “light” ($200 \mu\text{mol m}^{-2} \text{s}^{-1}$). The six open circles in the left hand graph are for measurements made by different methods on a different subset of the cores held at ITE, Bush in Edinburgh. These ITE data are repeated on the right hand graph though most of them there are obscured by other points. The lines were fitted to $E = ae^{bT}$, where E is the efflux ($\mu\text{mol m}^{-2} \text{h}^{-1}$), T is the Celsius temperature, a is the multiplier with the same units as E and dimensionless b determines the steepness of the curve. The numerical values were:

	“Dark”	Light
a ($\mu\text{mol m}^{-2} \text{h}^{-1}$)	4.1	15.7
b	0.1460	0.0908

The 0–22°C part of the “dark” line is repeated in the right hand graph for comparison with the “light” line.

3.4. Effect of watertable

Six cores of each of hollow, lawn and hummock peatland were maintained at 10°C. The watertable in each was moved independently (by adding distilled water, or removing water, from the top) on different random sequences among depths of 0, -5 , -10 , -15 , -20 and -25 cm. The watertable was allowed to remain at the new depth for 3–4 days before effluxes were measured. The results are shown in Fig. 3, where a straight line has been fitted to the three sets of results separately. The most striking feature is that all three lines are very similar, though in nature, where the watertable is much deeper below hummocks than it is below hollows and lawns, the efflux of CH_4 from hummocks is much less than it is from the other two microhabitats.

The CH_4 consumption values when the watertable is at depths greater than -20 cm are not very reliable as they are based on small differences in very small concentrations over short times.

3.5. Effect of rooted plants

There are numerous reports that interconnecting gas spaces in roots, stems and leaves of vascular plants facilitate gas transport to roots (e.g. Conway, 1936, 1937) and that CH_4 efflux may also be facilitated (e.g. Whiting and Chanton, 1992; Shannon *et al.*, 1996; MacDonald *et al.*, 1998). We tested this by comparing the transport of Ar from the headspace over a lawn core, dominated by *Sphagnum papillosum* with only three small plants of *Eriophorum vaginatum*, with transport into a hollow core dominated by *Menyanthes trifoliata* with an understorey of *Sphagnum cuspidatum*. For *Menyanthes* the quotient of leaf area/core area was 3.2. The cores were kept at 10°C and the watertable at a depth of -1 cm. First, the efflux of CH_4 was measured: for the *Sphagnum* core it was $18 \mu\text{mol m}^{-2} \text{h}^{-1}$ and for the *Menyanthes* core $46 \mu\text{mol m}^{-2} \text{h}^{-1}$. Then the headspace was filled with Ar and the concentration of Ar was followed at various depths. Finally, we froze the cores, cut off the top

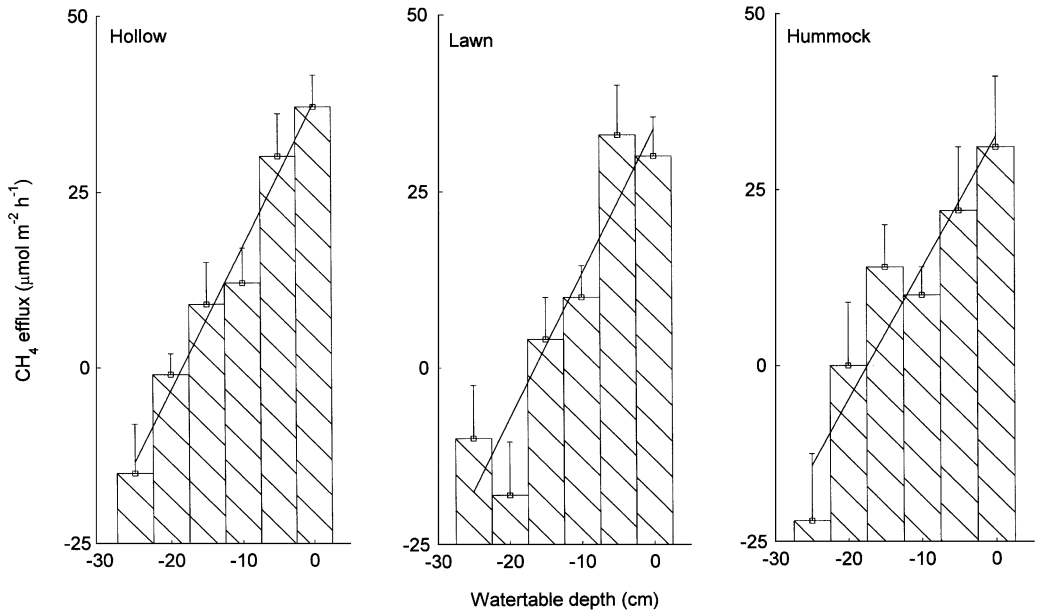


Fig. 3. Effect of watertable depth at 10°C on mean efflux of CH₄ from 30 cm diameter cores of peatland from three microhabitats: hollow, lawn and hummock. Bars show + 1 SE of measurements on six different cores. Measurements were made 3–4 d after the watertable had been moved to the chosen depth. These movements were made in random order. The function $E = sW + r$ was fitted, where E is the efflux ($\mu\text{mol m}^{-2} \text{h}^{-1}$), W is the watertable depth (cm), r is the offset with the same units as E , and s ($\mu\text{mol m}^{-2} \text{h}^{-1} \text{cm}^{-1}$) determines the steepness of the line. The numerical values were:

	Hollow	Lawn	Hummock
r ($\mu\text{mol m}^{-2} \text{h}^{-1}$)	37	34	33
s ($\mu\text{mol m}^{-2} \text{h}^{-1} \text{cm}^{-1}$)	2.03	2.05	1.87

10 cm, allowed it to melt, and picked out and measured the length of roots. In this depth the *Sphagnum*-dominated lawn core had 5.3 mm m^{-2} , and the *Menyanthes* dominated hollow core had 54 mm^{-2} . At the extremes the difference between live and dead roots was clear, but the majority of the roots were intermediate. We included all but recognise that a large proportion may have collapsed and been playing no further part in gas transport. An example of some of the Ar measurements is shown in Fig. 4.

For the *Sphagnum*-dominated core (lower line, S, in every case) the concentration began at about $0.02 \mu\text{mol cm}^{-3}$, which is the concentration in equilibrium with Ar in the air. At a height of -2.5 cm (i.e. 2.5 cm below the watertable) after about 900 min the concentration began to rise slowly. In all deeper cases there was no sign of any change. This was in marked contrast with the *Menyanthes*-dominated core in which the concentration increased very steeply down to -7.5 cm (though not by 17 h at -10 cm). It is clear that in this case the vascular plants provided an effective direct route for gas from the atmosphere to sites some distance into the peat, bypassing diffusion through the water and peat. We suppose that the same route is available for the reverse movement of CH₄ from its site of formation to the atmosphere. The

kinetics of Ar movement are analysed in more detail in Stephen *et al.* (1998).

3.6. Temperature and watertable in the field

The experimental site was Ellergower Moss in Galloway, southwest Scotland (Clymo and Pearce, 1995). It is an elliptical raised bog with axes about 600 and 900 m, maximum peat depth about 7.2 m, and has been forming for about 9000 yr. The march of temperature at -5 , -10 , -20 and -40 cm depth beneath three microhabitats (hollow, lawn, hummock) is shown in Fig. 5. The curves approximate sine curves. In Fig. 6 are shown the amplitude and phase shift parameters plotted against depth. In a homogeneous isotropic medium to which a sinusoidally varying heat load is applied one expects to find that, where A is the amplitude of the temperature curve, then e^A and the phase shift are linear with depth (Monteith, 1973). This they do seem to be and from the slopes one can calculate the year damping depth (d_y , cm) from amplitude and from phase shift as 132, 117 for the hollow; 130 and 127 for the lawn; and 116, 116 for the hummock. Given all the circumstances, this agreement is good. The relation $\kappa = \omega d^2/2$, where κ is thermal diffusivity, and ω is the angular frequency gives a mean value of thermal diffusivity of $0.15e^{-6} \text{ m}^2 \text{ s}^{-1}$

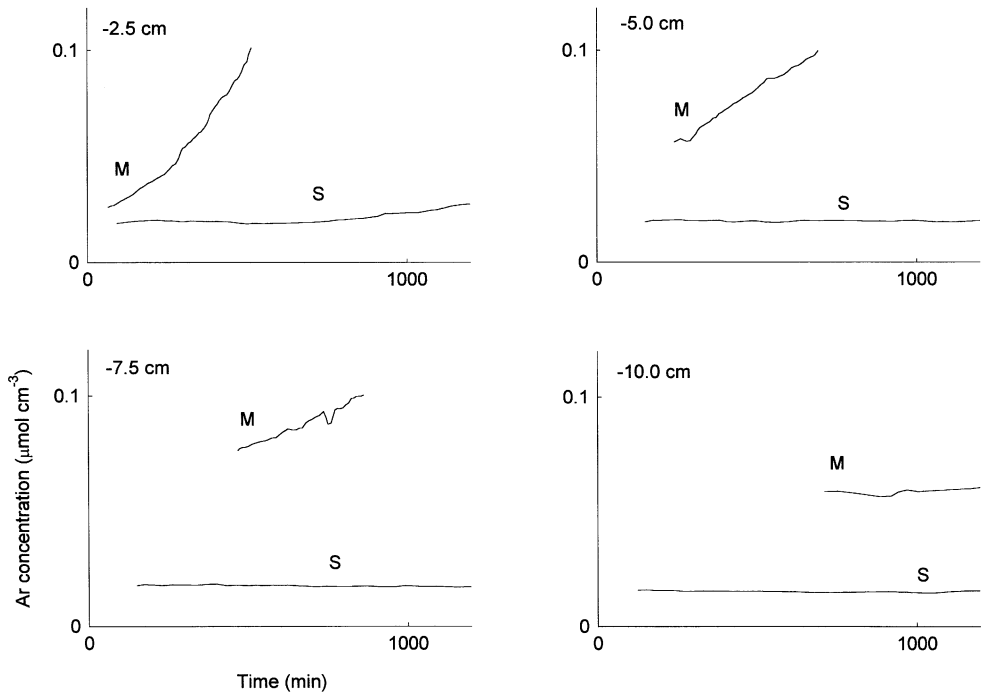


Fig. 4. Change of concentration of Ar at four heights (i.e. distances below the watertable) in a lawn core with *Sphagnum papillosum* and very few rooted plants (line S) and in a hollow core with *Menyanthes trifoliata* (line M) for which leaf area/core area was 3.2. The top of the core was covered by a closed chamber which was filled with Ar at room pressure (1 atm) at time zero.

while that of water is $0.14e^{-6}$. The mean d_Y is 123 cm, and thus the day damping depth, d_D is $123/\sqrt{365} = 6.4$ cm at which the amplitude is $1/e = 0.37$ of that at the surface, while at 25 cm depth, 4 damping depths, the amplitude of daily fluctuations is less than $1/e^4 = 2\%$ of that at the surface. It is clear from this simple analysis, and from Fig. 5, that daily fluctuations in surface temperature are strongly damped at 15–25 cm depth.

3.7. Calculated and measured efflux of CH_4 in the field

Finally, we calculate for the three microhabitats (hollow, lawn, hummock) the CH_4 efflux expected from the experimental responses to temperature and watertable reported here (Figs 2 and 3) driven by the temperature and watertable recorded at Ellergower Moss (Fig. 7). The watertable was measured in the hollow only, and has been assumed to behave in the same way for the other two microhabitats. This is wrong in detail (Bragg, 1982), but probably not by a great deal. Methane production has been assumed to be concentrated at a height of -10 cm, and to move up and down with the watertable as shown. It is the temperature at this position, obtained by interpolation in the recorded profiles that is shown in the top line. In Fig. 8 is shown the CH_4 efflux calculated using the temperature and watertable depth in Fig. 7. The E_T curve uses the temperature response only; The $E_{W,T}$ curve uses responses to both watertable depth

and temperature. For the lawn there is little difference, but for the hollow the $E_{W,T}$ value is consistently greater than that based on temperature only, while the reverse is true for the hummock (and especially so when the watertable drops during the summer).

In the left half of Fig. 9 is shown the mean CH_4 efflux for the whole year from the three microhabitats for different assumed heights of CH_4 production, and hence of the relevant temperature. It is clear that the height of this layer is of little importance in the calculations: all the lines are almost horizontal. But calculating with watertable as well as temperature produces substantially different results from those got using temperature alone. The latter are almost identical for all three microhabitats whereas all those who have measured effluxes in the field report greater values for hollows than for hummocks.

In the right half of Fig. 9 the calculated values are compared with the reported measured ones (Clymo and Pearce, 1995) at the same site at which the microclimate was recorded. The comparison is not exact because the measured values were spread over 1991–1994, whilst the microclimate measurements span 1991–1992 only. But the seasonal patterns were fairly similar in all these years. The rank correlation coefficient (0.52) though technically “significant” at $P = 0.01$ is only modest, but the calculated and measured values are clustered around the hoped for slope of 1.0.

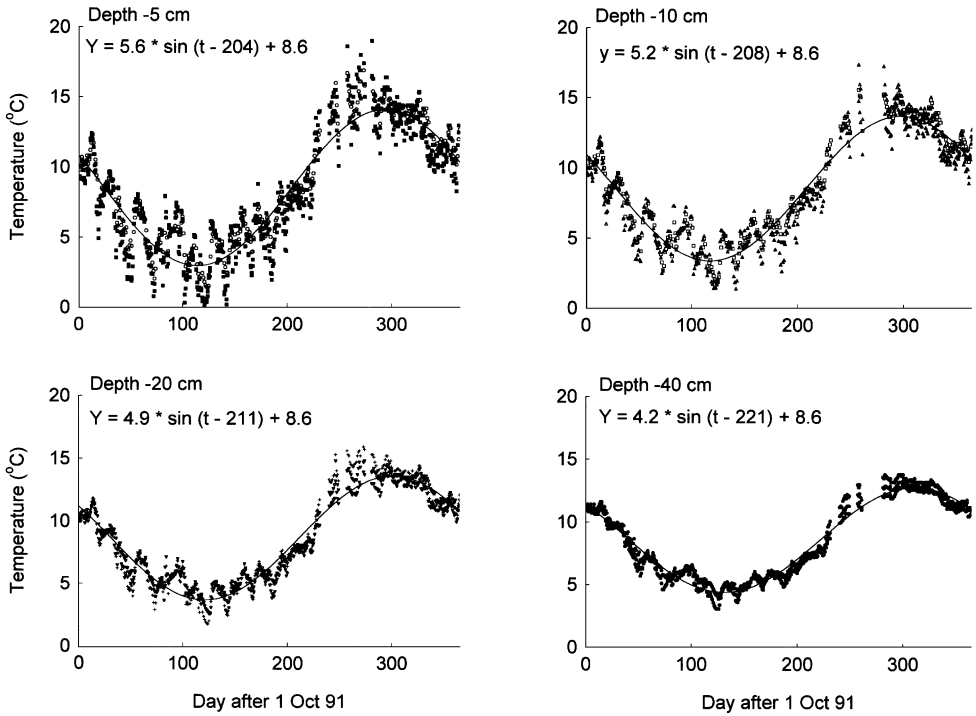


Fig. 5. Course of temperature at Ellergower Moss, southwest Scotland, during the hydrological year Oct. 91 to Sep. 92 at four depths beneath the surface. Each graph contains daily values for one hollow, one lawn, and one hummock microhabitat. The lines were fitted by least squares optimisation.

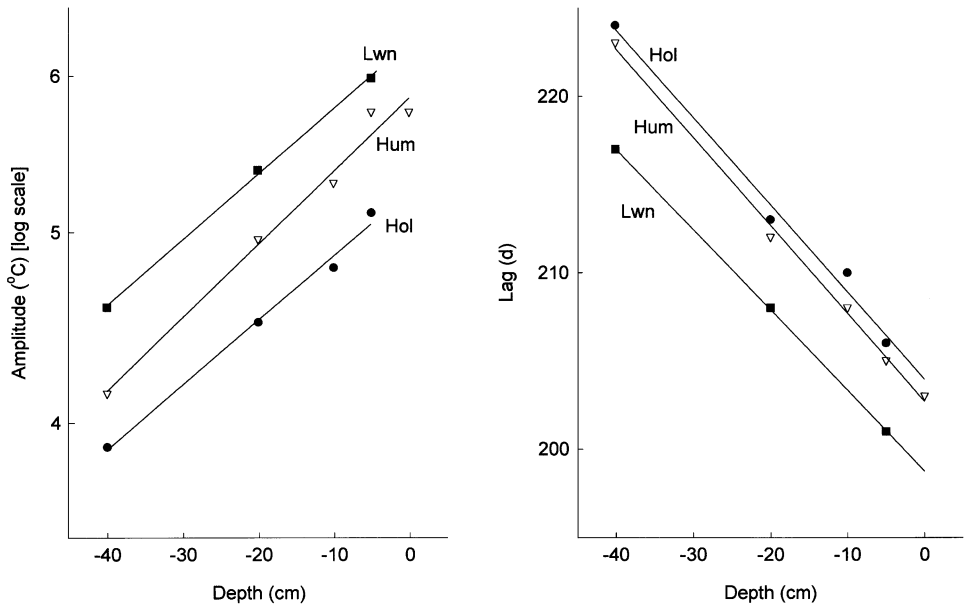


Fig. 6. Summary of parameters fitted separately for hollow, lawn and hummock measurements in Fig. 5. In the left graph straight lines were fitted to e^A vs depth (where A is the amplitude) and the axis is log transformed. The right graph is a standard linear plot.

4. DISCUSSION

4.1. The effect of temperature

Temperature has an effect that is close to exponential on CH_4 efflux. Some authors choose to report this

in terms of a Q_{10} : where we have used $E = ae^{bT}$ then $\ln(Q_{10}) = 10b$. For our data this gives Q_{10} of 2.5–4.3 which suggests a biologically dominated process rather than a physically dominated one. Other authors report the same relationship as the activation

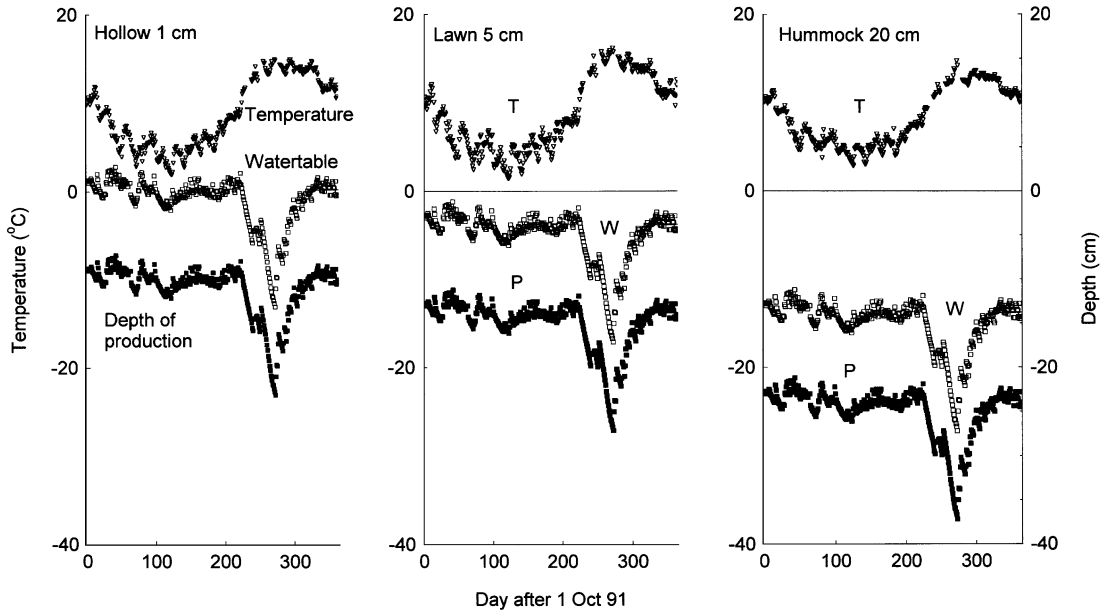


Fig. 7. Physical conditions in the three microhabitats used in calculations of CH_4 efflux at Ellergower Moss. The surface of the hollow was at a height of 1 cm relative to the mean watertable; the lawn was at 5 cm; and the hollow at 20 cm. The watertable was measured in the hollow and assumed to be the same for lawn and hummock but at the different depths shown in the middle curves, "Watertable" (W). The lowest curve, "Depth of production" (P), 10 cm below the watertable, is the assumed depth of generation of CH_4 . The temperature there was estimated by interpolation in profiles measured separately in all three microhabitats, and is shown in the top curve, "Temperature" (T).

energy in an Arrhenius plot. We think this is misleading: the phenomenon probably has complex causes.

4.2. The effects of light

In our experiments light had a small stimulatory effect on CH_4 efflux, as it did in the experiments of Thomas *et al.* (1996), but in contrast to those of King (1990). The three cases are different however. King (1990) used a wetland "sediment" with an overlying algal mat and water. He attributes the reduction in efflux in light to increased oxidation following increased photosynthesis by the algal mat. The other two experiments used peatland cores with the watertable below the surface. That some peatland vascular plants have interconnected gas spaces through which gases may move much more rapidly than by diffusion through water has been known for 60 yr (Conway, 1936, 1937) and is confirmed in our experiments with the passage of Ar into peat with or without *Menyanthes*. The presence of rooted plants in the experiments of Thomas *et al.* introduces a complication: they suggest that stomatal apertures varying with light and exudation of carbohydrates from roots may be parts of the explanation of the response. In our experiments, however, we excluded all but three tiny rooted plants. Photosynthesis by *Sphagnum* results in the production of carbohydrates, and these plants do have an internal system capable of transporting carbohydrates (Rydin and Clymo, 1989). But

it seems unlikely that this is capable of moving significant amounts of carbohydrate from the plant apices above the watertable, 20 cm or so down stems that are mostly dead, to the height of -15 cm that seems to be the main site of CH_4 production. Inhibition of CH_4 oxidation at the surface by light cannot be ruled out but seems unlikely.

4.3. The effects of watertable

That the efflux of CH_4 is lower from peatlands the lower the watertable in field conditions has been repeatedly recorded following the original observation by Clymo and Reddaway (1971). The interesting feature of the experiments reported here is that a similar effect was seen when the watertable was moved up and down in any particular core, and that the reduction was linear and independent of microhabitat. There is a well-developed potential to oxidise CH_4 in the peat both above and below the watertable (Nedwell and Watson, 1995). The potential to produce CH_4 is also present both above and below the watertable. Actual production at a high rate seems, however, to be limited to a thin layer (Fig. 1) probably by a delicate interaction of gradients of concentration, perhaps of O_2 and S^{2-} , changing in opposite senses (Arah and Stephen, 1998). Such thin layers are well-known in limnology. If a consortium of different species of bacteria is involved in CH_4 production then their needs may be conflicting. Optimum conditions

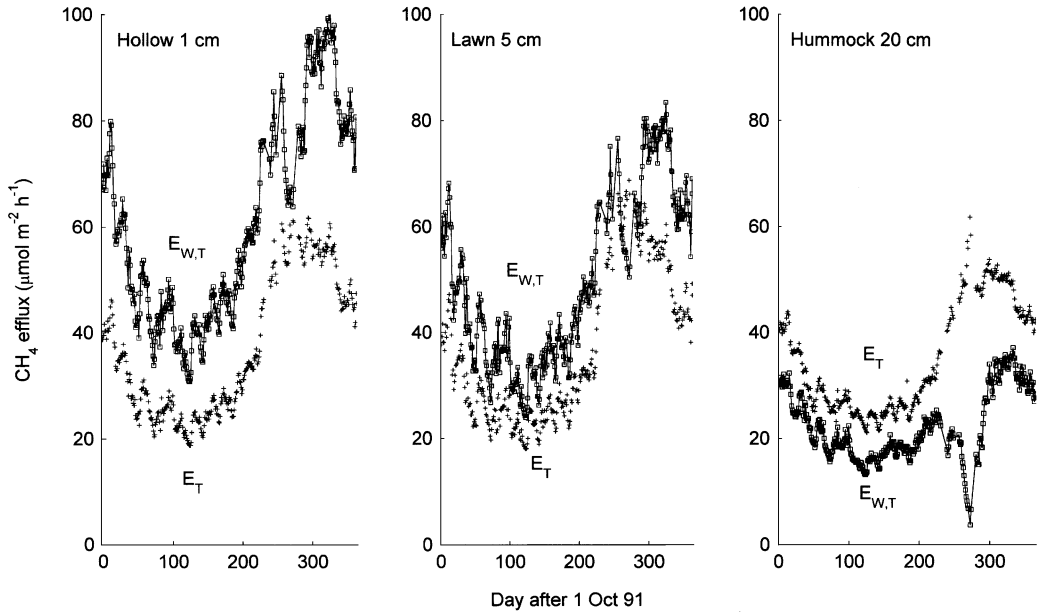


Fig. 8. Calculated CH_4 efflux from three microhabitats at Ellergower Moss using the responses to temperature (Fig. 2) and to watertable (Fig. 3) determined by the physical conditions (Fig. 7). The E_T curve uses temperature alone, the $E_{W,T}$ curve uses watertable and temperature. In the hollow $E_{W,T} > E_T$; in the lawn they are almost the same; in the hummock $E_T > E_{W,T}$.

for CH_4 production are probably sub-optimal for most—perhaps all—the consortium members. These facts are consistent with a mechanism (Clymo and Pearce, 1995, Fig. 5), common to all microhabitats, in which CH_4 is produced at much the same temperature-dependent rate at a height of about -15 cm (relative to the watertable), and is oxidised at a steady rate as it diffuses upward. The greater the thickness of the overlying material the greater the amount of CH_4 converted to CO_2 and the smaller the efflux of CH_4 . The thing that distinguishes the microhabitats is that in the field they happen to have the watertable at different depths. Differences in botanic composition seem to be unimportant. It may turn out that the efflux of CH_4 is more determined by the behaviour and activity of the CH_4 oxidisers than it is by the producers.

4.4. Calculations of field efflux

Both temperature and watertable are constantly changing in the field. Shifts in watertable are usually to be measured in mm d^{-1} except during heavy rain and after long drought. Daily temperature changes at the site of CH_4 production are strongly damped because the day damping depth is only 6–7 cm. Temperatures in the oxidation layer above it are more variable. The profile of CH_4 concentration changes rapidly in response to a change in watertable however and after 24 h a similar profile has re-established at the same height (relative to the watertable). It seems

that microbial activity can be started and stopped rather rapidly, consistent with the presence of the necessary organisms through out the surface layers. This does not rule out the possibility of longer-term changes resulting from population growth or resource depletion, but by then (in the field) conditions will probably have changed. The speed of microbial response and the relative slowness of change in temperature and watertable allow us to assume for calculation purposes that the CH_4 efflux responds directly to the current values of temperature at the postulated position of production and to watertable depth.

It turns out (Fig. 9) that the height we assume for the site of production is of no significance in these calculations, but the response to watertable fluctuations is very important.

In our experiments, and in the field measurements, we took care to try to minimise the extra complexity introduced by rooted plants when they are abundant. Thus, the median values of efflux from hollows in our work were less than $100 \mu\text{mol m}^{-2} \text{h}^{-1}$ while values 3–5 times this are often recorded from these hollows with abundant rooted plants.

The mean value over a year for the measured (Clymo and Pearce, 1995) and the calculated (this article, Fig. 9) efflux of CH_4 from hollows at Ellergower Moss was 62 and $60 \mu\text{mol m}^{-2} \text{h}^{-1}$, and for hummocks was 23 and $22 \mu\text{mol m}^{-2} \text{h}^{-1}$. This extraordinary agreement may be misleading though: the

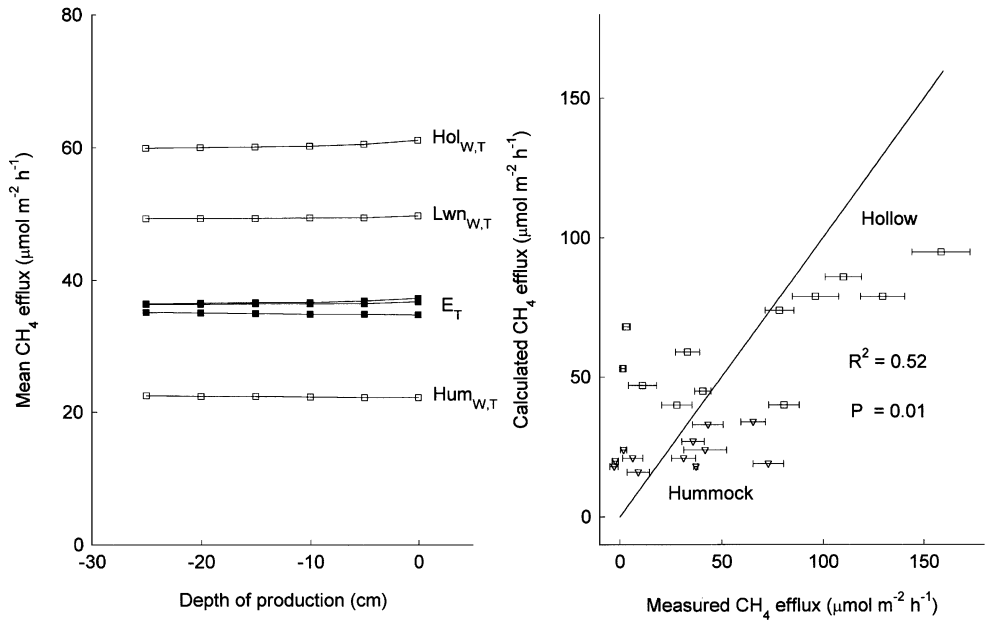


Fig. 9. Left: Calculated mean CH₄ efflux for Oct. 91–Sep. 92 assuming the depth at which CH₄ is produced (and therefore the relevant temperature) is between –0 and –25 cm height relative to the watertable. Results for hollow, lawn and hummock are shown. The central three lines, almost coincident, use temperature alone in the calculation. The other three use watertable and temperature. Right: Calculated CH₄ flux compared with that measured at Ellergower Moss at the same time of year as the meteorological records were made (Clymo and Pearce, 1995). R_s is Spearman's rank correlation coefficient. The line has slope = 1.0; it has not been fitted.

comparison of individual values in Fig. 9 shows considerable scatter.

Could these findings be applied to other peatlands? The temperature and watertable responses are probably fairly general but there are two main difficulties.

First, there is much variation in the proportion of rooted 'bypass' plants in the hollows and pools and these give corresponding variations in these main contributors to overall efflux: the hollows and pools are already the leaky boundaries, and rooted plants increase the leaks. Not only is it difficult to estimate the proportion of rooted plants but, at a higher level, it is difficult to make reliable estimates of the proportion of hollows and pools.

Secondly, it is easy to calculate the relevant temperature given the seasonal maximum and minimum, but it is not easy to calculate the variation in watertable height.

The real value of calculations of this kind is that they are alternative to direct measurements by micrometeorological or aircraft-borne methods. When all three eventually converge we may begin to have confidence in all.

Acknowledgements—We thank K. Lee and D. Duckworth for building the equipment; Dr K. Hargreaves for tending the climate recorder; and the TIGER programme of the NERC for financial support.

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