



## The role of *Eriophorum vaginatum* in CH<sub>4</sub> flux from an ombrotrophic peatland

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### Abstract

Vegetation composition was found to be an important factor controlling CH<sub>4</sub> emission from an ombrotrophic peatland in the UK, with significantly greater ( $P < 0.01$ ) CH<sub>4</sub> released from areas containing both *Eriophorum vaginatum* L. and *Sphagnum*, than from similar areas without *E. vaginatum*. Positive correlations were observed between the amount of *E. vaginatum* and CH<sub>4</sub> emission, with the best predictor of flux being the amount of below-ground biomass of this species ( $r^2 = 0.93$ ). A cutting experiment revealed that there was no significant difference ( $P > 0.05$ ) in CH<sub>4</sub> flux between plots with *E. vaginatum* stems cut above the water table and plots with intact vegetation, yet there was a 56% mean reduction in CH<sub>4</sub> efflux where stems were cut below the water table ( $P < 0.05$ ). The effect of *E. vaginatum* on CH<sub>4</sub> release was mimicked by the presence of inert glass tubes. These findings suggest that the main short-term role of *E. vaginatum* in the ecosystem is simply as a conduit for CH<sub>4</sub> release. The longer-term importance of *E. vaginatum* in controlling CH<sub>4</sub> fluxes through C substrate input was suggested by the positive correlation between the night-time CO<sub>2</sub> and CH<sub>4</sub> fluxes ( $r^2 = 0.70$ ), which only occurred when the vegetation was not senescent.

### Introduction

Almost 3% of the Earth's land surface is covered by peatlands (Matthews and Fung, 1987), a type of wetland ecosystem in which productivity exceeds biodegradation (Williams and Crawford, 1984). Due to their flooded nature, peatlands are a major source of atmospheric CH<sub>4</sub>, contributing an estimated 25–30% of total CH<sub>4</sub> released to the atmosphere each year (Cicerone and Oremland, 1988). The three mechanisms of CH<sub>4</sub> release from peatlands to the atmosphere are molecular diffusion, ebullition (bubbling) and plant-mediated transport (Topp and Pattey, 1997).

Many vascular plants growing in flooded wetland soils produce aerenchyma, a tissue that contains

extensive gas spaces (Sculthorpe, 1985). The aerenchyma acts as a ventilation system transporting oxygen to the root tips in saturated soil and also transports CH<sub>4</sub> and CO<sub>2</sub> to the atmosphere (Holzapfel-Pschorn et al., 1986). As such, these plants serve as direct conduits between reducing and oxidizing environments (Chanton et al., 1992) and can be responsible for up to 90% of the total CH<sub>4</sub> flux (Shannon et al., 1996).

In peatlands, where much of the C assimilated by plants is allocated to below-ground tissues (Wallen, 1986), plants also affect CH<sub>4</sub> dynamics through the translocation of photosynthate to their roots and, subsequently, to the rhizosphere (Van Veen et al., 1989). As a consequence, the rate of photosynthesis might be coupled to the rate of methanogenesis, greater C fixation leading to an increased provision of labile C to the roots and the rhizosphere and ultimately increasing substrate availability to methanogens.

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However, the positive effects of ventilation systems and photosynthesis on CH<sub>4</sub> emissions may be cancelled out by the dual function of aerenchymatous tissues in transporting O<sub>2</sub> to the roots (Roura-Carol and Freeman, 1999). This leads to the inhibition of the strictly anaerobic methanogenic bacteria (Watson et al., 1997) and the stimulation of methanotrophic bacteria, whose activity is constrained by O<sub>2</sub> transport from the roots to the otherwise anoxic rhizosphere (Roslev and King, 1994). The net emission of CH<sub>4</sub> is a balance between these processes.

The aim of this study was to determine how *E. vaginatum* affected the spatial patterns and magnitude of CH<sub>4</sub> release from an ombrotrophic peatland. The relative importance of the two CH<sub>4</sub> emission enhancement mechanisms, the conduit effect and the substrate production effect, were assessed.

## Methods

### Site description

The investigation was carried out at Roudsea Moss (NGR SD330820), an ombrotrophic peatland in the UK. The peat is classified as Longmoss series, within the Longmoss Association (Jarvis et al., 1984). The vegetation corresponds to M18 *Erica tetralix* – *Sphagnum papillosum* raised mire of the UK National Vegetation Classification (Rodwell, 1991). The majority of the experimental site was covered with a *Sphagnum* lawn community dominated by *Sphagnum papillosum* Lindb. and containing a number of ericaceous shrubs, for example, *Erica tetralix* L., *Andromeda polifolia* L. and *Calluna vulgaris* L. The cotton sedge *E. vaginatum* was abundant, often forming tussocks. The work concentrated on areas of *Sphagnum* lawn, with and without the presence of *E. vaginatum*.

The water table of the peatland was monitored on a weekly basis between October 1996 and September 1998, and during the time of the experiments described here, it fluctuated between 0 and 100 mm below the moss surface. The organic C content of the peat was in excess of 50%.

### Determining CH<sub>4</sub> and CO<sub>2</sub> flux

Soil CH<sub>4</sub> and CO<sub>2</sub> fluxes were determined using a flow-through chamber technique. Chambers consisted of a single Plexiglass cylinder (190 mm diameter, 275 mm tall) cut 50 mm into the peat. Two 9 mm holes were drilled into the cylinder to function as air

inlets and outlets. Ambient air was drawn through the chamber headspaces at 30 m<sup>3</sup> h<sup>-1</sup> into 100 m lengths of polytetrafluoroethylene tubing (PTFE), which carried the outlet headspace gas to a Perkin Elmer 8500 GC fitted with an electron-capture detector (ECD) and flame ionisation detector (FID). The gas stream of both the chamber inlet and outlet was automatically monitored for CH<sub>4</sub> and CO<sub>2</sub>. Trace gas flux rates were calculated from the difference between chamber input and output concentrations of the trace gas under study; for a full description of the gas analysis and data storage, see Ineson et al. (1998).

### Monitoring *E. vaginatum* and *Sphagnum* sites for trace gas flux

To evaluate the effect of presence or absence of *E. vaginatum* on peat CH<sub>4</sub> flux four open chambers per vegetation type were placed on plots of *Sphagnum* lawn with and without *E. vaginatum*. These plots were monitored continuously for a period of approximately three days on three separate occasions in September and October 1997. As higher CH<sub>4</sub> release was frequently observed from plots containing *E. vaginatum*, an additional experiment was performed to investigate whether the amount of CH<sub>4</sub> release was associated with the amount of *E. vaginatum*. The open chambers were placed on nine new areas of *Sphagnum* lawn, plots being selected to contain different shoot densities of *E. vaginatum* and their CH<sub>4</sub> emission rates were determined. Flux monitoring took place between the 6th–10th July and the 17th–20th July 1998. These plots were then removed as intact cores to a depth of 400 mm and the amount of *E. vaginatum* was determined as the number of green and brown shoots and the dry weight of the above and below-ground biomass of *E. vaginatum*.

### Role of *E. vaginatum* in gas transfer

It was hypothesised that *E. vaginatum* increased CH<sub>4</sub> release from plots simply by acting as a conduit for CH<sub>4</sub>, providing a pathway for CH<sub>4</sub> to travel from the peat to the atmosphere. To test this hypothesis, nine field plots with similar *E. vaginatum* shoot densities and with water tables at or just below the *Sphagnum* surface were monitored for CH<sub>4</sub> flux rates from the 10th July to the 13th July 1998 and allocated to experimental blocks. Treatments were then randomly assigned within each block and comprised: (i) cutting of *E. vaginatum* stems below the water table; (ii) cutting stems above the water table; (iii) leaving

stems intact (control). The chambers were removed and stems were cut with a scalpel and, where plants were cut above the water table, cutting took place at the shoot base where the shoots became green, leaving ca. 40 mm of stem above the *Sphagnum* surface. The control chambers were also removed and then replaced in their original positions so that treatment of all plots, with the exception of *E. vaginatum* cutting, was identical. The CH<sub>4</sub> flux rates of these plots were then monitored for a period of five days.

An additional experiment was established in September 1997 to investigate whether a simple physical conduit would increase CH<sub>4</sub> release from the peatland. The 'conduits' were inert glass tubes (1 mm diameter bore) with their ends covered with gas-permeable, water-impermeable tape. Seven tubes were inserted into the peat to a depth of 100 mm, with 50 mm of tube protruding above the *Sphagnum* surface, in four of eight plots covered with pure *Sphagnum* lawn (i.e. no graminoid species present). The end of the tube inserted into the peat went below the water table and CH<sub>4</sub> fluxes from all eight plots were measured for 24 h after tube insertion.

#### *Sphagnum* removal

The observed low CH<sub>4</sub> emissions from plots of 'pure' *Sphagnum* may have been because *Sphagnum* was associated with CH<sub>4</sub> oxidation. To test this hypothesis, eight plots of pure *Sphagnum* lawn were monitored to determine their baseline CH<sub>4</sub> flux rates for a period of 2 days in October 1997. Using these data, plots were allocated experimental blocks. From one randomly selected plot in each block, the *Sphagnum* layer was carefully peeled away by hand, to avoid disturbing the surface of the peat, and the *Sphagnum* discarded. All chambers, including controls, were removed and replaced before CH<sub>4</sub> flux monitoring was resumed for a period of 2 days.

#### Statistical analyses

All data analyses and statistical comparisons were performed using SAS (SAS Institute, 1988). Repeated measures ANOVA, or repeated measures blocked ANOVA, were used to analyse for treatment effects. Frequency distributions of model residuals were tested for normality ( $\alpha = 0.1$ ) using the Shapiro-Wilk test (Holder, 1985). Normalised residuals were achieved by log<sub>10</sub>-transforming data. In the glass tube experiment, residuals could not be normalised by a log<sub>10</sub>-transform and, so, data were ranked before being

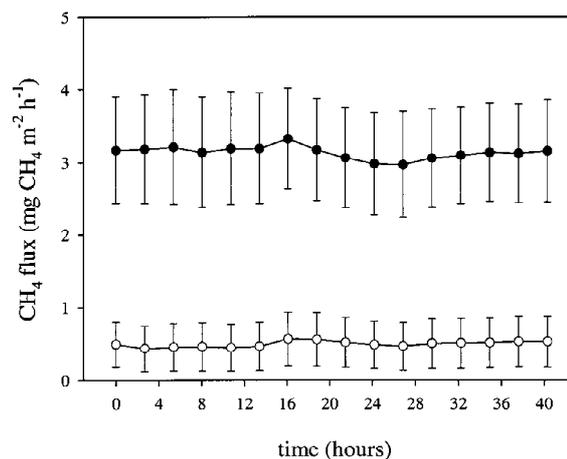


Figure 1. Mean CH<sub>4</sub> flux of experimental field plots with (●) and without (○) the presence of *E. vaginatum*. The dominant vegetation type in plots without *E. vaginatum* was *Sphagnum* spp. T=0 is the 1st October 1997, 15:00 hours. Standard errors of the means are shown as bars ( $n = 4$ ).

used in a repeated measures ANOVA; this is equivalent to the Kruskal-Wallis  $k$ -sample test designed for non-normal data (Campbell, 1989).

Relationships between CH<sub>4</sub> flux and *E. vaginatum* and CH<sub>4</sub> flux and CO<sub>2</sub> flux were determined using correlation and multiple-regression analysis (SAS Institute, 1988). Frequency distributions of residuals were tested for normality and data were log<sub>10</sub>-transformed to improve the residuals' fit to a normal distribution when necessary.

## Results

### *Monitoring E. vaginatum and Sphagnum sites for trace gas flux*

The site was a net producer of CH<sub>4</sub>, although the flux measured from areas that contained both *E. vaginatum* and *Sphagnum* was at least six times greater ( $P < 0.01$ ) than that from similar areas without *E. vaginatum* (see Figure 1).

Methane flux correlated with the number of green and brown *E. vaginatum* shoots, total shoot number, dry weight of above-ground biomass (green, brown and all shoots) and below-ground biomass. The weakest correlate was with number of brown shoots ( $r^2 = 0.63$ ). Below-ground biomass was found to be the best predictor of CH<sub>4</sub> flux ( $r^2 = 0.93$ , Figure 2) and, when other variables were added to the model using

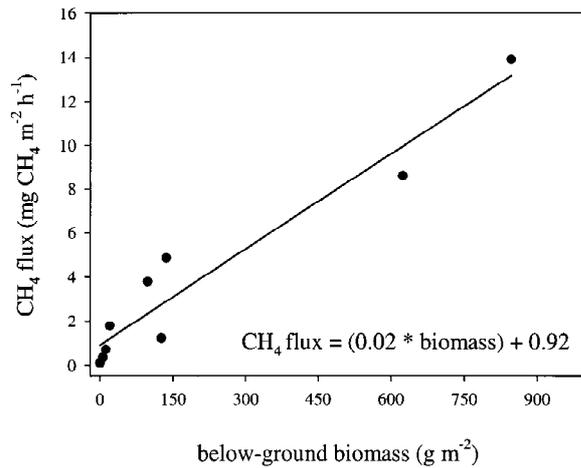


Figure 2. Relationship between the below-ground biomass of *E. vaginatum* and  $\text{CH}_4$  flux ( $n = 9$ ,  $r^2 = 0.93$ ,  $P < 0.001$ ) observed in July 1998 when the vascular vegetation was at peak biomass.

stepwise multiple regression (SAS Institute, 1988), no improvement in fit was achieved.

#### Role of *E. vaginatum* in gas transfer

Initial flux monitoring for a period of 3 days revealed that there were no significant differences ( $P > 0.05$ ) in  $\text{CH}_4$  flux from the plots prior to cutting. Following shoot cutting, mean  $\text{CH}_4$  emissions from plots where *E. vaginatum* had been cut below the water table were significantly lower ( $P < 0.05$ ) than emissions from intact plants and from plants which had been cut above the water table (Figure 3). The mean emission from plots with *E. vaginatum* cut below the water table was 44% of the flux from intact plants, whereas emissions from plots with intact plants and plants cut above the water table were not significantly different ( $P > 0.05$ ). Methane emissions were monitored for 5 days after shoot cutting took place and this pattern remained consistent, there being no indication that the release of  $\text{CH}_4$  from plants cut above the water table was decreasing from its pre-treatment level. The dip in  $\text{CH}_4$  emissions seen in Figure 3 resulted from the removal of all the chambers whilst shoot cutting took place and indicates the time taken for the flow-through system to re-stabilise to equilibrium concentrations after the chambers had been removed and replaced.

Methane flux from *Sphagnum* areas without and with glass tubes was  $5.1 \pm 4.2$  and  $111.5 \pm 53.2 \mu\text{g m}^{-2} \text{h}^{-1} \pm \text{SE}$ , respectively. The emissions were significantly higher ( $P < 0.01$ ) from areas with tubes. There was no significant impact on  $\text{CH}_4$  flux

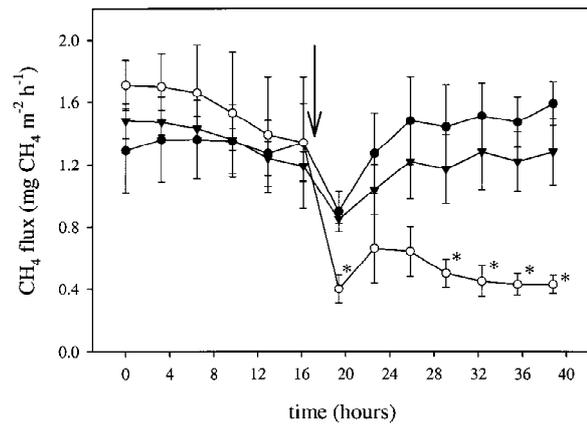


Figure 3. Mean  $\text{CH}_4$  flux of plots with intact shoots of *E. vaginatum* ( $\blacktriangledown$ ), *E. vaginatum* shoots cut above the water table ( $\bullet$ ) and *E. vaginatum* shoots cut below the water table ( $\circ$ ). T=0 is the 12th July 1998, 21:00 hours. The arrow indicates the point in time at which shoot cutting occurred. Standard errors of the means are shown ( $n = 3$ ). An asterisk marks a significant difference in flux ( $P < 0.05$ ) from control plots.

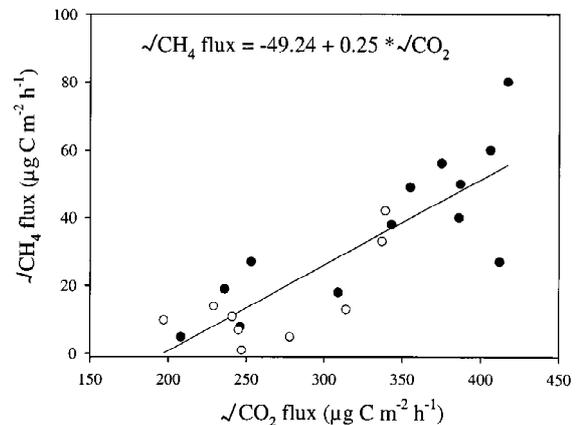


Figure 4. Relationship between night-time  $\text{CH}_4$  and  $\text{CO}_2$  flux of plots with ( $\bullet$ ) and without ( $\circ$ ) the presence of *E. vaginatum* ( $n = 22$ ,  $r^2 = 0.70$ ,  $P < 0.001$ ).

rates ( $P > 0.05$ ) when *Sphagnum* was removed from plots (data not shown).

#### Relationship between $\text{CO}_2$ and $\text{CH}_4$ fluxes

The night-time  $\text{CO}_2$  and  $\text{CH}_4$  fluxes pre-treatment, measured for the experiments that investigated trace gas fluxes from *Sphagnum* lawn areas with and without *E. vaginatum*, were used to investigate relationships between  $\text{CO}_2$  and  $\text{CH}_4$  fluxes at the site. During the growing season, night-time  $\text{CH}_4$  and  $\text{CO}_2$  fluxes were highly correlated ( $P < 0.001$ ;  $r^2 = 0.70$ ) in *Sphagnum* sites with and without *E. vaginatum*

(Figure 4). Only night-time flux values were used for these analyses, since CO<sub>2</sub> concentrations were greatly reduced within chambers in daylight hours due to photosynthesis. There was no significant correlation between CH<sub>4</sub> and CO<sub>2</sub> fluxes from the peat once the vegetation had started to senesce ( $P > 0.05$ ) and, at this time, the magnitude of CH<sub>4</sub> release was significantly lower ( $P < 0.05$ ) than when the vegetation was actively growing (data not shown).

## Discussion

### *Monitoring E. vaginatum and Sphagnum sites for trace gas flux*

Presence or absence of *E. vaginatum* appeared to control CH<sub>4</sub> release from areas of *Sphagnum* lawn. This was confirmed by the experiment in which chambers were placed over areas of *Sphagnum* with and without *E. vaginatum*. The significantly greater CH<sub>4</sub> emission observed from *Eriophorum* plots than from areas of *Sphagnum* has been reported in several other studies (Bartlett et al., 1992; Frenzel and Rudolph, 1998).

The mechanisms by which *E. vaginatum* could increase CH<sub>4</sub> emissions are by increasing C supply to the methanogens and/or by acting as a simple conduit for CH<sub>4</sub> (Schütz et al., 1990). Schimel (1995) concluded that the composition of the plant community and the ability to transport CH<sub>4</sub> was the most important determinant of flux and that measurements of total CH<sub>4</sub> production *per se* were not a good predictor of actual flux. Furthermore, Saarnio et al. (1998) measured similar CH<sub>4</sub> production potentials in monoliths containing either sedges or *Sphagnum* spp. and concluded that the 6–12 times greater release of CH<sub>4</sub> from the sedge monoliths was as an indicator of the great importance of CH<sub>4</sub> transport by vascular plants. The lateral movement of new substrate and CH<sub>4</sub> (Waddington and Roulet, 1997) will probably ensure that the concentration of CH<sub>4</sub> is relatively high at depth across the whole peatland, but for the CH<sub>4</sub> to escape to the atmosphere the presence of a conduit is required, as supported by the increased CH<sub>4</sub> release found from areas of *Sphagnum* with thin glass tubes inserted into the peat.

### *Correlation of CH<sub>4</sub> flux with E. vaginatum*

A strong, positive correlation between CH<sub>4</sub> emission and amount of *E. vaginatum* was observed, with the strongest relationship being with the amount of

below-ground biomass. This is unsurprising given the importance of aerenchyma in gas transport in wetland species (Daulat and Clymo, 1998; Lloyd et al., 1998; Torn and Chapin, 1993). In a growth chamber experiment with intact peat monoliths, Saarnio and Silvola (1999) found the rate of CH<sub>4</sub> flux to be strongly dependent on the number of *E. vaginatum* shoots. The release of CH<sub>4</sub> increased linearly with the number of *E. vaginatum* shoots at low shoot densities and became saturated according to a hyperbolic curve with increasing shoot density. The results of the present *in situ* field experiments are in support of their laboratory study. That we found correlations with both shoot density and the dry weight of above- and below-ground biomass is explained by the relationship between root biomass and stem cross-sectional area (Arenovski and Howes, 1992) and thus, as biomass increases the conduit potential of the plant also increases. Torn and Chapin (1993) found that flux tended to correlate with above-ground plant biomass of *Carex aquatilis* Wahlenb., and *Eriophorum angustifolium* Honck., with *C. aquatilis* accounting for most of the effect. In contrast to both the present study and that of Saarnio and Silvola (1999), no correlation was found between CH<sub>4</sub> flux and shoot number of any or all species.

That the strongest correlation was found with the amount of below-ground biomass in the current study was perhaps to be expected, as in many wetland species a large percentage of the living biomass is found in below-ground roots and rhizomes. The concentration of CH<sub>4</sub> in the gas-phase and as dissolved CH<sub>4</sub> within the peat is likely to be at saturation (Sebacher et al., 1985; Shannon et al., 1996) and thus, the rate-limiting step for CH<sub>4</sub> transport is the interface between the CH<sub>4</sub> saturated rhizosphere and the root aerenchyma (Chanton and Dacey, 1991; Kelker and Chanton, 1997; Schimel, 1995). Therefore, when the below-ground biomass of *E. vaginatum* increases, so too does the net emission of CH<sub>4</sub> at the surface. Frenzel and Rudolph (1998) speculated that since the below-ground parts of *Eriophorum* cover a wide area, they will act as a route for CH<sub>4</sub> release even from below *Sphagnum* lawns where no shoots are growing.

### *Role of E. vaginatum in gas transfer*

The fact that there was no significant difference in CH<sub>4</sub> emissions between the intact plants and those cut above the water table indicates that the *E. vaginatum* leaves were not providing resistance to gas flow, consistent with the results from similar studies with *E.*

*angustifolium* (Schimel, 1995), *Scheuchzeria palustris* L. (Shannon et al., 1996) and *Carex* (Kelker and Chanton, 1997). We hypothesize that any changes in stomatal aperture have little effect on CH<sub>4</sub> emission from *E. vaginatum*, as testified by the lack of a pronounced diurnal rhythm in CH<sub>4</sub> flux (see Figure 1). Similarly, no diurnal pattern in CH<sub>4</sub> flux was observed at the site during flux monitoring in July and August at the time of peak biomass of the vascular vegetation (data not shown). In contrast, Thomas et al. (1996) observed a diurnal effect on the release of CH<sub>4</sub> from *E. angustifolium* in a laboratory study with intact peat columns and attributed this to the opening and closure of the stomata. Stomatal response may vary with experimental conditions and it should be noted that the *in situ* experiment described here involved minimal modification of the environment, unlike many laboratory experiments which maximize control of the environment at the risk of modifying plant response.

It has been found that some wetland plants show relatively weak stomatal closure in the dark, perhaps explaining the lack of diurnal fluctuation in this study and in others (Morrissey et al., 1993; Torn and Chapin, 1993). It is also possible that the stomata are not the release site of CH<sub>4</sub>, since cuticular conductance is a significant pathway for CH<sub>4</sub> release in *Carex* spp., particularly in young and senescent leaves early and late in the growing season (Morrissey et al., 1993). Further, Nouchi et al. (1990) demonstrated that CH<sub>4</sub> is not released from the stomata of rice plants, rather from small micropores in the culm.

The absence of a reduction in CH<sub>4</sub> flux in darkness in the present study supports earlier assertions that CH<sub>4</sub> transport through plants is passive with respect to photosynthesis (Conrad, 1993; Sebacher et al., 1985; Torn and Chapin, 1993). Indeed, plants which rely solely on molecular diffusion for gas transport do not show large variations in CH<sub>4</sub> emission rates between day and night, for example *Carex rostrata* Stokes and *Carex limosa* L. (Whiting and Chanton, 1992). In contrast, pressure-induced flow of CH<sub>4</sub> in some wetland plants occurs by heating and pressurization of green, emergent leaves, which drives CH<sub>4</sub> into the roots and through old, brittle leaves to the atmosphere (Dacey, 1981; Yavitt and Knapp, 1998). The diurnal variation in CH<sub>4</sub> release from plants employing pressure-induced flow is considerably greater than CH<sub>4</sub> release from plants which transport gas by molecular diffusion (Sebacher et al., 1985).

A further implication of the cutting experiment is that the conduit effect predominates over the substrate

effect, at least in the short-term, as even plants with little or no photosynthetically active tissue continued to transport a similar amount of CH<sub>4</sub> as intact plants. Conrad (1993) reported that the production of CH<sub>4</sub> is probably greater than the emission of CH<sub>4</sub>, so that CH<sub>4</sub> accumulates in the soil and over short periods at least, the emission of CH<sub>4</sub> to the atmosphere is a function of the properties of the reservoir of CH<sub>4</sub> in the soil rather than of CH<sub>4</sub> production itself. This reservoir is connected to the atmosphere by the dense network of *E. vaginatum* shoots in peatlands (Frenzel and Rudolph, 1998). It is not possible to say from the present study how long plants cut above the water table would continue to transport CH<sub>4</sub> at the same rate as intact plants but it was clear that inert tubes carry out a similar function. It is likely that without continuous CH<sub>4</sub> production, CH<sub>4</sub> emission will gradually decrease until the produced CH<sub>4</sub> has been depleted.

The difference in flux between the intact plants and those cut below the water table may provide some indication of the amount of CH<sub>4</sub> release due to direct transport through the roots and stems of *E. vaginatum*. An immediate and significant decrease in CH<sub>4</sub> emissions following the removal or cutting of vascular vegetation has been reported in several other field (e.g. Kelker and Chanton, 1997; Torn and Chapin, 1993) and laboratory (e.g. Saarnio et al., 1998) studies, supporting the hypothesis that aerenchymatous plants provide the dominant pathway for CH<sub>4</sub> transport from the soil to the atmosphere. The significant reduction in CH<sub>4</sub> flux from plants cut below the water table may result from the much slower transfer to the atmosphere by diffusion through water and/or CH<sub>4</sub> oxidation in the surface layers where the frequent oxic conditions enable methanotrophs to thrive (Nedwell and Watson, 1995).

Given the importance of aerenchymatous plant tissue in controlling CH<sub>4</sub> fluxes, the significantly lower efflux from the areas of pure *Sphagnum* is not surprising since *Sphagnum* spp. have no roots or ventilation system and are generally not considered to have a role in the conduction of CH<sub>4</sub> (Thomas et al., 1996). It was hypothesized that the lower efflux could also have been attributed to a limitation of CH<sub>4</sub> release by *Sphagnum*, for example, through a direct link between methanotrophs and the plant. High rates of CH<sub>4</sub> oxidation have been reported in the moss layer (Vecherskaya et al., 1993) and surface (Whalen and Reeburgh, 1990; Whalen et al., 1996) of tundra soils. However, the removal of *Sphagnum* in the current study did not support this, with no significant change in CH<sub>4</sub> emissions

after *Sphagnum* removal, suggesting that *Sphagnum* did not limit CH<sub>4</sub> diffusion or production, or act as a site for CH<sub>4</sub> oxidation. This observation adds support to the 'conduit theory' for *E. vaginatum* because the tube experiment clearly showed that CH<sub>4</sub> was present at depths below *Sphagnum* but was escaping at a much slower rate, by molecular diffusion or ebullition, from the peat to the atmosphere.

#### *Relationship between CO<sub>2</sub> and CH<sub>4</sub> fluxes*

There was a positive correlation between night-time CH<sub>4</sub> flux and net CO<sub>2</sub> production, but only before the vegetation began to senesce. If net CO<sub>2</sub> production is taken as a function of overall microbial and plant activity, then this relationship suggests that in some areas of the *Sphagnum* lawn, conditions are more favourable for microbial and plant activity than others. This correlation suggests that methanogenic rates are either controlled by overall plant and microbial activity, or that edaphic conditions (e.g. peat temperature) which are favourable for plant and general microbial activity also favour methanogenesis. If methanogenic rates are controlled by overall microbial and plant activity, one reason for this may be that methanogens are poor competitors and probably have to rely on substrates not utilised by other microbes (Segers and Leffelaar, 1996). Greater overall microbial and plant activity would generate more methanogenic C substrates and, so, increase CH<sub>4</sub> production, although this could only be proved by <sup>13</sup>C or <sup>14</sup>C measurements.

The spatial variation in CO<sub>2</sub> and CH<sub>4</sub> fluxes implies that different areas of the peatland are more or less productive than others and, indeed, a positive correlation between net CH<sub>4</sub> emissions and primary productivity has been demonstrated in wetland ecosystems (Bellisario et al., 1999; Waddington et al., 1996; Whiting and Chanton, 1993). As the growing season ended, primary productivity decreased, potentially explaining why CH<sub>4</sub> and CO<sub>2</sub> fluxes no longer correlated during senescence of the vegetation. The decrease in CH<sub>4</sub> emissions as the vegetation began to senesce also supports the observation that the active surface vegetation exerts a strong control over CH<sub>4</sub> flux, as has already been detailed. Dise et al. (1993) reported a similar decline in CH<sub>4</sub> flux from a northern peatland in late August when the vegetation underwent senescence.

The site was a net emitter of CH<sub>4</sub> throughout the current study, as is typical for peat wetlands (see Clymo, 1987). The presence of *E. vaginatum* dom-

inated CH<sub>4</sub> emission from the peatland, probably by functioning as a conduit for CH<sub>4</sub> release from the peat to the atmosphere. This is consistent with the findings of Lloyd et al. (1998) and others on the importance of plants with aerenchyma in regulating CH<sub>4</sub> flux from peatlands. This has implications for the management of peatlands as sources or sinks for trace gases, since the results of this study suggest that any change leading to an increase in the coverage of these plants would lead to a concomitant increase in CH<sub>4</sub> emissions. As such, when estimating CH<sub>4</sub> flux from peatlands, it is important to quantify the role of vegetation with gas transporting tissues.

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