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REGULAR ARTICLE

A mesocosm study of the role of the sedge *Eriophorum angustifolium* in the efflux of methane—including that due to episodic ebullition—from peatlands

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Abstract
Background & Aim Vascular plants may reduce episodic ebullition losses of methane (CH_4) from peatlands. They transport CH_4 to the atmosphere, which may lead to a reduction in pore-water [CH_4], bubble formation and release. This effect may be compounded by rhizospheric oxidation and associated methanotrophy. However, any reduction in pore-water [CH_4] may be countered by root exudation (substrate for methanogens). The aim of this study was to determine how the presence of sedges affects CH_4 emissions from peatlands.
Methods Five pairs of peat cores were collected from a raised bog. One of each pair contained *Sphagnum cuspidatum* and *Eriophorum angustifolium* ('sedge' cores); the other was dominated by *S. cuspidatum* ('no-sedge'). From these the total CH_4 efflux—including that due to episodic ebullition—were measured. A partial-shading treatment helped isolate the potential effect of root exudation.
Results Sedge samples had significantly higher CH_4 fluxes than no-sedge samples, but episodic-ebullition fluxes were not significantly different. Between full-light and partially-shaded conditions, there was a significant increase in the difference in CH_4 fluxes between the sedge and no-sedge cores.
Conclusion The higher rates of CH_4 flux from the sedge cores cannot be explained simply by higher rates of CH_4 production due to rapid utilisation of exudates.

Keywords Peatlands · Methane flux · Ebullition · Vascular plants · *Eriophorum angustifolium*

Introduction

Many northern bogs are dominated by *Sphagnum* mosses, with sedges and ericaceous shrubs also being important components of the vegetation. It is known that some vascular plants, and sedges in particular, have an important effect on methane (CH_4) emissions from peatlands. Sedges can act as 'short-circuits' between the peat and the atmosphere, with the CH_4 moving through the aerenchyma and by-passing methanotrophic bacteria in the zone above the water table (e.g., Frenzel and Rudolph 1998; Greenup et al. 2000). Through root exudation they can provide substrate to the methanogens, thus potentially enhancing rates of CH_4 production (e.g., Öquist and Svensson 2002; Ström et al. 2003) and emission. They may also act as conduits for the transfer of oxygen to the rhizosphere—a process known as radial oxygen loss (ROL) or rhizospheric oxidation—with

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the oxygen both inhibiting archaeal CH_4 production and enhancing bacterial methanotrophy (Chanton 2005; Popp et al. 2000; Wheeler 1999). Although there is good evidence for each of these processes, there remains a lack of understanding of how they combine to affect total CH_4 emissions from bogs and, in particular, how they affect the formation and release to the atmosphere of CH_4-containing bubbles.

Recent studies, as summarised by Coulthard et al. (2009), have suggested that ebullition—the release of CH_4-containing bubbles to the atmosphere—may be the most important pathway of CH_4 loss from peatlands; i.e., that ebullition is more important than diffusion through the interstices within the peat and more important than plant-mediated transport. Ebullition may be divided into steady ebullition and episodic ebullition. Steady ebullition, if it occurs, refers to the steady stream of CH_4-containing bubbles released to the water table, an analogy being the steady release of bubbles (albeit ones containing CO_2) from vats of fermenting beer. The CH_4 in this steady stream of bubbles moving through the peat will then diffuse through the zone above the water table to the peatland surface and may be partly or wholly consumed by methanotrophs. CH_4-containing bubbles may also be released in short-lived (minutes to hours) bursts or episodes where fluxes are generally much higher and more variable than background steady fluxes. These periods of rapid CH_4 loss from the peatland occur when groups of bubbles or single large bubbles containing CH_4 move to the water table, and may be termed episodic ebullition. Because of their volume, these bubbles, and the CH_4 within them, will move en masse (advect) to the peatland surface from the water table, largely by-passing methanotrophic 'processing' (Rosenberry et al. 2006). Trapped bubbles may be released to the atmosphere when their buoyancy exceeds the forces keeping them in place (e.g., surface tension), and factors such as changes in atmospheric pressure and turbulent shaking of bog vegetation have been implicated in episodic bubble release (Tokida et al. 2005; David Fowler pers. comm.).

Chanton (2005) suggests that, because of their role as transporters of CH_4 to the atmosphere, vascular plants may lower pore-water $[CH_4]$ (square brackets denote concentration) by as much as 50%, with the effect that diffusion and bubble formation/episodic ebullition become secondary mechanisms of CH_4 transport. Many studies on the effects of vascular plants on ebullition have looked at inundated mineral sediments and emergent macrophytes (cf. Chanton 2005), and it remains unclear how vascular plants affect ebullition in peatlands, particularly bogs. Those studies that have been done on peats, such as the laboratory mesocosm investigations of Christensen et al. (2003) and Ström et al. (2005), present a somewhat contradictory picture which may, in part, be due to their (the studies') lack of replication: no more than two samples of any single peat type were investigated. Christensen et al. (2003) found that episodic ebullition may contribute as much as 20-50% of total CH_4 fluxes to the atmosphere when the cover of sedges such as *Carex rostrata* Stokes and *Eriophorum angustifolium* Honck. is "very dense" or "dense". Ström et al. (2005) found that the contribution for *C. rostrata* was about 23%, but only 3.5% for *Eriophorum vaginatum* L., which may suggest that ebullition varies in importance between species within the Eriophora. However, in a field study on a bog in S Estonia, Frenzel and Rudolph (1998) refer to the presence of a zone of bubbles that coincides with dense networks of roots and rhizomes of *E. vaginatum*, although they also suggest that the roots and rhizomes act as a trap for bubbles produced lower in the peat profile.

Hence, the picture of how vascular plants, and sedges in particular, affect episodic ebullition in peatlands remains unclear. To address this lack of clarity, we sought to address the following research question: how does the presence of sedges affect CH_4 emissions from bog peats, particularly emissions due to episodic ebullition? We chose to look at *E. angustifolium* because it is common in many Eurasian and North American bogs and because it is also found widely in minerotrophic conditions (fens). We posed and tested three hypotheses; each is given below, together with a brief rationale. These hypotheses were used to provide greater focus to the overall research question. Following Green and Baird (2011 in review) we use two terms to describe CH_4 efflux: 'steady flux' and 'episodic ebullition'. The latter has been defined already. The former is the combination of diffusion through the soil, diffusion through plant tissue, and steady ebullition, and, as such, is similar to the "steady emission" of Christensen et al. (2003). 'Steady' is used as shorthand here and does not mean that fluxes are truly steady; however, when measured in the absence of episodic ebullition, these three processes will give a linear increase in [CH_4] in the enclosed atmosphere of a flux chamber over short periods of time, and are probably steady over periods of tens of minutes to an hour or two (Christensen et al. 2003).

The hypotheses are:

Hypothesis 1: Steady CH_4 flux is higher in peat with *E. angustifolium* than in peat without any vascular plant cover.

Rationale: Because it is deep-rooting (Limpens et al. 2003), *E. angustifolium* can be expected to vent CH_4 from a large part of the peat profile straight to the atmosphere, by-passing methanotrophic processing in the zone between the water table and the ground surface (should such a zone exist). The presence of the sedge may also lead to higher rates of CH_4 production (and hence loss) via root exudation of recent photosynthate and through longer-term growth of rhizomes and roots which can provide substrate for methanogens when they decay (see Hypothesis 3). For Hypothesis 1 to hold, the inhibitory effects of rhizospheric oxidation have to be negligible, or secondary, to venting and enhanced CH_4 production.

Hypothesis 2: Episodic CH_4 flux (episodic ebullition) is lower in peat with *E. angustifolium* than in peat without any vascular plant cover.

Rationale: Two possibilities may be invoked to explain a reduction in episodic ebullition in the presence of *E. angustifolium*. First, the presence of the sedge reduces pore-water [CH_4] via rhizospheric oxidation, causing lower rates of CH_4 production and/or higher rates of methanotrophy, so that rates of bubble production and release are reduced. Secondly, pore-water [CH_4] is reduced via the enhanced rate of release of CH_4 through aerenchyma, with the effect again being that rates of bubble production and release are reduced.

Hypothesis 3: Any differences in steady CH_4 flux between peat with *E. angustifolium* and peat without any vascular plants decrease when the growing surface of the peatland is partially shaded. That is, steady CH_4 flux is related to vascular plant productivity and root exudation.

Rationale: CH_4 production may be enhanced by root exudates which act as substrate for methanogens (Joabsson et al. 1999; Ström et al. 2003; Waddington et al. 1996). Because root exudation is tightly coupled with plant productivity, photosynthesis is thought to be coupled with the rate of methanogenesis and therefore CH_4 emissions (Joabsson et al. 1999). Non-vascular plants such as *Sphagnum* do not provide substrate quickly to the zone of CH_4 production (any *Sphagnum*-derived substrate would have to diffuse through the pore network or be carried by mass water flow), so any relationship between shading and CH_4 efflux is likely due to root exudation from *E. angustifolium*. When partially shaded, the rate of carbon fixation by vascular plants should be reduced (Öquist and Svensson 2002; Ström et al. 2003); thus, a comparison of CH_4 fluxes under partially-shaded conditions with those under full-light conditions should reveal how *E. angustifolium* productivity affects CH_4 loss. The results of such a comparison might be confounded by rhizospheric oxidation if the latter is driven by active gas transport (i.e., mass or advective flow of gas through a plant) which varies with light intensity (Jackson and Armstrong 1999). However, the available evidence suggests that diffusion is the only mechanism of CH_4 transport in *E. angustifolium* (e.g., Frenzel and Rudolph 1998).

To test these hypotheses we focused on a single peatland microhabitat—bog hollows—and used a controlled-environment laboratory mesocosm approach. We used a paired design whereby adjacent samples of peat—one with an *E. angustifolium* cover and one with no vascular plants—were collected. We incubated the samples in two environmental cabinets and measured both the steady CH_4 flux (day and night) and the episodic-ebullition CH_4 flux. Net ecosystem (CO_2) exchange (NEE) was also measured. The peat samples were subjected to 42 days under full-light summer conditions, followed by 42 days with a 55% reduction in photosynthetically-active radiation (PAR), before being brought back into full-light conditions for a further 42 days. The latter period was used to check that there were no long-term trends in NEE that were unrelated to the transition from full-light to partially-shaded conditions. Henceforth, we term the different light treatments phases.

Materials and methods

Field site

The peat samples were collected from Longbridgemuir, a raised bog located near Dumfries, SW Scotland (54° 55’ 31” N 03° 14’ 37” W) (for a full description, see Green and Baird 2011 in review). We collected our samples from bog hollow microhabitats (cf. Belyea and Clymo 2001). The peat samples were taken from five separate hollows. From each hollow we extracted one sample co-dominated by *Sphagnum cuspidatum* Ehrh. ex Hoffm. and *E. angustifolium* (labelled ‘sedge’) and one adjacent sample (no more than 50-cm distant) containing just *S. cuspidatum* (i.e., a sample with no vascular plants) (labelled ‘no sedge’). The hollows from which the pairs of samples were extracted, contained poorly-decomposed peat consisting of the remains of *S. cuspidatum*, with some *E. angustifolium* remains where sedges were present. There were no visual differences between each member of a pair of samples, excepting the presence of sedges in one; that is, the peat type and degree of decomposition of the peat were the same between samples. In addition, because of their close proximity and because they were in the same micro-habitat, the samples would have shared very similar environmental conditions to each other (e.g., rainfall inputs, thermal regime). As far as could be ascertained, the only substantial difference between the samples was the presence of sedges in one of each pair. Fig. 1 shows one of the sampling sites, with the no-sedge and sedge areas from which the adjacent samples were taken. It can be seen from the picture that, apart from the sedge cover, the two sample locations are very similar. Thus, we had a paired design to our experiment which meant that we could analyse our data using paired or repeated-measures tests.

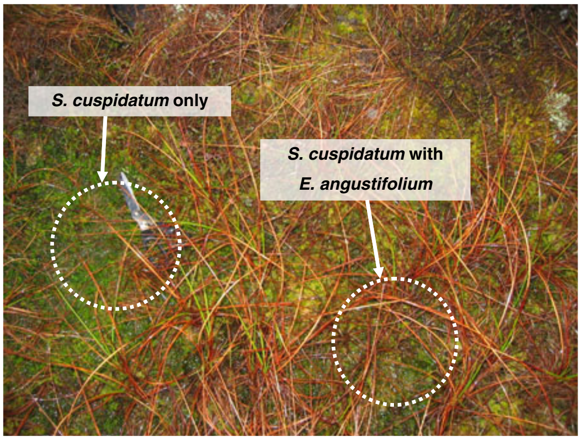

Fig. 1 View of the hollow from which the second pair of peat samples was taken. The peat in the hollow is dominated by poorly-decomposed *Sphagnum cuspidatum* remains. Scale: scissors are 20-cm long

Sample collection and incubations

The samples were extracted on 6th and 7th May 2009 using open-ended 20-cm inside-diameter, 50-cm deep polyvinyl chloride (PVC) cylinders. To extract the samples, the cylinders were placed on the peat surface and the peat around the outer edge of the cylinder was cut using gardening scissors to a depth of c. 2 cm. The cylinder was then pushed into the cut peat, and the process repeated until 50 cm depth was achieved. Core extraction took between one and two hours. More details may be found in Green and Baird (2011 in review) which reports on different samples and experiments from those described here. The samples were kept in an undrained state after collection by wrapping the PVC cylinders in tight-fitting, fully-waterproof, plastic bags. Within a few hours of collection, the samples were transferred into PVC holders fitted with water-table regulators, pore-water sampling ports, and fittings to allow chamber flux readings to be taken of the gas exchange from the top of the peat. When back in the laboratory the sides of these holders were enclosed in a 5-cm layer of insulation (vermiculite pellets), after which the samples were incubated within two Weiss-Gallenkamp Fitotron SGC097.CPX.F plant growth cabinets. Incubations started on 18th May 2009 and continued for 18 weeks until 18th September 2009. The cabinets were used to control and maintain ‘weather’ conditions typical of summer at Longbridgemuir, with a 14 h daylight period. Daylight temperatures were set to 15°C, and night-time temperatures to 12°C. The relative humidity was 76% and 89%, respectively, during the daytime and night-time settings. Daytime PAR was nominally 380 μm m^{-2} s^{-1} during the full-light phase, and 171 μm m^{-2} s^{-1} during the shading treatment (the latter being 45% of the full-light value).

We provided the peat samples with artificial rainfall. The water used for the rainfall was matched chemically with natural rainfall at the field site (Na^+= 2.07 mg L^{-1}, Mg^{2+}=0.46 mg L^{-1}, Ca^{2+}=0.28 mg L^{-1},

K^+=0.12 mg L^{-1}, NH_4^+=0.33 mg L^{-1}, NO_3^-= 0.74 mg L^{-1}, SO_4^{2-}=2.11 mg L^{-1}, Cl^-= 3.76 mg L^{-1}; pH adjusted to 5.17). A total of 150 mL (~ 5 mm) of artificial rainfall was added to each peat sample per week.

Water tables in the peat samples were set to a constant depth below the surface (1 cm below ground level) to reflect field conditions. Water-table levels were maintained using Mariotte regulators fitted to each peat sample holder; these contained He-sparged deionised water. Atmospheric pressure and (as a check) internal cabinet temperature were measured and logged by a 'Diver' pressure and temperature gauge (Van Essen Instruments) (pressure accuracy of~± 0.5 hPa and precision of~0.2 hPa; temperature accuracy of~± 0.5°C and precision of 0.2°C). Atmospheric pressure was measured because, as noted above, some studies have suggested a link between low pressure episodes and episodic ebullition events. PAR was measured daily above all samples using a Skye Instruments PAR Quantum Sensor to check that each peat sample was receiving equivalent amounts of incoming solar radiation. No significant differences were found between sedge and no-sedge samples. For example, during the first full-light treatment, the two groups had the following means and standard deviations of PAR photon flux density: no sedge=390.0, 20.5 μmol m^{-2} s^{-1}; sedge=384.1, 24.3 μmol m^{-2} s^{-1}) (p=0.853 [two-sample t-test]).

Steady CH_4 fluxes

The description here follows that given in Green and Baird (2011 in review). Steady fluxes were measured once a week by fitting acrylic flux chambers to water-filled collars on the top of the peat holders. Daytime measurements were made at or close to the middle of the daylight phase, while night-time measurements were made after two-three hours of darkness. Gel ice packs (hung within the chamber) were used to minimise the temperature increase of the air above the peat sample during chamber use. Small electric fans were used to circulate the chamber air. The chamber wall was drilled and fitted with an acrylic tube. On the inside of the chamber, a balloon was attached to the tube; this arrangement allowed the equalisation of pressure between the inside and outside of the chamber. Using disposable syringes with 21-gauge needles, 12-mL gas samples were extracted at 5-minute intervals for 30 min through a septum in the chamber wall. The effectiveness of the balloon and ice packs was checked by measuring chamber temperature and pressure during gas sampling using a Commeter C4141 thermometer-hygrometer-barometer (Comet Systems, Czech Republic; temperature precision 0.1°C, accuracy±0.4°C; pressure precision 0.1 hPa, accuracy±2 hPa). Each extraction of a gas sample was preceded by triplicate purges after septum penetration. Gas samples were transferred into 12-mL pre-evacuated vials (Labco Limited, High Wycombe, Buckinghamshire, UK) and were measured for their CH_4 content using an Agilent 7890A gas chromatograph (GC) system fitted with a flame ionisation detector (FID). CH_4 was separated on a stainless steel column packed with Porapak (Q 80/100) at 30°C with zero grade N_2 as the carrier gas. Standard analytical grade reference span gases were used to calibrate the GC, and thereafter inserted at regular intervals into the sample runs to check for drift.

The flux chamber data were used to test Hypotheses 1 and 3, for which only steady flux data were needed. Hence, any episodic ebullition fluxes during flux chamber measurements (indicated by sudden, step-like increases in chamber [CH_4]) were discounted, and only the steady component of the flux estimated. The slope of the regression line of chamber [CH_4] over time was used for estimating fluxes, provided $r^2 \geq 0.8$ and $p<0.05$. For situations where the change in chamber [CH_4] was<0.003 ppmv, fluxes were assumed to be zero. In all other cases the data were rejected.

Net ecosystem exchange

Net ecosystem exchange (NEE) provides a direct measure of the net CO_2 exchange between ecosystems and the atmosphere. NEE was measured to determine whether partial shading caused a reduction in the rate of carbon fixation by vascular plants. NEE was measured on a weekly basis using the flux chambers; the chamber gas samples used for CH_4 analysis were also used for CO_2 analysis using the same Agilent 7890A gas chromatograph (GC) system (details as above).

CO_2 exchanges were estimated using a similar protocol to that employed for estimating steady CH_4 fluxes. The slope of the regression line of chamber [CO_2] over time was used for estimating fluxes, provided $r^2 \geq 0.8$ and $p < 0.05$. For situations where changes in flux chamber [CO_2] were <1 ppmv, fluxes were assumed to be zero. In all other cases the data were rejected. We used the convention that a positive NEE indicates a net release of CO_2 to the atmosphere, while a negative value indicates a net uptake of CO_2 from the atmosphere. Thus, an increase in NEE would indicate less CO_2 being taken up by the peat samples or a greater rate of net CO_2 loss.

Episodic ebullition measurement

Water losses from the Mariotte regulators were recorded daily during the incubations (except at weekends). Water tables may fall due to evapotranspiration and also when trapped bubbles are released from the cores during episodic ebullition. After any drops, the water-table level is immediately restored by water flowing from the Mariotte regulator into the peat sample. The two processes can be separated by analysing the regulator data; evapotranspiration appears as a steady loss (when recorded daily) while episodic ebullition appears as large and sporadic losses in the daily time series data. To convert the volumetric release of bubbles to a CH_4 flux, it was assumed that the CH_4 content of bubbles was in equilibrium with the dissolved pore-water CH_4 (see below).

During bubble formation and build up, the water table may rise. To prevent the latter, each peat holder was fitted with an overflow pipe. Therefore, regardless of whether bubbles built up or were released, water-tables were held at a constant level.

Dissolved CH_4 content

Weekly measurements were made of pore-water [CH_4] at six depths: 7, 14, 22, 30, 38 and 46 cm. Pore water was extracted from mini-piezometers inserted horizontally through the side of the peat holder. The piezometers comprised perforated tubes, with a length of 4 cm, and an outside diameter of 0.8 cm. Approximately 20 mL of pore water was extracted via gravity flow from each port (in some ports, the flow rate was too slow for a sample to be obtained within an hour, so samples were extracted under suction). Of this volume, 12 mL was injected into 12-mL mini-vials (Labco Limited, High Wycombe, Buckinghamshire, UK), into which a 2-mL headspace of analytical grade Helium (He) was introduced via a syringe, causing pore water to be displaced through a separate bleed needle in the vial's septum (bleed needle was then removed). After shaking for 24 h, the headspace gas was analysed for CH_4 content using the GC method described above. The dissolved CH_4 contents were used in our calculations of episodic ebullition flux. We used the highest pore-water [CH_4] values from each peat core on each measurement occasion when estimating the CH_4 content of bubbles, so our calculations of episodic ebullition flux represent a higher-end estimate (see Episodic ebullition measurement).

Statistical analysis

For all statistical tests of the hypotheses, significance was accepted at $p \leq 0.05$. Statistical analyses were performed using SPSS version 16.0.0 (2007). Paired *t*-tests were used to address Hypotheses 1 and 2. For Hypotheses 1 and 2, the variable compared was, respectively, the untransformed mean steady and the mean episodic CH_4 flux in the sedge and no-sedge paired cores. The response variable for Hypothesis 3 was the untransformed mean steady CH_4 flux. A 2-way, repeated-measures ANOVA was used to test the hypothesis, with repeated measures applying to the full and partial light phases and to the sedge and no-sedge peat samples, The ANOVA was used to show if any differences between sedge and no-sedge samples changed according to light phase, thus providing a direct test of the hypothesis. The 2-way, repeated-measures ANOVA also provides an additional test of Hypothesis 1. In all tests, the data met the parametric assumptions of normality and equality of variance.

Results

Hypothesis 1

Fig. 2 shows the median steady CH_4 fluxes from the cores. It was found that the sedge samples had significantly higher CH_4 fluxes than the no-sedge samples under both the first full-light and partially-shaded phases (daylight full-light: $p=0.002$; daylight partially-shaded: $p=0.005$; night-time full-light: $p=0.002$; night-time partially-shaded: $p=0.003$). Therefore, Hypothesis 1 may be accepted for both the first full-light phase and the partially-shaded phase.

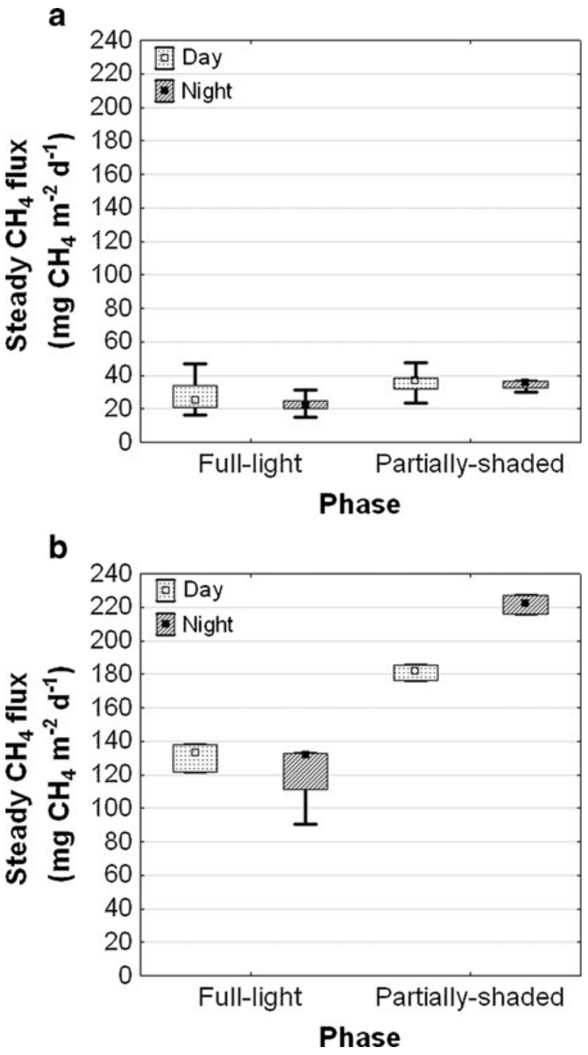

Fig. 2 Box plots of the steady CH_4 fluxes (i.e., excluding episodic ebullition) from the no-sedge (**a**) and the sedge (**b**) samples. The median is shown as a *filled* or *open square*, the inter-quartile range by the box or rectangle, and the minimum and maximum by the 'whiskers' extending from the box

As a supplement to the main hypothesis, for each of the sample types (either sedge or no-sedge) we compared day-time and night-time CH_4 fluxes for the first full-light phase. There was no-significant difference between day-time or night-time emissions (sedge $p=0.13$; no sedge $p=0.26$).

Hypothesis 2

Episodic ebullition was recorded 251 times across all of the cores over the first two light phases (full-light and partially-shaded). Episodic ebullition occurred in one or more cores on 66 of the total of 84 days (Fig. 3), with the number of incidences ranging from 2 to 66 for individual cores. When episodic ebullition occurred in a core, daily episodic ebullition fluxes ranged from 81.1 to 276 mg CH_4 m^{-2} d^{-1} in the sedge cores, and from 0.20 to 784 mg CH_4 m^{-2} d^{-1} in the no-sedge cores.

The mean episodic-ebullition flux (fluxes were combined for the first two light phases before being compared—see below) was not significantly different between sedge and no-sedge samples ($p=0.774$). Therefore, Hypothesis 2 may be rejected. Additional tests showed that mean episodic-ebullition flux did not differ between full-light and partially-shaded conditions (no-sedge $p=0.49$; sedge $p=0.96$). The data also showed that ebullition increased with decreasing atmospheric pressure, although this was statistically a rather weak link relationship ($r=0.1$; $p=0.004$ (first full-light and partially-shaded conditions combined)). Time-averaged episodic ebullition contributed, on average, 28.0 and 7.0% to total CH_4 flux, respectively, in the no-sedge and sedge samples.

Mean pore-water [CH_4] (which is~depth-averaged pore-water [CH_4] and also a measure of the dissolved CH_4 pool or stock in the samples) was significantly higher in the no-sedge cores ($p=0.027$) (2-way, repeated-measures ANOVA) (Fig. 4). There was no significant difference in mean pore-water [CH_4] between light phases ($p=0.268$) (Fig. 4). Maximum pore-water [CH_4] (not shown in Fig. 4) gave a similar result to the mean pore-water [CH_4] data, with the difference between sedge and no-sedge samples again being significant (no-sedge higher; $p=0.041$).

Hypothesis 3

The 2-way, repeated-measures ANOVA showed that there were significant differences ($p=0.002$) in steady CH_4 fluxes between the sedge and no-sedge samples, and also that these differences depended on light phase. However, unexpectedly, there was a significant increase in differences in fluxes between the two phases (interaction between phase and vegetation: $p=0.006$), when, according to the hypothesis, one would expect the differences to decrease.

Hypothesis 3 is predicated on the assumption that NEE is affected by shading, such that there is more carbon uptake by the ecosystem during full-light conditions than during partially-shaded conditions.

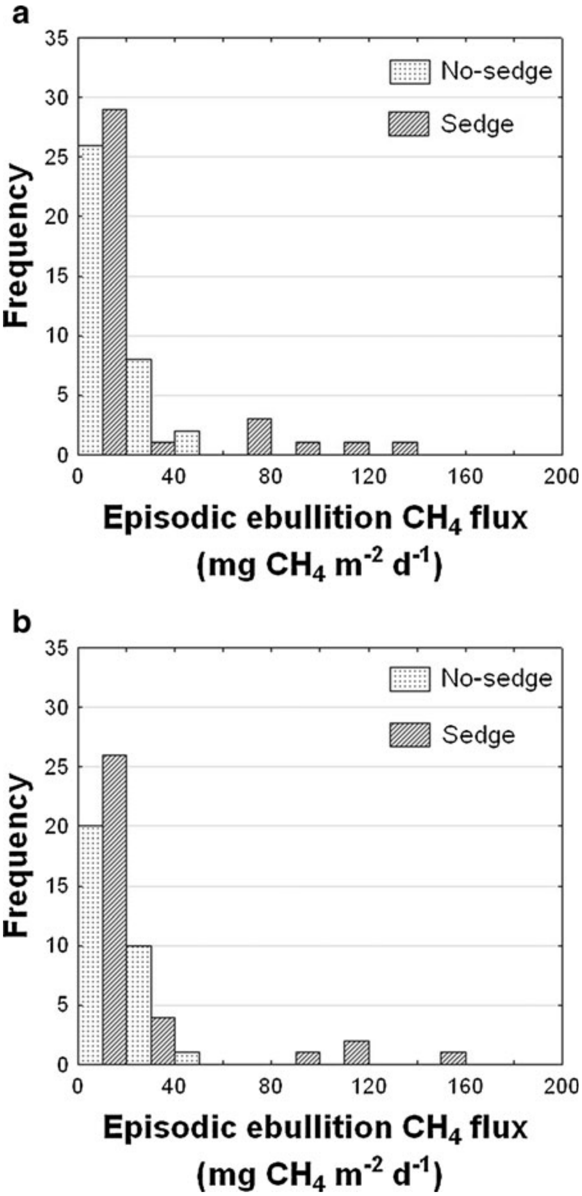

Fig. 3 Frequency distribution of episodic ebullition CH_4 fluxes for summer (**a**) and early autumn (**b**). The data are grouped according to vegetation type (sedge, no-sedge). Thus, each flux value used in the distribution represents a mean of five samples on a single measurement occasion

Using our sign convention, NEE is negative when there is a net uptake of CO_2 by the ecosystem; therefore, we would expect NEE to increase (become less negative) during partially-shaded conditions. This was indeed the case ($p=0.004$) (see Fig. 5). Therefore, despite the productivity of the sedge samples decreasing during the partially-shaded conditions, CH_4 emissions rose from these samples.

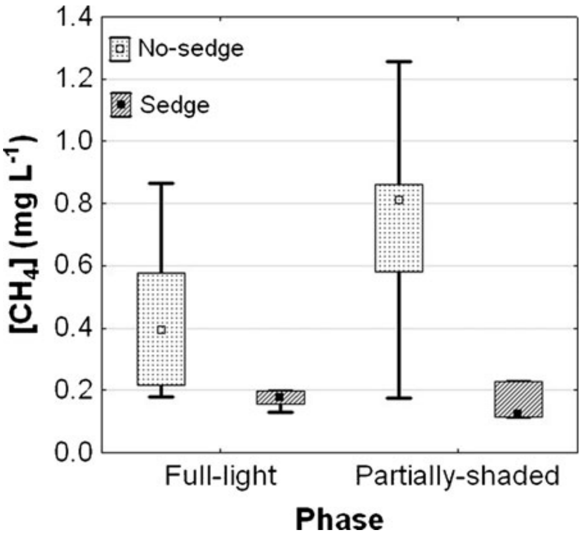

Fig. 4 Dissolved depth-averaged methane pore-water concentration (mg L^{-1}) disaggregated by no-sedge and sedge samples under the two light phases ($n=5$). The median is shown as a *filled* or *open square*, the inter-quartile range by the box or rectangle, and the minimum and maximum by the 'whiskers' extending from the box

Discussion

As expected, there was a significantly higher steady CH_4 flux from the cores containing sedges compared to those without (Fig. 2). On average, the no-sedge samples emitted ~17% of the steady CH_4 flux that is released by sedge cores, nearly a factor of six difference. Other studies that have compared sedge and no-sedge flux chamber emissions (roughly equivalent to our definition of steady emissions) have reported a wide range of differences. Whiting and Chanton (1992) compared CH_4 fluxes in a sub-Arctic Canadian fen between (i) plots dominated by *Carex limosa* L. and *C. rostrata* and (ii) areas where the sedges had been clipped. The vegetated plots had late-season emissions approximately 16 times higher than the clipped areas (approximately 80 vs 5 mg CH_4 m^{-2} d^{-1}). In a Swedish boreal raised bog, Waddington et al. (1996) assessed the role of *E. vaginatum* on CH_4 flux using clipping experiments on floating mat and marginal sites. Mean fluxes for the study period (summer) were 35.3 and 93.4 mg m^{-2} d^{-1} for floating mat clipped and natural areas, respectively, and 4.9 and 42.3 mg m^{-2} d^{-1}, respectively, in the marginal areas. Therefore, the presence of the sedge was associated with CH_4 emissions that were between 2.6 and 8.6

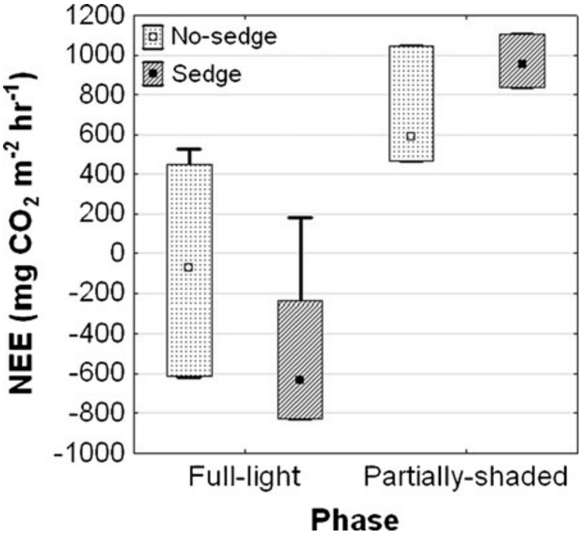

Fig. 5 Box plot of the NEE for no-sedge and sedge samples under full-light and shaded conditions. The median is shown as a *filled* or *open square*, the inter-quartile range by the box or rectangle, and the minimum and maximum by the 'whiskers' extending from the box

times higher than areas without the sedge. However, the differences between sedge and no-sedge areas were higher by nearly a factor of 60 on individual measurement occasions. Waddington et al. (1996) also reported on experiments on a fen site in Manitoba, Canada, in which the sedges were *C. rostrata* and *C. limosa*, and found that clipping reduced summer CH_4 fluxes on average by 30% (a factor of 1.4 difference between no-sedge and sedge conditions), a much more modest plant effect than that found by Whiting and Chanton (1992). Strack et al. (2006) investigated CH_4 dynamics in a poor fen in the St. Charles-de-Bellechasse peatland near Quebec, Canada using clipped and unclipped plots. Dominant sedges at the site were *Carex oligosperma* Michx., *C. limosa* and *Rhynchospora alba* (L.) Vahl., while dominant bryophytes were *Sphagnum papillosum* Lindb., *Sphagnum magellanicum* Brid., *Sphagnum cuspidatum* and *Polytrichum strictum* Brid.. Strack et al. (2006) found that the median spring/summer CH_4 flux from unclipped plots was nearly a factor of three higher than from clipped peats (41.0 vs 13.9 mg CH_4 m^{-2} d^{-1}).

The mean episodic-ebullition flux in our study was not significantly different between sedge and no-sedge samples, suggesting that episodic ebullition flux is not affected by the presence or absence of sedges, unlike steady CH_4 fluxes. To some extent, this result was not expected because of the suggestion of Chanton (2005) that vascular plants serve to lower pore-water [CH_4] and to lower rates of bubble formation and release. Our results suggest a 55% reduction in mean pore-water [CH_4] associated with sedge samples (full-light phase), similar to that reported in Chanton (2005). However, other workers have found higher pore-water [CH_4] in the presence of sedges, including Whiting and Chanton (1992) who report pore-water [CH_4] among roots of *Carex* spp. in vegetated plots more than 10 times the values in clipped plots. Nevertheless, the picture seems to be more complicated than implied by either Chanton (2005) or the data from Whiting and Chanton (1992). For example, Strack et al. (2006) obtained mixed results from their pore-water data, with unclipped plots having significantly higher pore-water [CH_4] than clipped plots at depths of 25 cm but with no significant differences at depths of 40 cm. Likewise, while Waddington et al. (1996) found that pore-water [CH_4] were lower in clipped plots on their Swedish raised bog site (see above), in other research sites in Canada where the dominant sedges were *Carex* spp., they found less clear cut differences in pore-water [CH_4]. What is clear from our findings is that it is unsafe to assume that ebullition losses of CH_4 are always lowered by the presence of sedges, even when the presence of the sedges is associated with a lowering of pore-water [CH_4]. Equally, it is important to note that we found no enhancement of episodic ebullition losses of CH_4 that could be attributed to sedges.

The absence of a difference in episodic ebullition losses of CH_4 between the no-sedge and sedge cores, despite differences in pore-water [CH_4], is difficult to explain without more detailed information on the processes controlling bubble formation. From a conventional understanding, one would expect rates of bubble formation to be reduced when pore-water [CH_4] are reduced, and such an assumption is made in many wetland CH_4 models (e.g., Walter et al. 1996) (see also the Introduction). However, it is also known that bubbles occur in peat soils when the pore-water [CH_4] is below the equilibrium solubility (e.g. Baird et al. 2004); in such circumstances, it is assumed that pore-water [CH_4] does reach and exceed the equilibrium solubility but only in microsites. This assumption may be right, but another possibility has apparently been overlooked by wetland scientists:

CH_4 bubbles may be produced directly by methanogens. Granular microbial consortia containing methanogens have been observed to produce bubbles of CH_4, with the bubbles emerging cyclically from pits within the microbial granules (Bochem et al. 1982). Thus, it is possible that pore-water [CH_4] are controlled by bubbles going into solution, rather than vice versa, and that the differences between the no-sedge and sedge samples may be explained by differences in the types of CH_4-producing microbial consortia within the different peat types.

Unexpectedly, rates of steady CH_4 loss from the sedge cores relative to the no-sedge cores increased despite the shading treatment leading to increases in NEE (i.e., less CO_2 uptake). The results from the test of Hypothesis 3 suggest that methanogens did not utilise exudates from the sedges, a suggestion also supported, in part at least, by the lack of any difference in steady CH_4 fluxes between daytime and night-time conditions (see Results—Hypothesis 1). This finding is the opposite of that of several other studies including Joabsson and Christensen (2001), Ström et al. (2003)—both on the same Arctic site in Greenland—and Waddington et al. (1996) on a site in northern central Sweden and at three sites in northern Manitoba, Canada. The difference between our findings and those from these cited studies may in part be due to differences in the vascular plant species that were investigated. In the site investigated by Joabsson and Christensen (2001) and Ström et al. (2003), the dominant vascular plants were the sedges *Eriophorum scheuchzeri* Hoppe and *Carex subspathacea* Wormsk. ex Hornem., and the grass *Dupontia fisheri* ssp. *psilosantha* (Rupr.) Hultén (mistakenly called a sedge by Ström et al. [2003]), while in the study of Waddington et al. (1996) the sedge species studied were *E. vaginatum* (at the Swedish bog site) and *C. rostrata* and *C. limosa* (at the Canadian sites). Christensen et al. (2003) suggested that the coupling between NEE and CH_4 emissions may vary according to species and plant density, and it is interesting that our findings appear to accord with those of Schimel (1995) who studied CH_4 dynamics in an Arctic peat soil dominated by *E. angustifolium*—the species looked at in our study. Schimel (1995) found that most CH_4 production could not be explained by root exudates acting as a substrate for methanogens. His study also shows substantial differences in CH_4 dynamics between peat dominated by *E. angustifolium* and peat dominated by *Carex aquatilis* Wahlenb., confirming the suggestion of Christensen et al. (2003).

Christensen et al. (2003) also proposed that stomatal opening (conductance) is not associated with plant-mediated CH_4 fluxes. Stomatal opening leads to enhanced gaseous movements (uptake or release) via diffusion through aerenchyma, assuming that a diffusion gradient exists. Stomatal opening and changes in stomatal aperture and gas exchange are physiologically coupled as plants respond to light, gas concentration (mainly CO_2), and water vapour pressure (Lambers et al. 1998). Stomata are light-responsive; hence, as PAR increases, the stomata open to their optimum size (for gas exchange), and as PAR decreases they close to limit water loss. Research by Nouchi et al. (1990) suggests that CH_4 is emitted from micro-pores in the leaf sheath rather than through the stomata; therefore, there would be no difference in steady CH_4 flux between diurnal phases—as is evident in our study (see Results—Hypothesis 1). However, some studies have reported that CH_4 flux is correlated with stomatal opening (Frye et al. 1994; Thomas et al. 1996), although this correlation tends to be associated with active transporters of CH_4, where gaseous exchange tends to be light-dependent (Chanton et al. 2002).

Plants may act as conduits for the transfer of oxygen to the rhizosphere, with the oxygen both inhibiting archaeal CH_4 production and enhancing bacterial methanotrophy (as discussed in the Introduction). Under partially-shaded conditions the converse is likely to occur as a result of a reduced O_2 concentration within the plant and in the rhizosphere—reducing conditions are likely to prevail. Stomatal aperture will change as PAR becomes the limiting factor in photosynthesis, leading to reduced movement of O_2 through the aerenchyma to the rhizosphere. Furthermore, as photosynthesis becomes limited, O_2 production is also suppressed within the plant; this may be inferred from our NEE results (see Results—Hypothesis 3). The higher steady CH_4 fluxes observed under partially-shaded conditions (Results—Hypothesis 3) may, therefore, be a result of lower rate of rhizospheric oxidation.

In the light of the findings from the test of Hypothesis 3, the higher rates of steady CH_4 flux from the sedge cores (Results—Hypothesis 1) cannot be explained by higher rates of CH_4 production due to rapid utilisation of exudates from the roots and rhizomes of the sedges. The higher rates of steady CH_4 flux from the sedge cores (Hypothesis 1) may then be explained by several mechanisms:

(i) The presence of sedges leads to higher CO_2 uptake (lower NEE) and therefore more substrate for methanogens—especially below-ground (Limpens et al. 2003)—only over *longer* (annual) timescales which leads to *generally* higher rates of CH_4 production and release from sedge-dominated areas. Our full-light NEE data (i.e., the 42-day full-light phase that preceded the 42-day partially-shaded phase) are consistent with this suggestion; we observed lower NEE (greater uptake) (Fig. 5) and higher steady CH_4 fluxes (Fig. 2) in sedge-dominated areas. Weighted (day plus night) mean (± one standard deviation) NEE was -694 ± 799 mg CO_2 m^{-2} d^{-1} for the sedge cores for the full-light phase, while for the no-sedge cores the value was -65.8 ± 552 mg CO_2 m^{-2} d^{-1}.

(ii) Sedges provide an additional route for CH_4 loss to the atmosphere so that total rates of transport are increased.

(iii) During CH_4 transport through the sedges, methanotrophic processing in the peat matrix is by-passed and, as Frenzel and Rudolph (1998) have shown, oxidation of CH_4 is negligible during its passage through *E. angustifolium*.

(iv) Some combination of (i) to (iii).

If mechanism (i) were the sole explanation for higher rates of steady loss from the sedge cores, we would also expect rates of ebullition to be higher in these cores and that was not the case (see Results—Hypothesis 2; Fig. 3; see also discussion above, this section). It is possible that CH_4 production was much higher in the sedge cores and that plant-mediated transport—mechanism (ii)—was sufficient to balance this enhanced production so that rates of bubble formation and release were similar between the sedge and no-sedge cores. However, the lower pore-water $[CH_4]$ content associated with sedge samples suggests that this was not the case (Fig. 4) (see also discussion above, this section).

It is difficult to envisage a situation in which mechanism (ii) is solely responsible for our observations because, in the absence of higher rates of CH_4 production in the presence of sedges, it would serve to lower pore-water $[CH_4]$ concentrations in the sedge samples compared to the no-sedge samples which would then lead to lower rates of steady CH_4 loss. In combination with (iii), mechanism (ii) could explain the steady CH_4 emission results, provided mechanism (iii) more than countered the reduced flux that would result from a reduction in pore-water $[CH_4]$ in the sedge samples.

Mechanism (iii) could, in theory, solely explain the differences in steady CH_4 fluxes but only if the presence of sedges served to provide an *alternative* pathway for CH_4 loss to the atmosphere and not an *additional* pathway to diffusion and steady ebullition through soil pores. However, if it provided an alternative pathway, we would not expect to see differences in pore-water $[CH_4]$ between the peat types.

Alone, no single mechanism can provide a satisfactory explanation of our data.

Conclusion

In a replicated study, we have shown that, although steady CH_4 emissions differ greatly between paired cores with and without *Eriophorum angustifolium* Honck., episodic ebullition fluxes do not differ. The higher rates of steady CH_4 flux from the sedge cores cannot be explained by higher rates of CH_4 production due to rapid utilisation of exudates from the roots and rhizomes of the sedges, a result that accords with the early work of Schimel (1995) and the idea that sedge effects on CH_4 emissions may be species-dependent. Finally, our observation of an increase in steady CH_4 flux under partially-shaded conditions may be due to a reduction in rhizospheric oxidation.

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