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## **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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1     **Title: A mesocosm study of the role of the sedge *Eriophorum angustifolium* in the efflux of**  
2                   **methane – including that due to episodic ebullition – from peatlands.**

3

4     **Running title: Sedges and ebullition methane efflux from peatlands**

5

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17    **Key words:** peatlands; methane flux; ebullition; vascular plants; *Eriophorum angustifolium*.

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24 **Abstract**

25 *Background & Aim* - Vascular plants may reduce episodic ebullition losses of methane (CH<sub>4</sub>)  
26 from peatlands. They transport CH<sub>4</sub> to the atmosphere, which may lead to a reduction in pore-  
27 water [CH<sub>4</sub>], bubble formation and release. This effect may be compounded by rhizospheric  
28 oxidation and associated methanotrophy. However, any reduction in pore-water [CH<sub>4</sub>] may be  
29 countered by root exudation (substrate for methanogens). The aim of this study was to determine  
30 how the presence of sedges affects CH<sub>4</sub> emissions from peatlands.

31 *Methods* - Five pairs of peat cores were collected from a raised bog. One of each pair contained  
32 *Sphagnum cuspidatum* and *Eriophorum angustifolium* ('sedge' cores); the other was dominated  
33 by *S. cuspidatum* ('no-sedge'). From these the total CH<sub>4</sub> efflux – including that due to episodic  
34 ebullition – were measured. A partial-shading treatment helped isolate the potential effect of root  
35 exudation.

36 *Results* - Sedge samples had significantly higher CH<sub>4</sub> fluxes than no-sedge samples, but  
37 episodic-ebullition fluxes were not significantly different. Between full-light and partially-  
38 shaded conditions, there was a significant increase in the difference in CH<sub>4</sub> fluxes between the  
39 sedge and no-sedge cores.

40 *Conclusion* - The higher rates of CH<sub>4</sub> flux from the sedge cores cannot be explained simply by  
41 higher rates of CH<sub>4</sub> production due to rapid utilisation of exudates.

42 **Introduction**

43 Many northern bogs are dominated by *Sphagnum* mosses, with sedges and ericaceous shrubs also  
44 being important components of the vegetation. It is known that some vascular plants, and sedges  
45 in particular, have an important effect on methane (CH<sub>4</sub>) emissions from peatlands. Sedges can  
46 act as ‘short-circuits’ between the peat and the atmosphere, with the CH<sub>4</sub> moving through the  
47 aerenchyma and by-passing methanotrophic bacteria in the zone above the water table (e.g.,  
48 Frenzel and Rudolph 1998; Greenup et al. 2000). Through root exudation they can provide  
49 substrate to the methanogens, thus potentially enhancing rates of CH<sub>4</sub> production (e.g., Öquist  
50 and Svensson 2002, Ström et al. 2003) and emission. They may also act as conduits for the  
51 transfer of oxygen to the rhizosphere – a process known as radial oxygen loss (ROL) or  
52 rhizospheric oxidation – with the oxygen both inhibiting archaeal CH<sub>4</sub> production and enhancing  
53 bacterial methanotrophy (Chanton 2005; Popp et al. 2000; Wheeler 1999). Although there is  
54 good evidence for each of these processes, there remains a lack of understanding of how they  
55 combine to affect total CH<sub>4</sub> emissions from bogs and, in particular, how they affect the formation  
56 and release to the atmosphere of CH<sub>4</sub>-containing bubbles.

57         Recent studies, as summarised by Coulthard et al. (2009), have suggested that ebullition –  
58 the release of CH<sub>4</sub>-containing bubbles to the atmosphere – may be the most important pathway  
59 of CH<sub>4</sub> loss from peatlands; i.e., that ebullition is more important than diffusion through the  
60 interstices within the peat and more important than plant-mediated transport. Ebullition may be  
61 divided into steady ebullition and episodic ebullition. Steady ebullition, if it occurs, refers to the  
62 steady stream of CH<sub>4</sub>-containing bubbles released to the water table, an analogy being the steady  
63 release of bubbles (albeit ones containing CO<sub>2</sub>) from vats of fermenting beer. The CH<sub>4</sub> in this  
64 steady stream of bubbles moving through the peat will then diffuse through the zone above the

65 water table to the peatland surface and may be partly or wholly consumed by methanotrophs.  
66 CH<sub>4</sub>-containing bubbles may also be released in short-lived (minutes to hours) bursts or episodes  
67 where fluxes are generally much higher and more variable than background steady fluxes. These  
68 periods of rapid CH<sub>4</sub> loss from the peatland occur when groups of bubbles or single large  
69 bubbles containing CH<sub>4</sub> move to the water table, and may be termed episodic ebullition. Because  
70 of their volume, these bubbles, and the CH<sub>4</sub> within them, will move en masse (advect) to the  
71 peatland surface from the water table, largely by-passing methanotrophic 'processing'  
72 (Rosenberry et al. 2006). Trapped bubbles may be released to the atmosphere when their  
73 buoyancy exceeds the forces keeping them in place (e.g., surface tension), and factors such as  
74 changes in atmospheric pressure and turbulent shaking of bog vegetation have been implicated in  
75 episodic bubble release (Tokida et al. 2005; David Fowler pers. comm.).

76 Chanton (2005) suggests that, because of their role as transporters of CH<sub>4</sub> to the  
77 atmosphere, vascular plants may lower pore-water [CH<sub>4</sub>] (square brackets denote concentration)  
78 by as much as 50%, with the effect that diffusion and bubble formation / episodic ebullition  
79 become secondary mechanisms of CH<sub>4</sub> transport. Many studies on the effects of vascular plants  
80 on ebullition have looked at inundated mineral sediments and emergent macrophytes (cf.  
81 Chanton 2005), and it remains unclear how vascular plants affect ebullition in peatlands,  
82 particularly bogs. Those studies that have been done on peats, such as the laboratory mesocosm  
83 investigations of Christensen et al. (2003) and Ström et al. (2005), present a somewhat  
84 contradictory picture which may, in part, be due to their (the studies') lack of replication: no  
85 more than two samples of any single peat type were investigated. Christensen et al. (2003) found  
86 that episodic ebullition may contribute as much as 20-50% of total CH<sub>4</sub> fluxes to the atmosphere  
87 when the cover of sedges such as *Carex rostrata* Stokes and *Eriophorum angustifolium* Honck.

88 is “very dense” or “dense”. Ström et al. (2005) found that the contribution for *C. rostrata* was  
89 about 23%, but only 3.5% for *Eriophorum vaginatum* L., which may suggest that ebullition  
90 varies in importance between species within the Eriophora. However, in a field study on a bog in  
91 S Estonia, Frenzel and Rudolph (1998) refer to the presence of a zone of bubbles that coincides  
92 with dense networks of roots and rhizomes of *E. vaginatum*, although they also suggest that the  
93 roots and rhizomes act as a trap for bubbles produced lower in the peat profile.

94 Hence, the picture of how vascular plants, and sedges in particular, affect episodic  
95 ebullition in peatlands remains unclear. To address this lack of clarity, we sought to address the  
96 following research question: how does the presence of sedges affect CH<sub>4</sub> emissions from bog  
97 peats, particularly emissions due to episodic ebullition? We chose to look at *E. angustifolium*  
98 because it is common in many Eurasian and North American bogs and because it is also found  
99 widely in minerotrophic conditions (fens). We posed and tested three hypotheses; each is given  
100 below, together with a brief rationale. These hypotheses were used to provide greater focus to the  
101 overall research question. Following Green and Baird (in review) we use two terms to describe  
102 CH<sub>4</sub> efflux: ‘steady flux’ and ‘episodic ebullition’. The latter has been defined already. The  
103 former is the combination of diffusion through the soil, diffusion through plant tissue, and steady  
104 ebullition, and, as such, is similar to the “steady emission” of Christensen et al. (2003). ‘Steady’  
105 is used as shorthand here and does not mean that fluxes are truly steady; however, when  
106 measured in the absence of episodic ebullition, these three processes will give a linear increase in  
107 [CH<sub>4</sub>] in the enclosed atmosphere of a flux chamber over short periods of time, and are probably  
108 steady over periods of tens of minutes to an hour or two (Christensen et al. 2003).

109 The hypotheses are:

110 **Hypothesis 1:** Steady CH<sub>4</sub> flux is higher in peat with *E. angustifolium* than in peat without any

111 vascular plant cover.

112 **Rationale:** Because it is deep-rooting (Limpens et al. 2003), *E. angustifolium* can be expected to  
113 vent methane (CH<sub>4</sub>) from a large part of the peat profile straight to the atmosphere, by-passing  
114 methanotrophic processing in the zone between the water table and the ground surface (should  
115 such a zone exist). The presence of the sedge may also lead to higher rates of CH<sub>4</sub> production  
116 (and hence loss) via root exudation of recent photosynthate and through longer-term growth of  
117 rhizomes and roots which can provide substrate for methanogens when they decay (see  
118 Hypothesis 3). For Hypothesis 1 to hold, the inhibitory effects of rhizospheric oxidation have to  
119 be negligible, or secondary, to venting and enhanced CH<sub>4</sub> production.

120 **Hypothesis 2:** Episodic CH<sub>4</sub> flux (episodic ebullition) is lower in peat with *E. angustifolium* than  
121 in peat without any vascular plant cover.

122 **Rationale:** Two possibilities may be invoked to explain a reduction in episodic ebullition in the  
123 presence of *E. angustifolium*. First, the presence of the sedge reduces pore-water [CH<sub>4</sub>] via  
124 rhizospheric oxidation, causing lower rates of CH<sub>4</sub> production and/or higher rates of  
125 methanotrophy, so that rates of bubble production and release are reduced. Secondly, pore-water  
126 [CH<sub>4</sub>] is reduced via the enhanced rate of release of CH<sub>4</sub> through aerenchyma, with the effect  
127 again being that rates of bubble production and release are reduced.

128 **Hypothesis 3:** Any differences in steady CH<sub>4</sub> flux between peat with *E. angustifolium* and peat  
129 without any vascular plants decrease when the growing surface of the peatland is partially  
130 shaded. That is, steady CH<sub>4</sub> flux is related to vascular plant productivity and root exudation.

131 **Rationale:** CH<sub>4</sub> production may be enhanced by root exudates which act as substrate for  
132 methanogens (Joabsson et al. 1999; Ström et al. 2003; Waddington et al. 1996). Because root  
133 exudation is tightly coupled with plant productivity, photosynthesis is thought to be coupled with

134 the rate of methanogenesis and therefore CH<sub>4</sub> emissions (Joabsson et al. 1999). Non-vascular  
135 plants such as *Sphagnum* do not provide substrate quickly to the zone of CH<sub>4</sub> production (any  
136 *Sphagnum*-derived substrate would have to diffuse through the pore network or be carried by  
137 mass water flow), so any relationship between shading and CH<sub>4</sub> efflux is likely due to root  
138 exudation from *E. angustifolium*. When partially shaded, the rate of carbon fixation by vascular  
139 plants should be reduced (Öquist and Svensson 2002; Ström et al. 2003); thus, a comparison of  
140 CH<sub>4</sub> fluxes under partially-shaded conditions with those under full-light conditions should reveal  
141 how *E. angustifolium* productivity affects CH<sub>4</sub> loss. The results of such a comparison might be  
142 confounded by rhizospheric oxidation if the latter is driven by active gas transport (i.e., mass or  
143 advective flow of gas through a plant) which varies with light intensity (Jackson and Armstrong  
144 1999). However, the available evidence suggests that diffusion is the only mechanism of CH<sub>4</sub>  
145 transport in the *E. angustifolium* (e.g., Frenzel and Rudolph 1998).

146         To test these hypotheses we focused on a single peatland microhabitat – bog hollows –  
147 and used a controlled-environment laboratory mesocosm approach. We used a paired design  
148 whereby adjacent samples of peat – one with an *E. angustifolium* cover and one with no vascular  
149 plants – were collected. We incubated the samples in two environmental cabinets and measured  
150 both the steady CH<sub>4</sub> flux (day and night) and the episodic-ebullition CH<sub>4</sub> flux. Net ecosystem  
151 (CO<sub>2</sub>) exchange (NEE) was also measured. The peat samples were subjected to 42 days under  
152 full-light summer conditions, followed by 42 days with a 55% reduction in photosynthetically-  
153 active radiation (PAR), before being brought back into full-light conditions for a further 42 days.  
154 The latter period was used to check that there were no long-term trends in NEE that were  
155 unrelated to the transition from full-light to partially-shaded conditions. Henceforth, we term the  
156 different light treatments phases.



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## 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 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. Figure 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.

180 *Sample collection and incubations*

181 The samples were extracted on 6<sup>th</sup> and 7<sup>th</sup> May 2009 using open-ended 20-cm inside-diameter,  
182 50-cm deep polyvinyl chloride (PVC) cylinders. To extract the samples, the cylinders were  
183 placed on the peat surface and the peat around the outer edge of the cylinder was cut using  
184 gardening scissors to a depth of c. 2 cm. The cylinder was then pushed into the cut peat, and the  
185 process repeated until 50 cm depth was achieved. Core extraction took between one and two  
186 hours. More details may be found in Green and Baird (in review) which reports on different  
187 samples and experiments from those described here. The samples were kept in an undrained state  
188 after collection by wrapping the PVC cylinders in tight-fitting, fully-waterproof, plastic bags.  
189 Within a few hours of collection, the samples were transferred into PVC holders fitted with  
190 water-table regulators, pore-water sampling ports, and fittings to allow chamber flux readings to  
191 be taken of the gas exchange from the top of the peat. When back in the laboratory the sides of  
192 these holders were enclosed in a 5-cm layer of insulation (vermiculite pellets), after which the  
193 samples were incubated within two Weiss-Gallenkamp Fitotron SGC097.CPX.F plant growth  
194 cabinets. Incubations started on 18<sup>th</sup> May 2009 and continued for 18 weeks until 18<sup>th</sup> September  
195 2009. The cabinets were used to control and maintain ‘weather’ conditions typical of summer at  
196 Longbridgemuir, with a 14 hour daylight period. Daylight temperatures were set to 15 °C, and  
197 night-time temperatures to 12 °C. The relative humidity was 76% and 89%, respectively, during  
198 the daytime and night-time settings. Daytime PAR was nominally 380  $\mu\text{m m}^{-2} \text{s}^{-1}$  during the full-  
199 light phase, and 171  $\mu\text{m m}^{-2} \text{s}^{-1}$  during the shading treatment (the latter being 45% of the full-  
200 light value).

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

203  $\text{Ca}^{2+} = 0.28 \text{ mg L}^{-1}$ ,  $\text{K}^{+} = 0.12 \text{ mg L}^{-1}$ ,  $\text{NH}_4^{+} = 0.33 \text{ mg L}^{-1}$ ,  $\text{NO}_3^{-} = 0.74 \text{ mg L}^{-1}$ ,  $\text{SO}_4^{2-} = 2.11 \text{ mg}$   
204  $\text{L}^{-1}$ ,  $\text{Cl}^{-} = 3.76 \text{ mg L}^{-1}$ ; pH adjusted to 5.17). A total of 150 mL (~ 5 mm) of artificial rainfall was  
205 added to each peat sample per week.

206 Water tables in the peat samples were set to a constant depth below the surface (1 cm  
207 below ground level) to reflect field conditions. Water-table levels were maintained using  
208 Mariotte regulators fitted to each peat sample holder; these contained He-sparged deionised  
209 water. Atmospheric pressure and (as a check) internal cabinet temperature were measured and  
210 logged by a 'Diver' pressure and temperature gauge (Van Essen Instruments) (pressure accuracy  
211 of  $\sim \pm 0.5 \text{ hPa}$  and precision of  $\sim 0.2 \text{ hPa}$ ; temperature accuracy of  $\sim \pm 0.5 \text{ }^{\circ}\text{C}$  and precision of  
212  $0.2 \text{ }^{\circ}\text{C}$ ). Atmospheric pressure was measured because, as noted above, some studies have  
213 suggested a link between low pressure episodes and episodic ebullition events. PAR was  
214 measured daily above all samples using a Skye Instruments PAR Quantum Sensor to check that  
215 each peat sample was receiving equivalent amounts of incoming solar radiation. No significant  
216 differences were found between sedge and no-sedge samples. For example, during the first full-  
217 light treatment, the two groups had the following means and standard deviations of PAR photon  
218 flux density: no sedge =  $390.0, 20.5 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ; sedge =  $384.1, 24.3 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$  ( $p = 0.853$   
219 [two-sample  $t$ -test]).

220

### 221 *Steady CH<sub>4</sub> fluxes*

222 The description here follows that given in Green and Baird (in review). Steady fluxes were  
223 measured once a week by fitting acrylic flux chambers to water-filled collars on the top of the  
224 peat holders. Daytime measurements were made at or close to the middle of the daylight phase,  
225 while night-time measurements were made after two-three hours of darkness. Gel ice packs

226 (hung within the chamber) were used to minimise the temperature increase of the air above the  
227 peat sample during chamber use. Small electric fans were used to circulate the chamber air. The  
228 chamber wall was drilled and fitted with an acrylic tube. On the inside of the chamber, a balloon  
229 was attached to the tube; this arrangement allowed the equalisation of pressure between the  
230 inside and outside of the chamber. Using disposable syringes with 21-gauge needles, 12-mL gas  
231 samples were extracted at five-minute intervals for 30 minutes through a septum in the chamber  
232 wall. The effectiveness of the balloon and ice packs was checked by measuring chamber  
233 temperature and pressure during gas sampling using a Commeter C4141 thermometer-  
234 hygrometer-barometer (Comet Systems, Czech Republic; temperature precision 0.1 °C, accuracy  
235  $\pm 0.4$  °C; pressure precision 0.1 hPa, accuracy  $\pm 2$  hPa). Each extraction of a gas sample was  
236 preceded by triplicate purges after septum penetration. Gas samples were transferred into 12-mL  
237 pre-evacuated vials (Labco Limited, High Wycombe, Buckinghamshire, UK) and were measured  
238 for their CH<sub>4</sub> content using an Agilent 7890A gas chromatograph (GC) system fitted with a  
239 flame ionisation detector (FID). CH<sub>4</sub> was separated on a stainless steel column packed with  
240 Porapak (Q 80/100) at 30°C with zero grade N<sub>2</sub> as the carrier gas. Standard analytical grade  
241 reference span gases were used to calibrate the GC, and thereafter inserted at regular intervals  
242 into the sample runs to check for drift.

243         The flux chamber data were used to test Hypotheses 1 and 3, for which only steady flux  
244 data were needed. Hence, any episodic ebullition fluxes during flux chamber measurements  
245 (indicated by sudden, step-like increases in chamber [CH<sub>4</sub>]) were discounted, and only the steady  
246 component of the flux estimated. The slope of the regression line of chamber [CH<sub>4</sub>] over time  
247 was used for estimating fluxes, provided  $r^2 \geq 0.8$  and  $p < 0.05$ . For situations where the change in  
248 chamber [CH<sub>4</sub>] was  $< 0.003$  ppmv, fluxes were assumed to be zero. In all other cases the data

249 were rejected.

250

### 251 *Net ecosystem exchange*

252 Net ecosystem exchange (NEE) provides a direct measure of the net CO<sub>2</sub> exchange between  
253 ecosystems and the atmosphere. NEE was measured to determine whether partial shading caused  
254 a reduction in the rate of carbon fixation by vascular plants. NEE was measured on a weekly  
255 basis using the flux chambers; the chamber gas samples used for CH<sub>4</sub> analysis were also used for  
256 CO<sub>2</sub> analysis using the same Agilent 7890A gas chromatograph (GC) system (details as above).

257 CO<sub>2</sub> exchanges were estimated using a similar protocol to that employed for estimating  
258 steady CH<sub>4</sub> fluxes. The slope of the regression line of chamber [CO<sub>2</sub>] over time was used for  
259 estimating fluxes, provided  $r^2 \geq 0.8$  and  $p < 0.05$ . For situations where changes in flux chamber  
260 [CO<sub>2</sub>] were  $< 1$  ppmv, fluxes were assumed to be zero. In all other cases the data were rejected.  
261 We used the convention that a positive NEE indicates a net release of CO<sub>2</sub> to the atmosphere,  
262 while a negative value indicates a net uptake of CO<sub>2</sub> from the atmosphere. Thus, an increase in  
263 NEE would indicate less CO<sub>2</sub> being taken up by the peat samples or a greater rate of net CO<sub>2</sub>  
264 loss.

265

### 266 *Episodic ebullition measurement*

267 Water losses from the Mariotte regulators were recorded daily during the incubations (except at  
268 weekends). Water tables may fall due to evapotranspiration and also when trapped bubbles are  
269 released from the cores during episodic ebullition. After any drops, the water-table level is  
270 immediately restored by water flowing from the Mariotte regulator into the peat sample. The two  
271 processes can be separated by analysing the regulator data; evapotranspiration appears as a

272 steady loss (when recorded daily) while episodic ebullition appears as large and sporadic losses  
273 in the daily time series data. To convert the volumetric release of bubbles to a CH<sub>4</sub> flux, it was  
274 assumed that the CH<sub>4</sub> content of bubbles was in equilibrium with the dissolved pore-water CH<sub>4</sub>  
275 (see below).

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

279

### 280 *Dissolved CH<sub>4</sub> content*

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

295

## 296 ***Statistical analysis***

297 For all statistical tests of the hypotheses, significance was accepted at  $p \leq 0.05$ . Statistical  
298 analyses were performed using SPSS version 16.0.0 (2007). Paired *t*-tests were used to address  
299 Hypotheses 1 and 2. For Hypotheses 1 and 2, the variable compared was, respectively, the  
300 untransformed mean steady and the mean episodic CH<sub>4</sub> flux in the sedge and no-sedge paired  
301 cores. The response variable for Hypothesis 3 was the untransformed mean steady CH<sub>4</sub> flux. A  
302 2-way, repeated-measures ANOVA was used to test the hypothesis, with repeated measures  
303 applying to the full and partial light phases and to the sedge and no-sedge peat samples, The  
304 ANOVA was used to show if any differences between sedge and no-sedge samples changed  
305 according to light phase, thus providing a direct test of the hypothesis. The 2-way, repeated-  
306 measures ANOVA also provides an additional test of Hypothesis 1. In all tests, the data met the  
307 parametric assumptions of normality and equality of variance.

308

## 309 **Results**

### 310 ***Hypothesis 1***

311 Figure 2 shows the mean steady CH<sub>4</sub> fluxes from the cores. It was found that the sedge samples  
312 had significantly higher CH<sub>4</sub> fluxes than the no-sedge samples under both the first full-light and  
313 partially-shaded phases (daylight full-light:  $p = 0.002$ ; daylight partially-shaded:  $p = 0.005$ ;  
314 night-time full-light:  $p = 0.002$ ; night-time partially-shaded:  $p = 0.003$ ). Therefore, Hypothesis 1  
315 may be accepted for both the first full-light phase and the partially-shaded phase.

316 As a supplement to the main hypothesis, for each of the sample types (either sedge or no-  
317 sedge) we compared day-time and night-time CH<sub>4</sub> fluxes for the first full-light phase. There was

318 no-significant difference between day-time or night-time emissions (sedge  $p = 0.13$ ; no sedge  $p =$   
319 0.26).

320

### 321 ***Hypothesis 2***

322 Episodic ebullition was recorded 251 times across all of the cores over the first two light phases  
323 (full-light and partially-shaded). Episodic ebullition occurred in one or more cores on 66 of the  
324 total of 84 days (Figure 3), with the number of incidences ranging from 2 to 66 for individual  
325 cores. When episodic ebullition occurred in a core, daily episodic ebullition fluxes ranged from  
326 81.1 to 276 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> in the sedge cores, and from 0.20 to 784 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> in the no-  
327 sedge cores.

328         The mean episodic-ebullition flux (fluxes were combined for the first two light phases  
329 before being compared – see below) was not significantly different between sedge and no-sedge  
330 samples ( $p = 0.774$ ). Therefore, Hypothesis 2 may be rejected. Additional tests showed that mean  
331 episodic-ebullition flux did not differ between full-light and partially-shaded conditions (no-  
332 sedge  $p = 0.49$ ; sedge  $p = 0.96$ ). The data also showed that ebullition increased with decreasing  
333 atmospheric pressure, although this was a statistically a rather weak link relationship ( $r = 0.1$ ;  $p$   
334 = 0.004 (first full-light and partially-shaded conditions combined)). Time-averaged episodic  
335 ebullition contributed, on average, 28.0 and 7.0% to total CH<sub>4</sub> flux, respectively, in the no-sedge  
336 and sedge samples.

337         Mean pore-water [CH<sub>4</sub>] (which is ~ depth-averaged pore-water [CH<sub>4</sub>] and also a measure  
338 of the dissolved CH<sub>4</sub> pool or stock in the samples) was significantly higher in the no-sedge cores  
339 ( $p = 0.027$ ) (2-way, repeated-measures ANOVA) (Figure 4). There was no significant difference  
340 in mean pore-water [CH<sub>4</sub>] between light phases ( $p = 0.268$ ) (Figure 4). Maximum pore-water



341 [CH<sub>4</sub>] (not shown in Figure 4) gave a similar result to the mean pore-water [CH<sub>4</sub>] data, with the  
342 difference between sedge and no-sedge samples again being significant (no-sedge higher;  $p =$   
343 0.041).

344

### 345 *Hypothesis 3*

346 The 2-way, repeated-measures ANOVA showed that there were significant differences ( $p =$   
347 0.002) in steady CH<sub>4</sub> fluxes between the sedge and no-sedge samples, and also that these  
348 differences depended on light phase. However, unexpectedly, there was a significant increase in  
349 differences in fluxes between the two phases (interaction between phase and vegetation:  $p =$   
350 0.006), when, according to the hypothesis, one would expect the differences to decrease.

351 Hypothesis 3 is predicated on the assumption that NEE is affected by shading, such that  
352 there is more carbon uptake by the ecosystem during full-light conditions than during partially-  
353 shaded conditions. Using our sign convention, NEE is negative when there is a net uptake of CO<sub>2</sub>  
354 by the ecosystem; therefore, we would expect NEE to increase (become less negative) during  
355 partially-shaded conditions. This was indeed the case ( $p = 0.004$ ) (see Figure 5). Therefore,  
356 despite the productivity of the sedge samples decreasing during the partially-shaded conditions,  
357 CH<sub>4</sub> emissions rose from these samples.

358

### 359 **Discussion**

360 As expected, there was a significantly higher steady CH<sub>4</sub> flux from the cores containing sedges  
361 compared to those without (Figure 2). On average, the no-sedge samples emitted ~17% of the  
362 steady CH<sub>4</sub> flux that is released by sedge cores, nearly a factor of six difference. Other studies  
363 that have compared sedge and no-sedge flux chamber emissions (roughly equivalent to our

364 definition of steady emissions) have reported a wide range of differences. Whiting and Chanton  
365 (1992) compared CH<sub>4</sub> fluxes in a sub-Arctic Canadian fen between (i) plots dominated by *Carex*  
366 *limosa* L. and *C. rostrata* and (ii) areas where the sedges had been clipped. The vegetated plots  
367 had late-season emissions approximately 16 times higher than the clipped areas (approximately  
368 80 vs 5 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup>). In a Swedish boreal raised bog, Waddington et al. (1996) assessed the  
369 role of *E. vaginatum* on CH<sub>4</sub> flux using clipping experiments on floating mat and marginal sites.  
370 Mean fluxes for the study period (summer) were 35.3 and 93.4 mg m<sup>-2</sup> d<sup>-1</sup> for floating mat  
371 clipped and natural areas, respectively, and 4.9 and 42.3 mg m<sup>-2</sup> d<sup>-1</sup>, respectively, in the marginal  
372 areas. Therefore, the presence of the sedge was associated with CH<sub>4</sub> emissions that were between  
373 2.6 and 8.6 times higher than areas without the sedge. However, the differences between sedge  
374 and no-sedge areas were higher by nearly a factor of 60 on individual measurement occasions.  
375 Waddington et al. (1996) also reported on experiments on a fen site in Manitoba, Canada, in  
376 which the sedges were *C. rostrata* and *C. limosa*, and found that clipping reduced summer CH<sub>4</sub>  
377 fluxes on average by 30 % (a factor of 1.4 difference between no-sedge and sedge conditions), a  
378 much more modest plant effect than that found by Whiting and Chanton (1992). Strack et al.  
379 (2006) investigated CH<sub>4</sub> dynamics in a poor fen in the St. Charles-de-Bellechasse peatland near  
380 Quebec, Canada using clipped and unclipped plots. Dominant sedges at the site were *Carex*  
381 *oligosperma* Michx., *C. limosa* and *Rhynchospora alba* (L.) Vahl., while dominant bryophytes  
382 were *Sphagnum papillosum* Lindb., *Sphagnum magellanicum* Brid., *Sphagnum cuspidatum* and  
383 *Polytrichum strictum* Brid.. Strack et al. (2006) found that the median spring/summer CH<sub>4</sub> flux  
384 from unclipped plots was nearly a factor of three higher than from clipped peats (41.0 vs 13.9 mg  
385 CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup>).

386           The mean episodic-ebullition flux in our study was not significantly different between  
387 sedge and no-sedge samples, suggesting that episodic ebullition flux is not affected by the  
388 presence or absence of sedges, unlike steady CH<sub>4</sub> fluxes. To some extent, this result was not  
389 expected because of the suggestion of Chanton (2005) that vascular plants serve to lower pore-  
390 water [CH<sub>4</sub>] and to lower rates of bubble formation and release. Our results suggest a 55%  
391 reduction in mean pore-water [CH<sub>4</sub>] associated with sedge samples (full-light phase), similar to  
392 that reported in Chanton (2005). However, other workers have found higher pore-water [CH<sub>4</sub>] in  
393 the presence of sedges, including Whiting and Chanton (1992) who report pore-water [CH<sub>4</sub>]  
394 among roots of *Carex* spp. in vegetated plots more than 10 times the values in clipped plots.  
395 Nevertheless, the picture seems to be more complicated than implied by either Chanton (2005) or  
396 the data from Whiting and Chanton (1992). For example, Strack et al. (2006) obtained mixed  
397 results from their pore-water data, with unclipped plots having significantly higher pore-water  
398 [CH<sub>4</sub>] than clipped plots at depths of 25 cm but with no significant differences at depths of 40  
399 cm. Likewise, while Waddington et al. (1996) found that pore-water [CH<sub>4</sub>] were lower in clipped  
400 plots on their Swedish raised bog site (see above), in other research sites in Canada where the  
401 dominant sedges were *Carex* spp., they found less clear cut differences in pore-water [CH<sub>4</sub>].  
402 What is clear from our findings is that it is unsafe to assume that ebullition losses of CH<sub>4</sub> are  
403 always lowered by the presence of sedges, even when the presence of the sedges is associated  
404 with a lowering of pore-water [CH<sub>4</sub>]. Equally, it is important to note that we found no  
405 enhancement of episodic ebullition losses of CH<sub>4</sub> that could be attributed to sedges.

406           The absence of a difference in episodic ebullition losses of CH<sub>4</sub> between the no-sedge  
407 and sedge cores, despite differences in pore-water [CH<sub>4</sub>], is difficult to explain without more  
408 detailed information on the processes controlling bubble formation. From a conventional

409 understanding, one would expect rates of bubble formation to be reduced when pore-water [CH<sub>4</sub>]  
410 are reduced, and such an assumption is made in many wetland CH<sub>4</sub> models (e.g., Walter et al.  
411 1996) (see also the Introduction). However, it is also known that bubbles occur in peat soils  
412 when the pore-water [CH<sub>4</sub>] is below the equilibrium solubility (e.g. Baird et al. 2004); in such  
413 circumstances, it is assumed that pore-water [CH<sub>4</sub>] does reach and exceed the equilibrium  
414 solubility but only in microsites. This assumption may be right, but another possibility has  
415 apparently been overlooked by wetland scientists: CH<sub>4</sub> bubbles may be produced directly by  
416 methanogens. Granular microbial consortia containing methanogens have been observed to  
417 produce bubbles of CH<sub>4</sub>, with the bubbles emerging cyclically from pits within the microbial  
418 granules (Bochum et al. 1982). Thus, it is possible that pore-water [CH<sub>4</sub>] are controlled by  
419 bubbles going into solution, rather than *vice versa*, and that the differences between the no-sedge  
420 and sedge samples may be explained by differences in the types of CH<sub>4</sub>-producing microbial  
421 consortia within the different peat types.

422         Unexpectedly, rates of steady CH<sub>4</sub> loss from the sedge cores relative to the no-sedge  
423 cores increased despite the shading treatment leading to increases in NEE (i.e., less CO<sub>2</sub> uptake).  
424 The results from the test of Hypothesis 3 suggest that methanogens did not utilise exudates from  
425 the sedges, a suggestion also supported, in part at least, by the lack of any difference in steady  
426 CH<sub>4</sub> fluxes between daytime and night-time conditions (see Results – Hypothesis 1). This finding  
427 is the opposite of that of several other studies including Joabsson and Christensen (2001), Ström  
428 et al. (2003) – both on the same Arctic site in Greenland – and Waddington et al. (1996) on a site  
429 in northern central Sweden and at three sites in northern Manitoba, Canada. The difference  
430 between our findings and those from these cited studies may in part be due to differences in the  
431 vascular plant species that were investigated. In the site investigated by Joabsson and

432 Christensen (2001) and Ström et al. (2003), the dominant vascular plants were the sedges  
433 *Eriophorum scheuchzeri* Hoppe and *Carex subspathacea* Wormsk. ex Hornem., and the grass  
434 *Dupontia fisheri* ssp. *psilosantha* (Rupr.) Hultén (mistakenly called a sedge by Ström et al.  
435 [2003]), while in the study of Waddington et al. (1996) the sedge species studied were *E.*  
436 *vaginatum* (at the Swedish bog site) and *C. rostrata* and *C. limosa* (at the Canadian sites).  
437 Christensen et al. (2003) suggested that the coupling between NEE and CH<sub>4</sub> emissions may vary  
438 according to species and plant density, and it is interesting that our findings appear to accord  
439 with those of Schimel (1995) who studied CH<sub>4</sub> dynamics in an Arctic peat soil dominated by *E.*  
440 *angustifolium* – the species looked at in our study. Schimel (1995) found that most CH<sub>4</sub>  
441 production could not be explained by root exudates acting as a substrate for methanogens. His  
442 study also shows substantial differences in CH<sub>4</sub> dynamics between peat dominated by *E.*  
443 *angustifolium* and peat dominated by *Carex aquatilis* Wahlenb., confirming the suggestion of  
444 Christensen et al. (2003).

445 Christensen et al. (2003) also proposed that stomatal opening (conductance) is not  
446 associated with plant-mediated CH<sub>4</sub> fluxes. Stomatal opening leads to enhanced gaseous  
447 movements (uptake or release) via diffusion through aerenchyma, assuming that a diffusion  
448 gradient exists. Stomatal opening and changes in stomatal aperture and gas exchange are  
449 physiologically coupled as plants respond to light, gas concentration (mainly CO<sub>2</sub>), and water  
450 vapour pressure (Lambers et al. 1998). Stomata are light-responsive; hence, as PAR increases,  
451 the stomata open to their optimum size (for gas exchange), and as PAR decreases they close to  
452 limit water loss. Research by Nouchi et al. (1990) suggests that CH<sub>4</sub> is emitted from micro-pores  
453 in the leaf sheath rather than through the stomata; therefore, there would be no difference in  
454 steady CH<sub>4</sub> flux between diurnal phases – as is evident in our study (see Results – Hypothesis 1).

455 However, some studies have reported that CH<sub>4</sub> flux is correlated with stomatal opening (Frye et  
456 al. 1994; Thomas et al. 1996), although this correlation tends to be associated with active  
457 transporters of CH<sub>4</sub>, where gaseous exchange tends to be light-dependent (Chanton et al. 2002).

458         Plants may act as conduits for the transfer of oxygen to the rhizosphere, with the oxygen  
459 both inhibiting archaeal CH<sub>4</sub> production and enhancing bacterial methanotrophy (as discussed in  
460 the Introduction). Under partially-shaded conditions the converse is likely to occur as a result of  
461 a reduced O<sub>2</sub> concentration within the plant and in the rhizosphere – reducing conditions are  
462 likely to prevail. Stomatal aperture will change as PAR becomes the limiting factor in  
463 photosynthesis, leading to reduced movement of O<sub>2</sub> through the aerenchyma to the rhizosphere.  
464 Furthermore, as photosynthesis becomes limited, O<sub>2</sub> production is also suppressed within the  
465 plant; this may be inferred from our NEE results (see Results – Hypothesis 3). The higher steady  
466 CH<sub>4</sub> fluxes observed under partially-shaded conditions (Results – Hypothesis 3) may, therefore,  
467 be a result of lower rate of rhizospheric oxidation.

468         In the light of the findings from the test of Hypothesis 3, the higher rates of steady CH<sub>4</sub>  
469 flux from the sedge cores (Results – Hypothesis 1) cannot be explained by higher rates of CH<sub>4</sub>  
470 production due to rapid utilisation of exudates from the roots and rhizomes of the sedges. The  
471 higher rates of steady CH<sub>4</sub> flux from the sedge cores (Hypothesis 1) may then be explained by  
472 several mechanisms:

473         (i) The presence of sedges leads to higher CO<sub>2</sub> uptake (lower NEE) and therefore more  
474 substrate for methanogens – especially below-ground (Limpens et al. 2003) – only over *longer*  
475 (annual) timescales which leads to *generally* higher rates of CH<sub>4</sub> production and release from  
476 sedge-dominated areas. Our full-light NEE data (i.e., the 42-day full-light phase that preceded  
477 the 42-day partially-shaded phase) are consistent with this suggestion; we observed lower NEE

478 (greater uptake) (Figure 5) and higher steady CH<sub>4</sub> fluxes (Figure 2) in sedge-dominated areas.  
479 Weighted (day plus night) mean ( $\pm$  one standard deviation) NEE was  $-694 \pm 799$  mg CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>  
480 for the sedge cores for the full-light phase, while for the no-sedge cores the value was  $-65.8 \pm$   
481  $552$  mg CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>.

482 (ii) Sedges provide an additional route for CH<sub>4</sub> loss to the atmosphere so that total rates  
483 of transport are increased.

484 (iii) During CH<sub>4</sub> transport through the sedges, methanotrophic processing in the peat  
485 matrix is by-passed and, as Frenzel and Rudolph (1998) have shown, oxidation of CH<sub>4</sub> is  
486 negligible during its passage through *E. angustifolium*.

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

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

496 It is difficult to envisage a situation in which mechanism (ii) is solely responsible for our  
497 observations because, in the absence of higher rates of CH<sub>4</sub> production in the presence of sedges,  
498 it would serve to lower pore-water [CH<sub>4</sub>] concentrations in the sedge samples compared to the  
499 no-sedge samples which would then lead to lower rates of steady CH<sub>4</sub> loss. In combination with  
500 (iii), mechanism (ii) could explain the steady CH<sub>4</sub> emission results, provided mechanism (iii)

501 more than countered the reduced flux that would result from a reduction in pore-water [CH<sub>4</sub>] in  
502 the sedge samples.

503 Mechanism (iii) could, in theory, solely explain the differences in steady CH<sub>4</sub> fluxes but  
504 only if the presence of sedges served to provide an *alternative* pathway for CH<sub>4</sub> loss to the  
505 atmosphere and not an *additional* pathway to diffusion and steady ebullition through soil pores.  
506 However, if it provided an alternative pathway, we would not expect to see differences in pore-  
507 water [CH<sub>4</sub>] between the peat types.

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

509

## 510 **Conclusion**

511 In a replicated study, we have shown that, although steady CH<sub>4</sub> emissions differ greatly between  
512 paired cores with and without *Eriophorum angustifolium* Honck., episodic ebullition fluxes do  
513 not differ. The higher rates of steady CH<sub>4</sub> flux from the sedge cores cannot be explained by  
514 higher rates of CH<sub>4</sub> production due to rapid utilisation of exudates from the roots and rhizomes  
515 of the sedges, a result that accords with the early work of Schimel (1995) and the idea that sedge  
516 effects on CH<sub>4</sub> emissions may be species-dependent. Finally, our observation of an increase in  
517 steady CH<sub>4</sub> flux under partially-shaded conditions may be due to a reduction in rhizospheric  
518 oxidation.

519

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525

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602

603 Figure captions.

604

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

608

609

610 **Figure 2.** Box plots of the steady CH<sub>4</sub> fluxes (i.e., excluding episodic ebullition) from the no-  
611 sedge (Figure 2a) and the sedge (Figure 2b) samples. The median is shown as a filled or open  
612 square, the inter-quartile range by the box or rectangle, and the minimum and maximum by the  
613 ‘whiskers’ extending from the box.  
614  
615

616 **Figure 3.** Frequency distribution of episodic ebullition CH<sub>4</sub> fluxes for summer (Figure 3a) and  
617 early autumn (Figure 3b). The data are grouped according to vegetation type (sedge, no-sedge).  
618 Thus, each flux value used in the distribution represents a mean of five samples on a single  
619 measurement occasion.  
620  
621

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

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