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1 **Effect of water table on greenhouse gas**
2 **emissions from peatland mesocosms**

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11 Peatland landscapes typically exhibit large variations in greenhouse gas (GHG) emissions due to
12 microtopographic and vegetation heterogeneity. As many peatland budgets are extrapolated from
13 small-scale chamber measurements it is important to both quantify and understand the processes
14 underlying this spatial variability. Here we carried out a mesocosm study which allowed a
15 comparison to be made between different microtopographic features and vegetation communities,
16 in response to conditions of both static and changing water table. Three mesocosm types
17 (hummocks + *Juncus effusus*, hummocks + *Eriophorum vaginatum*, and hollows dominated by
18 moss) were subjected to 2 water table treatments (0-5 cm and 30-35 cm depth). Measurements
19 were made of soil-atmosphere GHG exchange, GHG concentration within the peat profile and soil
20 water solute concentrations. After 14 weeks the high water table group was drained and the low
21 water table group flooded. Measurement intensity was then increased to examine the immediate
22 response to change in water table position.

23 Mean CO₂, CH₄ and N₂O exchange across all chambers was 39.8 μg m⁻² s⁻¹, 54.7 μg m⁻² h⁻¹ and -
24 2.9 μg m⁻² h⁻¹, respectively. Hence the GHG budget was dominated in this case by CO₂ exchange.
25 CO₂ and N₂O emissions were highest in the low water table treatment group; CH₄ emissions were
26 highest in the saturated mesocosms. We observed a strong interaction between mesocosm type and
27 water table for CH₄ emissions. In contrast to many previous studies, we found that the presence of
28 aerenchyma-containing vegetation reduced CH₄ emissions. A significant pulse in both CH₄ and
29 N₂O emissions occurred within 1-2 days of switching the water table treatments. This pulsing
30 could potentially lead to significant underestimation of landscape annual GHG budgets when
31 widely spaced chamber measurements are upscaled.

32 *Greenhouse gases; Water table; Vegetation; Microtopography; Peatland;*
33 *Mesocosm;*

1 **Introduction:**

2 Northern peatlands are estimated to contain 455 Gt of carbon (Gorham 1991),
3 representing approximately a third of the estimated total global soil carbon pool.
4 They are considered to be net sinks of CO₂ and net sources of CH₄ (Bartlett and
5 Harriss 1993; Gorham 1991; Huttunen et al. 2003), though annual and inter-annual
6 variation can be extremely high. Peatlands also represent an important source of
7 dissolved organic carbon to drainage waters (Urban et al. 1989; Billett et al. 2004;
8 Dawson et al. 2004). As soluble nitrogen is often limited, soil-atmosphere fluxes
9 of N₂O tend to be small, although with a global warming potential of 298 (IPCC
10 2007) they can still contribute significantly to the total GHG budget. Some of the
11 primary consequences of climate change, including increased temperatures,
12 increased drought and increased frequency and intensity of rainfall events, are
13 likely to directly influence peatland ecosystems. This in addition to management
14 practices such as peatland drainage, means that it is becoming increasingly
15 important to accurately predict the biospheric feedbacks of peatlands to climate.

16 The main controls on soil carbon and nitrogen cycling in peatlands are a)
17 temperature, as it controls the rate of microbial activity; b) water table depth as it
18 determines the depth of the oxic/anoxic boundary and redox level within the soil;
19 and c) plant community composition and structure which influences the quantity
20 and quality of organic substrate available, and can alter the aerobic capacity of the
21 peat by transporting O₂ to the rhizosphere (Bartlett and Harriss 1993; Dise et al.
22 1993; Ström et al. 2003; Whiting and Chanton 1996; Yavitt et al. 1997). In the
23 same way that certain plant species have the ability to transport O₂ from the
24 atmosphere to the rhizosphere, they can provide a direct pathway for many GHGs
25 to the atmosphere, bypassing the aerobic peat horizon (Bartlett and Harriss 1993;
26 Minkinen and Laine 2006). Such plant mediated transport has been demonstrated
27 to account for >80% of CH₄ emissions from rice paddies (Butterbach-Bahl et al.
28 1997; Yu et al. 1997).

29 The microtopographic pattern of elevated hummocks, wetter hollows and
30 submerged pools, typical of many peatlands, can cause significant variation in soil
31 environmental conditions (Nungesser 2003). Such differences are further
32 reinforced by the colonisation of distinct plant communities. As a result GHG

1 production, emission and consumption within peatlands can vary considerably at
2 scales $<1 \text{ m}^2$. Problems arise when gas exchange measurements, made using
3 chambers of usually $<0.5 \text{ m}^2$, require up-scaling to catchment level.

4 The influence of water table depth on CO_2 and CH_4 soil-atmosphere exchange has
5 been studied repeatedly using flask experiments on disturbed peat (Blodau and
6 Moore 2003a; Öquist and Sundh 1998), measurements on relatively undisturbed
7 peat cores (Aerts and Ludwig 1997; Moore and Dalva 1993), and field studies
8 (Hargreaves and Fowler 1998; MacDonald et al. 1998). Only a small number of
9 controlled experiments have been carried out with the vegetation structure intact
10 (Blodau et al. 2004; Blodau and Moore 2003a). Fewer still have compared
11 different vegetation/microtopography types (though examples include: Updegraff
12 et al. 2001), despite studies showing that the influence of vegetation is species-
13 specific (Butterbach-Bahl et al. 1997; Ström et al. 2005). Such comparisons are
14 important as the relative coverage of each community type may be altered
15 following ecological succession resulting from long-term environmental change
16 (Strack et al. 2006; Weltzin et al. 2003). The general consensus from these studies
17 is that lowering the water table increases C mineralization and decreases CH_4
18 emissions. Studies into the effects of water table depth on peatland N_2O emissions
19 include those by Aerts and Ludwig (1997) and Regina et al. (1999); they conclude
20 that lowering the water table depth leads to a net increase in N_2O emissions.

21 The aims of this study are: a) to compare the greenhouse gas budget (with
22 emphasis on CH_4 and N_2O) and temperature response of peatland mesocosms
23 under high and low water table conditions; b) to quantify the immediate CH_4 and
24 N_2O exchange response to a sudden changes in water table depth; and c) to assess
25 the influence of vegetation/microtopography on these responses.

26 **Materials and Methods:**

27 **Site Description**

28 Cores were collected from Auchencorth peatland ($55^\circ 47' 34\text{N}$; $3^\circ 14' 35\text{W}$),
29 approximately 17 km south west of Edinburgh (Scotland). Mean annual
30 precipitation at the site (1995-2006) is 1016 mm (Coyle, unpublished data, 2008)

1 with maximum and minimum monthly mean temperatures (1971-2000) of 19 °C
2 in July and 0.7 °C in January respectively (www.metoffice.gov.uk).

3 The catchment is a 335 ha grass dominated, lowland ombrotrophic peatland with
4 an elevation range of 249 to 300 m (Billett et al. 2004). The land-use is primarily
5 low intensity sheep grazing, though overgrown ditches are evidence of past
6 drainage. The vegetation is a patchy mix of coarse grasses and soft rush covering
7 a *Sphagnum* base layer. *Calluna vulgaris* is present in the south-west of the
8 catchment where drainage is better. The microtopography consists of a series of
9 hummocks and hollows. Hummocks are typically small (~40 cm diameter, ~30
10 cm height) and dominated by either a mix of *Deschamsia flexuosa* and
11 *Eriophorum vaginatum*, or *Juncus effusus*. Hollows refer to the areas between
12 hummocks and are dominated by mosses (*Sphagnum papilloso* and *Polytrichum*
13 *commune*) and a thinner layer of grasses; hollows often become submerged after
14 periods of intense or sustained rainfall. Water table at the site generally fluctuates
15 between the peat surface and ~20 cm depth, although during dry periods it is often
16 drawn down to >35 cm (Coyle, unpublished data, 2008). The mean water
17 extractable DOC is 312 ± 15.9 (SE) $\mu\text{g C g}^{-1}$ dry soil and KCL extractable NO_3^-
18 and NH_4^+ are 4.45 ± 0.48 (SE) and 21.8 ± 1.85 (SE) $\mu\text{g N g}^{-1}$ dry soil, respectively
19 (Dinsmore, unpublished data, 2008). Total N and S deposition at the site are 16.5
20 $\text{kg N ha}^{-1} \text{ a}^{-1}$ and $6.9 \text{ kg S ha}^{-1} \text{ a}^{-1}$ respectively (Smith, personal communication,
21 2008).

22 To minimise variation in factors other than microtopography, the cores were all
23 collected within an area of approximately 10 m^2 . Peat depth at the sample site was
24 approximately 0.5 m, overlaying a mineral subsoil. Peat core pH ranged from 3.8-
25 4.3, typical of the catchment as a whole which ranges from 3.6-4.6 (Dinsmore,
26 unpublished data). Mean bulk density was 0.12 g cm^{-3} .

27 **Experimental Design**

28 Three distinct peatland topographic/vegetation features were identified as
29 comprising the majority of the field heterogeneity; hollows, hummocks dominated
30 by the rush *Juncus effusus*, and hummocks dominated by a mixture of grass and
31 sedge. Eight cores were collected from each ecotope in December 2006; 24 cores
32 in total. A 30 cm diameter, 50 cm long, stainless-steel, cylindrical corer was used

1 to cut into the peat. The core was then dug out, cut to size and immediately
2 transferred to near-parallel sided buckets (30 cm diameter, 41 cm height) with as
3 little disturbance to the soil as possible. The following terminology will be used
4 henceforth in reference to the 3 different mesocosm types: hummock + *J. effusus*
5 (Juncus/Hummock), hummock + grass and sedge (Sedge/Hummock), hollow
6 (Hollow).

7 Dip wells, consisting of perforated pipes inserted into the soil and sealed at the top
8 with rubber bungs, were placed into each mesocosm. Deep and shallow soil
9 atmosphere wells were created by inserting water tight, gas permeable tubing
10 (Accurel[®], Gut et al. 1998) horizontally into the mesocosms at depths of 10 cm
11 and 30 cm below the soil surface. The Accurel[®] was sealed to gas tight tubing
12 (using Plasti Dip[®]) which was then extended to the mesocosm surface for sample
13 collection (Fig. 1); the surface sampling port was closed to the atmosphere using a
14 3-way tap. Mesocosms were individually placed within larger buckets and the
15 space between filled with polystyrene chips to insulate and mimic field conditions
16 (Fig. 1). Each mesocosm was assigned to either a high or low water table group,
17 leading to a repeated measures factorial design. The mesocosms were arranged
18 using a randomised block design into 6 rows of 4 under a rain shelter, located
19 outside the Centre for Ecology and Hydrology Edinburgh, approximately 10 km
20 from the Auchencorth Moss field site. Mesocosms were allowed to acclimatise *in-*
21 *situ* for 4 weeks before measurements began.

22 **Static water table treatment**

23 From core collection until the end of May 2007, water table depth was held
24 constant by daily inspection and manually refilling with rain water collected on-
25 site. The mean ion concentrations in rainwater ($\text{mmol m}^{-2} \text{ week}^{-1}$), measured from
26 June to October 2006, were as follows: Sodium 0.56; Ammonium 0.26; Potassium
27 0.05; Calcium 0.37; Magnesium 0.13; Chloride 0.85; Nitrate 0.36; Sulphate 0.34
28 (Cape et al., pre-publication, 2008). Water table depth in the high and low water
29 table groups was held at 0-5 cm and 30-35 cm below the soil surface, respectively.
30 Weekly measurements of CH₄ and N₂O were made using static chambers. A clear
31 plastic lid was sealed to each mesocosm and air samples collected at time zero,
32 after 20 minutes and after 40 minutes. Soil air samples were collected weekly
33 from the gas permeable tubing, and water samples collected fortnightly from the

1 dip wells. Soil temperature at ~5 cm was measured at the same time as flux
2 measurements and soil atmosphere sampling. Total mesocosm net ecosystem
3 exchange (NEE) was measured using a static chamber connected to a PP-Systems
4 EGM-4 infrared gas analyser, which measures CO₂ concentrations every 4
5 seconds. Measurements were made under 4 different light conditions produced
6 using full sunlight, 1 shade cloth, 2 shade cloths and a black out cloth and
7 combined to produce light response curves. Photosynthetically active radiation
8 (PAR) and temperature were measured inside the NEE chamber alongside CO₂
9 concentration. Photosynthesis was calculated as total NEE minus the combined
10 plant and soil respiration (NEE under dark conditions).

11 **Rewetting/Draining**

12 At the end of May 2007 (after approximately 14 weeks of measurements), the
13 water table treatments were reversed. Drainage of the saturated mesocosms was
14 achieved using a siphon placed in the dip well; re-wetting of the drier mesocosms
15 was carried out by periodic watering over a 2 day period. Thereafter, CH₄ and
16 N₂O fluxes were measured and solute samples collected daily for one week and
17 then every 2 days for a second week.

18 **Analytical methods**

19 Both chamber and soil atmosphere samples were analysed using a HP5890 Series
20 II gas chromatograph (detection limits: CO₂ < 199 ppmv, CH₄ < 1.26 ppmv, N₂O
21 < 0.2 ppmv). Water samples were analysed for DOC and DIC on a Rosemount-
22 Dohrmann DC-80 total organic carbon analyser (detection range 0.1 to 4000
23 ppmv), using ultraviolet oxidation and sparging with N₂ to remove acidified
24 inorganic carbon. NO₃⁻ and NH₄⁺ were analysed on a dual channel CHEMLAB
25 continuous flow colorimetric analyser (detection range NH₄⁺-N: 0.25 to 3.0 ppmv;
26 NO₃⁻-N: 0.25 to 5.0 ppmv).

27 **Statistical Analysis**

28 Repeated measures MANOVA was used when testing the significance of
29 mesocosm type and water table treatment on measured variables; an interaction
30 term was also included in the model specification. ANOVA was used when
31 considering mesocosm respiration, photosynthesis and NEE, with temperature as

1 a covariate where appropriate. Quoted test results refer to Pillai's test statistic
2 (Townend 2002) unless stated otherwise. Normality was assessed using the
3 Kolmogorov-Smirnov test (Townend 2002) and datasets adjusted, where
4 appropriate, using log transformations. Temperature responses were tested using
5 regression; trend lines are compared using multiple regression with temperature,
6 group identifier (e.g. water table treatment 1 or 2 referring to high and low
7 respectively), and temperature*group as independent variables. Depending on the
8 normality of the data, correlations were carried out using either Pearson's product-
9 moment or Spearman's rank correlation (Townend 2002). Where mean values are
10 quoted, the \pm value that follows refers to the standard error of the mean unless
11 otherwise stated. Analyses were carried out in 'Minitab15'.

12 **Results:**

13 **Comparison of mesocosm types/peatland features**

14 The observed differences in species composition (Fig. 2) within the mesocosms
15 was shown to be highly statistically significant using MANOVA ($F = 6.36$, $p <$
16 0.01). All 3 mesocosm types had an average coverage of more than 60% moss.
17 The 'Sedge/Hummock' group was dominated by grass and moss, and also
18 contained a significant amount of the sedge *E. vaginatum*. The 'Hollow' group
19 was dominated primarily by mosses and the 'Juncus/Hummock' group, whilst still
20 being dominated by moss and grass, also contained an average of 40% *J. effusus*
21 coverage. Small but significant differences were apparent in soil pH across
22 mesocosm types; 'Juncus/Hummock' 4.2 ± 0.1 (SD), 'Sedge/Hummock' 3.9 ± 0.1
23 (SD), 'Hollow' 4.0 ± 0.1 (SD).

24 **Static water table treatment**

25 *Uptake/Emissions*

26 Mean combined plant and soil respiration across replicates during the static water
27 table portion of the study ranged from 92 to 167 $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 1).
28 Respiration was highest in the 'Sedge/Hummock' group. In both the
29 'Sedge/Hummock' and 'Hollow' mesocosms, respiration was higher in the low
30 water table group; no difference was observed in the 'Juncus/Hummock' group.

1 Although the observed patterns were not statistically significant, this was
2 expected due to the low level of replication. Light response curves were used to
3 predict photosynthesis at a PAR of $210 \mu\text{mol m}^{-2} \text{s}^{-1}$, the mean PAR at the
4 Auchencorth field site over the measurement period (Coyle, unpublished data).
5 Photosynthesis (Table 1) was highest in the 'Juncus/Hummock' mesocosms,
6 followed by the 'Sedge/Hummock' and finally the 'Hollow' mesocosms ($F =$
7 5.25 , $p < 0.05$). The effect of water table depth on photosynthesis was
8 insignificant ($F = 3.68$, $p < 0.10$); however, lower water tables indicated a 44%,
9 36% and 21% decrease in photosynthesis in the 'Juncus/Hummock',
10 'Sedge/Hummock' and 'Hollow' mesocosms, respectively. The resulting NEE
11 calculated from the respiration and photosynthesis data showed no significant
12 effect of either mesocosm type or water table position. However, in general the
13 lower water table treatment increased the flux of CO_2 to the atmosphere (Table 1).
14 The 'Juncus/Hummock' mesocosms in the high water table treatment were the
15 only group to show a net CO_2 uptake.

16 Mean CH_4 fluxes from individual chambers over the 14 week period of static
17 water table treatment ranged from -30.7 to $358 \mu\text{g CH}_4 \text{m}^{-2} \text{h}^{-1}$; mean N_2O fluxes
18 over the same period ranged from -17.3 to $12.5 \mu\text{g N}_2\text{O m}^{-2} \text{h}^{-1}$. Averages across
19 chamber types and water table levels for both CH_4 and N_2O are presented in Table
20 1. Variation in mean CH_4 flux was high within all groups, and neither water table
21 level nor mesocosm type alone had a significant effect on CH_4 efflux; the effect of
22 water table was almost significant ($F = 3.41$, $p < 0.10$). However, there was a
23 significant interaction effect ($F = 1.65$, $p < 0.05$). Only in the high water table
24 group did mesocosm type have a significant effect on CH_4 flux (Hollow >
25 Sedge/Hummock > Juncus/Hummock). A highly significant increasing trend in
26 mean CH_4 flux ($r^2 = 0.59$, $p < 0.01$) was observed in the 'Sedge/Hummock' time
27 series plot (Fig. 3). When the experiment began mean CH_4 emissions from the
28 'Sedge/Hummock' mesocosms were similar in magnitude to the
29 'Juncus/Hummock' mesocosms; however, from early April onwards the
30 'Sedge/Hummock' mesocosms were more similar to the 'Hollow' mesocosms.
31 Mean CH_4 flux in all groups was positive, representing a net emission; however,
32 uptake was measured at least once throughout the experiment in all but 2 of the
33 mesocosms.

1 There was a net uptake of N₂O in 21 of the 24 mesocosms over the 14 week
2 period reflected in a net uptake across all chamber types irrespective of water
3 table (Table 1); however, variation was extremely high. No significant effect of
4 either water table depth or mesocosm type on N₂O flux was observed using
5 Pillai's MANOVA test. However, using the Lawley-Hotelling (Townend 2002)
6 MANOVA post-hoc, the interaction effect was statistically significant ($F = 1.72$, p
7 < 0.05); again mesocosm type was only important in the high water table
8 treatment.

9 *Below ground concentrations*

10 Mean CO₂ concentrations in the deep and shallow soil atmosphere wells were 764
11 ± 52 and 680 ± 25 ppmv respectively; mean CH₄ concentrations 127 ± 52 and 111
12 ± 37 ppmv and mean N₂O concentrations 0.38 ± 0.01 and 0.37 ± 0.01 ppmv
13 (Table 2). Strong positive correlations were found between the deep and shallow
14 well concentrations for CO₂ ($r = 0.90$, $p < 0.01$) and N₂O ($r = 0.93$, $p < 0.01$).
15 However, no correlation was observed between CH₄ concentrations in the deep
16 and shallow wells ($r = -0.10$, $p = 0.80$). Variability in the measured CH₄
17 concentrations was large, ranging from below the detection limit to 5755 ppmv,
18 suggesting the presence of pockets of high CH₄ concentrations within the peat
19 profile. No water table or mesocosm type effects were observed for CO₂ or N₂O
20 concentrations (Table 2). Although not statistically significant, CH₄
21 concentrations appeared to be higher in the high water table treatment. The
22 highest concentrations were observed in the 'Sedge/Hummock' mesocosms,
23 where the water table effect was also most pronounced, followed by the
24 'Hollows', and lastly the 'Juncus/Hummock' group, where no visible difference
25 was apparent between high and low water table.

26 Soil solution DOC concentrations ranged from 8.0-124 mg l⁻¹ with a mean of $43 \pm$
27 2.1 mg l⁻¹. Concentrations of DIC, NO₃⁻ and NH₄⁺ covered a much smaller range
28 with mean values of 3.61 ± 0.26 , 0.03 ± 0.01 and 1.16 ± 0.09 mg l⁻¹ respectively.
29 No consistent patterns were observed across mesocosm type or water table
30 treatment in soil water solute concentrations.

1 *Temperature sensitivity*

2 Both high and low water table groups showed a highly significant CH₄ response
3 ($p < 0.01$) to natural variations in soil temperature (Fig. 4a) during the static water
4 table period. In the high water table group CH₄ emissions increased with
5 increasing temperature ($r^2 = 0.50$); in the low water table group increasing
6 temperature led to a decrease in emissions ($r^2 = 0.26$). The slopes of the 2
7 different trend lines were significantly different ($t = -4.51$, $p < 0.001$), with a
8 much stronger response to temperature in the high water table group. The N₂O
9 flux responded positively to increased soil temperature ($r^2 = 0.28$) with no
10 significant difference in the trend lines between water table treatments (Fig. 4b).
11 The N₂O flux showed a switch from uptake to emissions between approximately
12 7.5 and 8.5°C.

13 The temperature response of CH₄ in the high water table treatment group,
14 separated by mesocosm type is shown in Fig. 5. The trend lines for the
15 'Sedge/Hummock' ($r^2 = 0.62$, $p < 0.01$) and 'Hollow' ($r^2 = 0.43$, $p < 0.05$)
16 mesocosms were offset (i.e. the 'Hollow' mesocosms had higher CH₄ emissions)
17 though the slope of the lines (i.e. the response to increasing temperature) were
18 similar. The slope of the 'Juncus/Hummock' trend line was negligible and not
19 significant at $p < 0.05$. Mesocosm type had no significant effect on CH₄ response
20 in the low water table treatment group. As variability around all trend lines was
21 great and as measurements were only made over a very limited temperature range,
22 it would be misleading to present Q₁₀ values for the data.

23 **Response to draining/rewetting**

24 After the initial 14 week static water table treatment, the water table levels in the 2
25 treatments were switched. Over a 2 day period the high water table group was
26 drained to a new water table depth of 30-35 cm, and the low water table group
27 was wetted up until water table depth reached 0-5 cm.

28 A significant and immediate pulse, raising the CH₄ flux rate to over 160 $\mu\text{g m}^{-2} \text{h}^{-1}$
29 above what it was prior to rewetting, was observed in both the 'Hollow' and the
30 'Sedge/Hummock' mesocosms; a similar, though slightly lower pulse was
31 observed a day later in the 'Juncus/Hummock' mesocosms (Fig. 6a). The CH₄
32 flux returned to a rate similar to its pre-change mean before rising more slowly

1 again after approximately 8-10 days. The rate of increase in the latter stage of the
2 response was greatest in the 'Sedge/Hummock' mesocosms, followed by the
3 'Hollow' mesocosms; very little increase was observed in the 'Juncus/Hummock'
4 mesocosms. To test the significance of differences between mesocosm types, the
5 post-change period was split into 3 separate time intervals; days 0-5, 5-10 and 10-
6 15. Each section was analyzed independently using a repeated measures
7 MANOVA test. The test confirmed the statistical significance of the differences in
8 mesocosm types between days 10-15 after rewetting ($F = 4.00$, $p < 0.01$).

9 A pulse of CH_4 , similar to that caused by rewetting was also seen in response to
10 drainage (Fig. 6c). However, the magnitude of this pulse was approximately 700
11 $\mu\text{g m}^{-2} \text{h}^{-1}$ above the pre-change mean in both the 'Sedge/Hummock' and the
12 'Hollow' mesocosms, and more than $200 \mu\text{g m}^{-2} \text{h}^{-1}$ above the pre-change mean in
13 the 'Juncus/Hummock' mesocosms; in all cases significantly higher than after
14 rewetting. After ~8 days the fluxes appeared to level off at approximately -10 , -70
15 and $-120 \mu\text{g m}^{-2} \text{h}^{-1}$ below the pre-change mean in the 'Juncus/Hummock',
16 'Sedge/Hummock' and 'Hollow' mesocosms, respectively. The effect of
17 mesocosm type on response to drainage was only significant between days 5-10
18 ($F = 2.95$, $p < 0.05$)

19 In both the rewetting and the draining treatments, peaks in the N_2O response
20 occurred after 2 days (Fig. 6b and d). The pulse effect occurred only in the
21 'Hollow' mesocosms after rewetting, and in both the 'Hollow' and
22 'Juncus/Hummock' mesocosms after draining. After the initial pulse, all
23 mesocosms, both in the rewetting and drainage treatments followed a very similar
24 pattern in terms of N_2O response. This response showed no correlation with
25 temperature.

26 Solute concentrations were also collected and analysed for DOC, DIC, NH_4^+ and
27 NO_3^- during both the rewetting and draining experiments. However, no significant
28 response to draining/rewetting was observed.

1 **Discussion:**

2 **Comparison between mesocosms and field conditions**

3 Mean NEE across the different water table treatments and mesocosm types ranged
4 from -65 to 123 $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 1). During the same study period, mean
5 NEE measured at the Auchencorth Moss field site using eddy covariance was -8.4
6 $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Coyle, unpublished data). Despite the low replication, different
7 conditions, and different measurement technique, the field site NEE is still within
8 the range measured here. Mean CH_4 and N_2O fluxes ranged from 0.19 to 191 μg
9 $\text{CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ and from -3.4 to -0.55 $\mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$ (Table 1). Fortnightly field
10 measurements over comparable vegetation types during the same period gave a
11 mean CH_4 and N_2O flux of $9.9 \pm 4.1 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ and $-3.3 \pm 1.5 \mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$
12 (Dinsmore, unpublished data); again the field mean is within the range measured
13 in this study. Mean mesocosm DOC and NH_4^+ concentrations were approximately
14 double the mean concentrations measured in the field. The higher DOC and NH_4^+
15 concentrations in the mesocosms may indicate an increase in mineralization
16 caused by the death of plant roots cut during mesocosm collection; this may also
17 explain why our mesocosms had a net CO_2 emission whilst field measurements
18 over the same period showed a net uptake. DIC and NO_3^- concentrations were
19 similar between field and mesocosms. In response to a number of GHGs and
20 solutes, our mesocosms therefore appear to represent field conditions relatively
21 well.

22 **Effect of water table depth and mesocosm type**

23 Although not statistically significant our results demonstrated that under lower
24 water table conditions respiration increased and photosynthesis decreased. This is
25 consistent with similar studies (e.g. Blodau et al. 2004; Moore and Roulet 1993),
26 as water table controls the depth of the oxic peat layer, and hence the volume of
27 peat where aerobic decomposition can occur (Moore and Dalva 1993; Silvola et
28 al. 1996). However, the relationship between water table depth and respiration is
29 not linear throughout the profile with several authors reporting a breakdown in the
30 relationship below ~30 cm (e.g. Silvola 1996; Lafleur et al. 2005). Blodau et al.
31 (2004) demonstrated a drop in photosynthesis of 24% and 42% in two different
32 Canadian peatlands, associated with a 30 cm drop in water level; similarly, in this

1 study we measured a drop of between 21-44% with a similar water level change.
2 In mesocosms dominated by *J. effusus* and *E. vaginatum*, Ström et al. (2005)
3 measured mean respiration rates of $78 \mu\text{g m}^{-2} \text{s}^{-1}$ and $121 \mu\text{g m}^{-2} \text{s}^{-1}$ respectively,
4 similar to the $100 \mu\text{g m}^{-2} \text{s}^{-1}$ and $123 \mu\text{g m}^{-2} \text{s}^{-1}$ for *J. effusus* and *E. vaginatum* in
5 this study. The response of ecosystems to water table manipulations has
6 previously been shown to be dominated primarily by processes associated with
7 respiration rather than photosynthesis (Funk et al. 1994). As such, in both this
8 study and others (for example Blodau and Moore 2003a; Chimner and Cooper
9 2003; Moore and Dalva 1993), the net effect of lowered water tables is an increase
10 in CO_2 flux to the atmosphere. However, despite the agreement with similar
11 studies, these results should not be directly extrapolated to predict the ecosystem
12 response to longer-term water table draw-down. Laiho (2006) highlights the
13 importance of differentiating between ‘wet’ and ‘dry’ sites. If deeper soil layers
14 are continuously exposed to aerobic decomposition, the carbon at depth becomes
15 highly recalcitrant. The associated decrease in decomposition potential is likely to
16 negate the effect of an increased aerobic zone. Several other studies have also
17 argued that in ‘dry’ peats, large relative changes in respiration at depth have little
18 effect on surface fluxes due to the low contribution of deeper peat to total
19 respiration (Blodau et al. 2007; Knorr et al. 2007; Lafleur et al. 2005). As the
20 natural water table regime at Auchencorth often exposes deeper layers to aerobic
21 conditions it is unsurprising that the relationship found here was small and not
22 statistically significant.

23 In accordance with previous studies (Aerts and Ludwig 1997; Moore and Dalva
24 1993), we measured higher CH_4 emissions in our high water table treatment. In
25 the high water table group, the effect of mesocosm type on CH_4 emissions was
26 highly significant. Based on both current literature and our photosynthesis data
27 (Table 1), we expected the order ‘Juncus/Hummock’ > ‘Sedge/Hummock’ >
28 ‘Hollow’ due to the potential for plant-mediated transport and substrate release
29 (Greenup et al. 2000; Shannon et al. 1996; Yu et al. 1997). In this study we found
30 the opposite to be true. Emissions were lower in the ‘Juncus/Hummock’ and the
31 ‘Sedge/Hummock’ mesocosms, both of which contained a large proportion of
32 aerenchyma containing plants (*J. effusus*, *D. flexuosa* and *E. vaginatum*).

1 As well as providing a transport route for CH₄, aerenchyma also transports O₂ into
2 the rhizosphere and can significantly alter the redox state of saturated peat,
3 resulting in decreased methanogenesis and increased oxidation (Visser et al. 2000;
4 Wiebner et al. 2002). Lombardi et al. (1997) measured CH₄ oxidation potentials
5 of 44-318 mg m⁻² d⁻¹ in the rhizosphere of common aerenchymous wetland
6 species. The amount of radial oxygen loss through the plant roots is likely to be
7 dependent on photosynthetic activity (Roura-Carol and Freeman 1999). In the low
8 water table treatment group, due to the limited depth of our mesocosms, only a
9 very shallow anoxic layer for methanogenesis is likely to have existed. The
10 absence of a significant CH₄ reservoir for plant roots to tap into may have
11 restricted the potential for plant-mediated transport. Although the majority of
12 studies have found a positive effect of vascular plants on CH₄ emissions, a few
13 have reported results similar to this study, where emission inhibition by
14 rhizospheric oxidation appears to be greater than the increase in emissions via
15 plant-mediated transport and enhanced substrate release (Grünfeld and Brix 1999;
16 Kutzbach et al. 2004). Similarly Arah and Stephen (1998) found that increasing
17 the root-mediated transport potential in a CH₄ flux model resulted in decreased net
18 emissions due to the increase in oxidation outweighing increased CH₄ transport.

19 The increase in CH₄ emissions from the 'Sedge/Hummock' mesocosms
20 throughout the study period (Fig. 3) may indicate a seasonal shift in the balance of
21 positive and negative effects of vascular plants on CH₄ emissions. The conduit
22 potential of aerenchyma containing plants is likely to increase seasonally due to
23 the relationship between root biomass and stem cross-sectional area (Arenovski
24 and Howes 1992; Waddington et al. 1996). The production of deep roots reaching
25 the anoxic peat layer (Wein 1973), or increased substrate release early in the
26 growing season (Saarnio et al. 2004), may also cause seasonal changes in plant-
27 related emissions. The earlier initiation of *E. vaginatum* growth than *Juncus*
28 *effusus* (Wein 1973) may explain why a similar increasing trend is not observed in
29 the 'Juncus/Hummock' mesocosms. Longer-term measurements are needed to test
30 this hypothesis.

31 The pattern of below ground CH₄ concentrations ('Sedge/Hummock' > 'Hollow')
32 was opposite to that seen in surface emissions ('Hollow' > 'Sedge/Hummock').
33 This suggests that although more CH₄ is produced in the 'Sedge/Hummock'

1 mesocosms, there is a barrier preventing soil-atmosphere transfer. This could be
2 either oxidation in the rhizosphere (assuming soil atmosphere wells did not
3 sample the rhizosphere), or a physical barrier such as the thick layer of hummock
4 biomass preventing diffusion across the soil-atmosphere boundary. As bubble
5 formation does not occur until partial pressures of >0.21 atm (Fechner-Levy and
6 Hemond 1996), this is unlikely to be important in our mesocosms. The extremely
7 high variability in soil-atmosphere CH_4 concentrations and the lack of correlation
8 between shallow and deep wells may indicate spatial heterogeneity in rates of
9 production and oxidation within the soil profile caused by plant roots. High
10 concentrations in the Sedge/Hummock mesocosms may also be due to substrate
11 availability. *E. vaginatum* has previously been shown to release much higher
12 quantities of acetate, a substrate of major importance to CH_4 production, than *J.*
13 *effusus* (Ström et al. 2005).

14 Relatively few conclusions can be drawn from the pattern of N_2O fluxes and
15 concentrations due to the very high temporal variability. Low NO_3^- concentrations
16 in soil water may indicate low nitrification rates. An increased rate of nitrification
17 has been observed after water-table drawdown in several studies (Neill 1995;
18 Regina et al. 1996). Similarly in this study, although not significant,
19 concentrations of NO_3^- were higher in the low water table treatment in both
20 'Sedge/Hummock' and 'Hollow' mesocosms. Alternatively, the low NO_3^- pool
21 may be a consequence of high turnover rates. N_2O consumption from complete
22 denitrification may be the dominant process controlling N_2O fluxes to and from
23 this system.

24 **Temperature response**

25 The clear difference in the temperature response of CH_4 emissions between the
26 high and low water table groups (Fig. 4) was likely a result of different processes
27 contributing to the net flux. In anoxic (high water table) conditions the dominant
28 process was methanogenesis which increases emissions as microbial activity
29 increases in response to increasing temperature. This is in agreement with
30 previous studies which show a stronger temperature response in methanogenesis
31 than methanotrophy (Dunfield et al. 1993). In oxic (low water table) conditions
32 methanotrophy as well as methanogenesis contributed to the net flux, dampening
33 the overall response. The responses of both the 'Hollow' and the

1 'Sedge/Hummock' mesocosms were similar, suggesting a common dominant
2 process (methanogenesis). The 'Juncus/Hummock' however, more closely
3 resembled the response of the low water table group, indicating that
4 methanotrophy was also important. This supports the assertion that rhizospheric
5 oxidation was important in the 'Juncus/Hummock' mesocosms. The temperature
6 responses here appeared to be linear compared to the exponential responses
7 observed in other studies (Dise et al. 1993; MacDonald et al. 1998). However,
8 this may simply be a consequence of the limited range of temperatures our
9 mesocosms were exposed to.

10 We found a positive linear response of N₂O emissions to temperature with a
11 switch from consumption to production between approximately 7.5 and 8.5°C.
12 This suggests that N₂O producing processes are more responsive to temperature
13 than N₂O consumption processes. Water table position had no effect on the
14 magnitude of the N₂O temperature response. Further work is required to assess the
15 validity of the observed switch from consumption to production as N₂O fluxes in
16 this study are low and variability high.

17 **Pulsing effect**

18 After switching water table positions, both drainage and rewetting produced
19 evidence of a significant pulse in CH₄ and N₂O emissions within 1 or 2 days. This
20 pulse may be the direct result of the physical disturbance (water table shift)
21 causing a release of CH₄ and N₂O from below ground reservoirs. Episodic pulsing
22 after water table drawdown was seen by both Moore et al. (1990) and Shurpali et
23 al. (1993) and was attributed to degassing due to reduced hydrostatic pressure.
24 Alternatively, pulses may be a biological response to increased substrate
25 availability from enhanced biomass recycling or redox-induced chemical
26 breakdown (Blodau and Moore 2003b). Similar pulses in mineralization rates
27 have been observed in response to water level fluctuations (Aerts and Ludwig
28 1997). After the initial pulse, the CH₄ response to drainage occurred faster than
29 the response to rewetting. This is consistent with previous studies (Whalen and
30 Reeburgh 2000). N₂O fluxes were similar across all mesocosm types and water
31 table positions.

1 **Implications**

2 From continuous water table measurements made at the Auchencorth Moss
3 peatland in 2007 (Coyle, unpublished data), a rise in water table by more than 20
4 cm in less than 48 hours occurred 9 times in 8 months. Assuming emissions in
5 both CH₄ and N₂O peak each time this occurs and the peak lasts approximately 24
6 hours, fortnightly field measurements may fail to capture these peaks. The results
7 from the mesocosm study suggest that CH₄ pulsing after rewetting could
8 potentially contribute an additional 16% to the average annual flux. Using the
9 same assumptions, net N₂O flux could switch from a net sink of 0.008 to a net
10 source of 0.02 μg m⁻² h⁻¹ (Dinsmore et al., unpublished data, 2008). Although this
11 is only a rough calculation and the assumptions are large, it illustrates the
12 potential importance of these emission pulses after a sudden rise in field water
13 table levels. No such calculation was carried out on the pulses observed after
14 drainage as it is extremely unlikely that a water table drop of this magnitude
15 would occur over only 2 days in the field. Further work is required to assess the
16 actual implications of this pulsing under natural field conditions.

17 Using the 100 year global warming potentials published by the IPCC (2007), the
18 GHG fluxes in CO₂ equivalents for each group of mesocosms was calculated
19 (Table 3). In this system, CO₂ fluxes dominate the budget entirely. CH₄ fluxes are
20 an order of magnitude smaller than in many studies (e.g. Dowrick et al. 2006;
21 Hargreaves and Fowler 1998; Minkkinen et al. 2002; Minkkinen and Laine 2006;
22 Roulet et al. 2007), though studies such as MacDonald et al (1998) found similar
23 values in Scottish blanket peats. Fluxes of CO₂-equivalents from N₂O are in the
24 same order of magnitude as CO₂-equivalents from CH₄. Lowering the water table
25 by 30 cm greatly increased the net flux of CO₂-equivalents to the atmosphere,
26 which was dominated by NEE. Of the different mesocosm types, only the *J.*
27 *effusus* dominated hummocks show a net uptake of CO₂-equivalents. Hence it is
28 important to accurately account for the relative proportions of each community
29 type when up-scaling chamber measurements made in the field.

30 **Conclusions:**

31 Our results agree with previous studies on the flux responses to low water table
32 conditions. We have also demonstrated the strong interaction between water table

1 depth and vegetation. The effect of vegetation within the mesocosms was counter
2 to what we had originally hypothesised based on the available literature. What
3 determines the ratio between flux enhancing and flux inhibiting mechanisms in
4 plant communities is still largely unclear and may be related to both site-specific
5 and species-specific variables, which may change seasonally with plant growth
6 stage. Despite the uncertainty in the mechanisms involved, it is clear that species
7 composition has a dramatic effect on ecosystem functioning, and as such it is
8 important that community type is considered when up-scaling chamber
9 measurements. It also highlights the need to include some form of vegetation
10 succession in models used to predict long-term effects of landscape management
11 and environmental change on GHG budgets.

12 We observed a pulse in both CH₄ and N₂O emissions occurring between 1-2 days
13 after manually changing the depth of the water table by \pm 30 cm. Though further
14 work is required to quantify the importance of this pulse under field conditions, it
15 can be concluded that low frequency chamber measurements may significantly
16 underestimate mean annual emissions.

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22

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1 **Figure Legends**

2 **Fig. 1** Illustration of mesocosm design. Note diagram is not to scale

3 **Fig. 2** Vegetation composition within different mesocosm types. Error bars represent standard
4 deviations. Rush refers only to *J. effusus* and sedge to *Eriophorum vaginatum*. The grass was
5 predominantly *Deschamsia flexuosa*; *Agrostis stolonifera*, *Anthoxanthum odoratum*, *Festuca*
6 *ovina*, and *Molinia caerulea* are also present in some mesocosms. The dominant mosses are
7 *Sphagnum papillosum* and *Polytrichum commune*. The herb species present were *Potentilla erecta*
8 and *Galium saxatile*

9 **Fig. 3** Time series of mean CH₄ emissions in high water table group during static water table
10 treatment

11 **Fig. 4** (a) CH₄ and (b) N₂O flux response to temperature in high and low water table treatment
12 groups

13 **Fig. 5** CH₄ flux response to temperature in high water table treatment separated by mesocosm type

14 **Fig. 6** Change in flux relative to mean prior to water table switch; a) and b) illustrate response to
15 rewetting, c) and d) illustrate response to draining. Positive values represent an increase from pre-
16 change mean; negative values indicate a decrease in flux rate from the pre-change mean

1

2 **Tables**

3 **Table 1 Mean (\pm SE) fluxes of CO₂, CH₄ and N₂O separated by water table depth and**
 4 **mesocosm type. Values of CO₂ are based on 2 sampling occasions; values for CH₄ and N₂O**
 5 **represent weekly fluxes the full 14 week static water table treatment. Note different units for**
 6 **CO₂.**

	Juncus/Hummock		Sedge/Hummock		Hollow	
	High	Low	High	Low	High	Low
CO ₂ ($\mu\text{g m}^{-2} \text{s}^{-1}$)						
Respiration	101 \pm 12	102 \pm 7.6	124 \pm 10	167 \pm 26	92 \pm 7.1	105 \pm 5.8
Photosynthesis*	165 \pm 75	92 \pm 25	69 \pm 24	44 \pm 10	45 \pm 13	36 \pm 3.8
NEE	-65 \pm 53	9.1 \pm 11	55 \pm 22	123 \pm 19	58 \pm 12	70 \pm 3.8
CH ₄ ($\mu\text{g m}^{-2} \text{h}^{-1}$)	11 \pm 5.2	0.19 \pm 5.2	117 \pm 28	3.2 \pm 3.4	191 \pm 27	5.8 \pm 4.9
N ₂ O ($\mu\text{g m}^{-2} \text{h}^{-1}$)	-3.2 \pm 2.2	-0.82 \pm 2.1	-3.4 \pm 2.1	-1.8 \pm 1.7	-0.55 \pm 1.5	-0.85 \pm 2.0

7

8 * Photosynthesis based on PAR = 210 $\mu\text{mol m}^{-2} \text{s}^{-1}$

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2 **Table 2 Mean (\pm SE) concentrations of CO₂, CH₄ and N₂O in soil atmosphere wells during**
 3 **static water table treatment. Units are ppmv**

	Juncus/Hummock		Sedge/Hummock		Hollow	
	High	Low	High	Low	High	Low
CO ₂						
Shallow	694 \pm 88	722 \pm 63	711 \pm 71	687 \pm 80	574 \pm 63	695 \pm 74
Deep	739 \pm 89	924 \pm 203	726 \pm 105	756 \pm 102	801 \pm 160	639 \pm 60
CH ₄						
Shallow	19 \pm 8.2	7.1 \pm 2.6	484 \pm 173	88 \pm 77	39 \pm 14	29 \pm 13
Deep	19 \pm 4.1	28 \pm 8.2	222 \pm 148	42 \pm 24	433 \pm 148	17 \pm 9.3
N ₂ O						
Shallow	0.39 \pm 0.02	0.42 \pm 0.03	0.37 \pm 0.02	0.38 \pm 0.01	0.31 \pm 0.01	0.37 \pm 0.01
Deep	0.44 \pm 0.04	0.41 \pm 0.04	0.37 \pm 0.01	0.38 \pm 0.01	0.31 \pm 0.01	0.39 \pm 0.01

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2 **Table 3 GHG fluxes from mesocosms using 100 yr global warming potentials of 298 for N₂O**
 3 **and 25 for CH₄ (IPCC 2007). Flux units are mg CO₂-eq m⁻² d⁻¹ ± SE; positive and negative**
 4 **values represent emissions and uptake respectively**

	Water table	CO ₂	CH ₄	N ₂ O	Net CO ₂ -eq
Juncus/Hummock	High	-5592 ± 3264	6.7 ± 5.5	-23 ± 29	-5608
	Low	792 ± 936	6.2 ± 5.8	-6.0 ± 27	792
Sedge/Hummock	High	4776 ± 1656	70 ± 30	-25 ± 26	4822
	Low	10608 ± 1176	1.9 ± 3.6	-13 ± 22	10597
Hollow	High	4008 ± 912	115 ± 29	-4.1 ± 19	4119
	Low	6024 ± 288	3.4 ± 5.3	-6.0 ± 25	6021

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