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Biotic controls on CO_2 and CH_4 exchange in wetlands – a closed environment study

TORBEN R. CHRISTENSEN[1,*], NICOLAI PANIKOV[1,2,3], MIHAIL MASTEPANOV[1,2], ANNA JOABSSON[1], ANGELA STEWART[1], MATS ÖQUIST[4], MARTIN SOMMERKORN[1], SEBASTIAN REYNAUD[1] and BO SVENSSON[4]

*[1]Climate Impacts Group, Department of Ecology (now: Department of Physical Geography and Ecosystem Analysis), Lund University, S-223 62 Lund, Sweden; [2]Russian Academy of Sciences, Institute of Microbiology, Moscow, 117811, Russia; [3]Dept. of Chemistry & Chemical Biology, Stevens Institute of Technology, NJ, United States; [4]Department of Water and Environmental Studies, Linköping University, S-581 83 Linköping, Sweden; *Author for correspondence*

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Abstract. Wetlands are significant sources of the important greenhouse gas CH_4. Here we explore the use of an experimental system developed for the determination of continuous fluxes of CO_2 and CH_4 in closed ecosystem monoliths including the capture of $^{14}CO_2$ and $^{14}CH_4$ following pulse labelling with $^{14}CO_2$. We show that, in the ecosystem studied, ebullition (bubble emission) may account for 18 to 50% of the total CH_4 emission, representing fluxes that have been difficult to estimate accurately in the past. Furthermore, using plant removal and ^{14}C labelling techniques, we use the system to detail the direct influence of vascular plants on CH_4 emission. This influence is observed to be dependent on the amount of vascular plants present. The results that may be produced using the presented experimental set-up have implications for an improved understanding of wetland ecosystem/atmosphere interactions, including possible feedback effects on climate change. In recent years much attention has been devoted to ascertaining and subsequently using the relationship between net ecosystem productivity and CH_4 emission as a basis for extrapolation of fluxes across large areas. The experimental system presented may be used to study the complex relationship between vascular plants and CH_4 emission and here we show examples of how this may vary considerably in nature between and even within ecosystems.

Introduction

Growing evidence from recent climate and biogeochemical studies indicates that carbon cycling in boreal and arctic wetlands strongly influences the global climate (IPCC (Intergovernmental Panel on Climate Change) 1995). In particular, exchange of the greenhouse gases CO_2 and CH_4 is important, both for the dynamics of the "natural" climate and for possible man-induced climate change. Northern peatlands and wet tundra regions contain large amounts of stored organic carbon, and their potential for exchange of greenhouse gases (CO_2, CH_4) with the atmosphere is therefore great (Gorham 1991; Oechel et al. 1993, 2000; Christensen et al. 1999).

In general, these ecosystems are known to be sinks for atmospheric CO_2 through the accumulation of peat, and significant sources of CH_4 through the prevailing favourable conditions for anaerobic decomposition. Although the controls on these trace gas fluxes are fairly well known qualitatively, an integrated quantitative understanding of the controls on the dynamics of these fluxes and, in particular, the interactions between them is still lacking. For example, there is currently an apparent discrepancy between source estimates of CH_4 made by atmospheric models and ground-based flux studies (Hein et al. 1997; Reeburgh et al. 1998; Walter and Heimann 2000). Likewise there has, in recent years, been a lot of attention devoted to the use of measures of net ecosystem productivity (NEP) as a possible indicator of CH_4 fluxes at a large scale (Whiting and Chanton 1993), but the mechanistic reasons and the dynamics of this relationship for differing vegetation types are currently not well understood (Joabsson et al. 1999).

Although micrometeorological measurements of landscape CH_4 fluxes are increasing in number (Fan et al. 1992; Fowler et al. 1995; Friborg et al. 1997; Christensen et al. 2000), chamber flux measurements dominate the body of empirical data available on environmental and climatic controls on wetland soil respiration and CH_4 emission (e.g., Crill et al. (1988) and Whalen and Reeburgh (1992), Roulet et al. (1994), Christensen (1993), Christensen et al. (1995)). However, chamber studies in general have problems dealing with the episodic fluxes and differences in the experimental and data treatment techniques (e.g., criteria for acceptance of flux measurements based on linear increase in chamber concentration with time) may have led to difficulties in comparing flux measurements in the past. So far, few studies have been able to accurately separate out the processes of diffusion and bubbling, and quantify the individual process relationships with the soil climate. Here we document the application of an experimental system where such emission processes may be clearly separated and evaluated against underlying mechanisms controlling the actual CH_4 production.

Plant productivity exerts a very important biological control on methane production and this interaction between ecosystem productivity and CH_4 formation has been studied at scales ranging from below-ground microbial investigations (Panikov 1995; Thomas et al. 1996), over plot scale flux measurements (Whiting and Chanton 1992; Waddington et al. 1996; Bubier et al. 1995; Nykänen et al. 1995; Christensen et al. 2000) to large scale vegetation models linked to methane parameterisations (Cao et al. 1996; Christensen et al. 1996). Various studies have attributed this relationship to mechanisms such as stimulation of methanogenesis by increasing C-substrate availability (input of organic substances to soil through root exudation and litter production; Chanton et al. (1995) and Dannenberg and Conrad (1999)) and also through an enhancement of gas transport from the methanogenic soil layer to the atmosphere via root aerenchyma acting as gas conduits by-passing zones of potential CH_4 oxidation in the soil (Waddington et al. 1996; Frenzel and Rudolph 1998; Frenzel and Karofeld 2000; Kelker and Chanton 1997; King et al. 1998; Schimel 1995; Verville et al. 1998). With this study we use a combination of established and new techniques and document an experimental system by which to evaluate the relative importance of these processes in controlling the net CH_4 flux.

For many years the use of $^{14}CO_2$ labelling of plant material has proven a powerful tool in agricultural studies of plant allocation patterns. Similar techniques using ^{13}C as tracer have been applied in the study of gaseous emissions of CO_2 and CH_4 from rice paddies (Minoda and Kimura 1994; Minoda et al. 1996). In northern wetland and tundra environments the use of ^{14}C labelling has so far been limited to studies of above and belowground growth rates of mosses and vascular plants (Tieszen et al. 1974; Saarinen et al. 1992; Wallén 1992) and of monocultures (Megonigal et al. 1999). Few studies have adopted this technique for whole system studies of the carbon flow in northern ecosystems including the turnover time for organic carbon leading to the release of CH_4 (King and Reeburgh 2002). Here we present an experimental system with the potential to elucidate important details in the dynamics of this linkage for northern wetland ecosystems. We show examples of how one may use this system to study the role of vascular plants in the turnover of C and quantify the turnover rate for different organic pools. In doing so we detail under specific environmental conditions for a particular ecosystem the time lag from C fixation to CH_4 emission using ^{14}C labelling.

Methods

Experimental set-up and sites

A schematic illustration showing the basic experimental set-up can be seen in Figure 1. The system can be applied for steady-state chamber measurements in connection with “long-term” experiments (weeks-months). For short-term experiments to investigate the response to immediate manipulations, the system may be used in a closed chamber mode such that the airflow is returned from the INNOVA multigas analyser to the chamber in a closed flow non-steady state system.

In the results reported on here the material has been from three very different wetland ecosystems in Sweden (Table 1). The Kopparås mire monolith (south-central Sweden) was used for most experiments, the Holmeja mire monolith (southernmost temperate Sweden) and the Stordalen mire monolith (sub-arctic Sweden) contributed to the comparison of flux patterns.

Monolith sampling

Peat monoliths, 25 × 25 cm and 40 cm deep, were taken from the three sites (Table 1). The Holmeja monolith was sampled in June 2000, the Kopparås monoliths were collected in November 1998 and the Stordalen monolith was taken in frozen state in the spring of 1999. All monoliths were allowed time (ranging from weeks to several months) to obtain stable rates of photosynthesis and dark respiration (only the Stordalen monolith showed a limited actual growth during the experiment) under the given environmental conditions. The monolith from Stordalen sampled in the frozen state was thawed under gradually increasing daylengths and

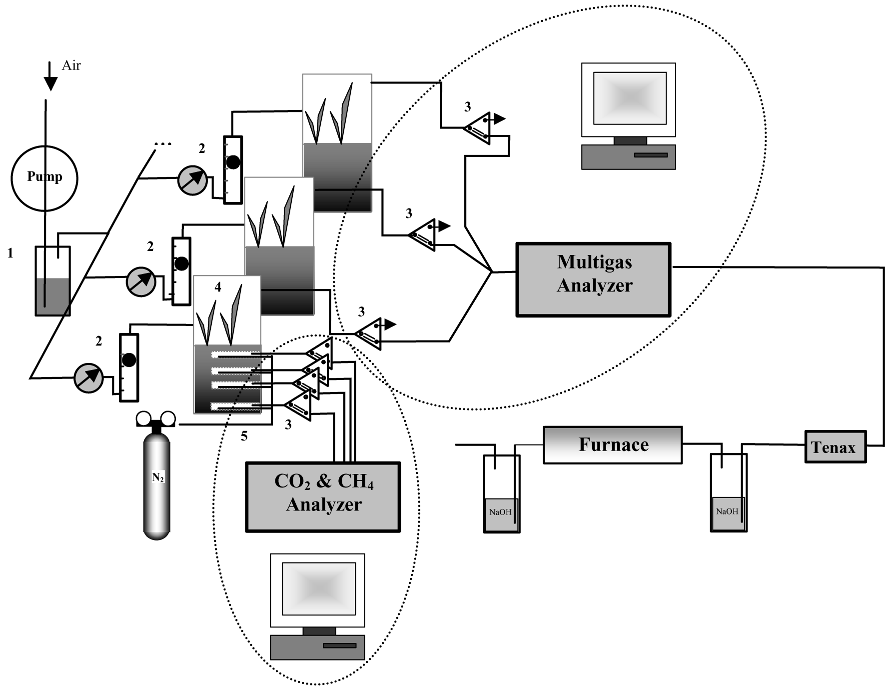

Figure 1. A schematic drawing of the experimental monolith set-up. The ambient air is passed through humidifier filter (1) and split into flow through 1–6 chambers (4) containing vegetated peat cores. Flowstat, rotameters (2) and solenoid valves (3) control airflow. The photoacoustic multigas (IR) gas analyzer (INNOVA 1312) operates continuously and records the concentration of CO_2 and CH_4 in the output air. The PC is used for data logging and for controlling the solenoid valves. The second PC and the second set of solenoid valves are used to record subsurface concentration of dissolved gases by membrane inlet probes (5). Results from these measurements are not shown here. In experiments with plant labeling with $^{14}CO_2$, the outflow air is subsequently passed through TENAX (retains non-methane hydrocarbons), NaOH trap and furnace (850 °C) to oxidize CH_4 to CO_2. Periodically NaOH aliquots and Tenax resins are counted for radioactivity by the scintillation technique.

temperatures. The sampling area of the Kopparås site has been thoroughly described by Malmer (1962). Stordalen was a site in the tundra part of the International Biological Programme (IBP) and is described in detail by Sonesson (1980). The Holmeja site is newly established and very little baseline information is therefore available.

At all sites aluminium frames were inserted into the ground while cutting around them with a sharp knife (at the frozen Stordalen a chain saw was necessary for this cutting). The frames were then lifted up containing the peat monoliths. The monoliths were transported to the laboratory within six hours and incubated under constant light (220 μmol m^{-2} s^{-1}) and moisture conditions at 15 °C before the experiment began. The depth of the water-table below the moss surface varied from 4 to 10 cm between the monoliths, which corresponded with the variation found in the field. Similar techniques of bringing in peat cores for laboratory CO_2 and CH_4 flux

Table 1. Site characteristics where the monoliths used in this study are from. All monoliths had a 40 cm peat-layer below the vegetated surface. The temperature averages refer to annual, warmest month and coldest month respectively.

Site	Location	Dominant vegetation	Temperature average (annual, warmest month, coldest month)	Vascular vegetation density
Holmeja	55°30′ N, 13°15′ E	*Carex rostrata*, *Eriophorum angustifolium*	7.8, 17.4, −0.8	Very dense
Kopparåsen	57°7.5′ N, 14°30′ E	*Eriophorum angustifolium, Sphagnum magellanicum, S. papillosum*	6.5, 16.6, −2.8	Dense
Stordalen	68°22′N, 19°03′E	*Eriophorum vaginatum*, *Drepanocladus* spp.	−0.9, 12.8, −10.1	Sparse

experiments have been used by e.g., Billings et al. (1982) and Thomas et al. (1996), Daulat and Clymo et al. (1998).

Monolith set-up in the laboratory

The cores were all placed in a temperature-controlled room at 19 °C and exposed to 300 μmol m^{-2} sec^{-1} (200 μmol m^{-2} sec^{-1} during the acclimation period before the experiments started) of photosynthetically active radiation. For comparative reasons in the results presented here all monoliths were exposed to the same conditions and kept at a day/night cycle of 12 hours each. For some of the monoliths a 12 hour light period is short compared to natural conditions but it was kept at this length here for the active photosynthesis not to "burn out" too soon in the experiment. The 19 °C is rather high as soil temperature for most of the monoliths compared to what they would see under natural conditions but for practical and comparative reasons this was the compromise temperature applied in the results presented here. A waterbath placed below the lights helped to minimise diurnal temperature variations. Transparent Plexiglas covers were sealed to the monoliths using silicone and flushed continuously with ambient air at an average flow rate of 800 ml min^{-1}. The air humidity was maintained at a constant level (Figure 1). Flowstat, rotameters and solenoid valves controlled the airflow. A photoacoustic multigas (IR) gas analyzer (INNOVA 1312) operated continuously and recorded the concentration of CO_2 and CH_4 in the input and output air. A PC was used for data logging and for controlling the solenoid valves.

Flux calculations and manipulations

Respiration was considered as the night-time flux and is presented as hourly mean values from an hour after light was switched off till light went back on. Net ecosystem exchange (NEE) was defined as the day-time flux, again as hourly mean values from one hour after the lamps went on and until they were switched off. Daily daytime gross photosynthesis values could then be estimated from the difference between the respiration and NEE.

The episodic and/or bubble fluxes can be filtered out by setting up an appropriate window for absolute fluxes identified as "steady emission" (*SE*). By isolating fluxes over an arbitrary defined baseline we can integrate under the peaks and thereby quantify the proportion of ebullition relative to the *SE*. The difference between *SE* and total emission (*TE*) gives gas ebullition (*GE*): $GE = TE - SE$. To compare different monoliths with differing *TE* we have to use relative rather than absolute measures of steady emission, so we introduce the specific steady emission: $se = SE/TE$.

There are methods to determine statistically and through chromatographic algorithms when a flux is significantly different from a "baseline". Any choice of method will be arbitrary and for full transparency and comparability we used the simplest possible arbitrary method and defined the baselines visually at a fixed fluxrate. The position of the individual baseline fluxes were set as 25 mg C/h/m^2

for Holmeja; 10 mg C/h/m^2 for the Kopparås 1 and 2 and 20 mg C/h/m^2 for Stordalen.

We carried out an experiment on a third Kopparås 3 “sister monolith” to the two others. In this experiment the vascular plants were removed incrementally to study the immediate effects of vascular plant presence on the CH_4 fluxes. The individual vascular plant tillers were very carefully pulled out including as much as possible of the root system one by one. Between each removal flux measurements were carried out after a few hours of stabilisation. The dry weight biomass of the material from each removal (shoot and root biomass) was quantified.

^{14}C labelling.

In the $^{14}CO_2$ experiment a total of 18.5 MBq was added as a sodium [^{14}C]bicarbonate (*Amersham Pharmacia Biotech*) solution in two repeated labellings in equal proportions (i.e. 9.5 MBq) on one monolith: on 1 April and 17 May 1999 respectively. A second monolith received a higher dose of 74 MBq on 8 November 1999 and the returned $^{14}CH_4$ and $^{14}CO_2$ were followed over a period of a minimum of 35 days following each labelling. In all labellings phosphoric acid was added to acidify the sodium bicarbonate in the chamber and release the ^{14}C as $^{14}CO_2$. Labelling was carried out over a two to three hour period before flushing the chamber completely.

To measure continuously the emitted $^{14}CO_2$ and $^{14}CH_4$ the outflow air was passed through TENAX (retains non-methane hydrocarbons), NaOH solution (0.1 M) to trap $^{14}CO_2$ and a furnace (850 °C) to oxidize $^{14}CH_4$ to $^{14}CO_2$ which was subsequently trapped in a second NaOH trap. Periodically NaOH aliquots and Tenax resins were counted for radioactivity by the standard scintillation technique. Opti-Flour™ (CIAB) was used as scintillation cocktail and counting was on a Packard Tri-Carb 2100TR liquid scintillation analyser.

In the post-experiment analyses of ^{14}C activity in the plants and peat the organic material was dried and sub samples of all fractions (living and dead plants, roots, peat etc.) were oxidised in a Packard sample oxidiser and the CO_2 trapped in Carbo-Sorb^R scintillation cocktail.

Results

Continuous flow flux dynamics – “long-term” isothermal incubations

Figures 2 and 3 show data from month-long incubations of different monoliths from Sweden (Table 1) using the INNOVA set-up illustrated in Figure 1 and with a two minute time resolution on the concentration (and hence flux) measurements. Average respiration rates, NEE and estimated gross photosynthesis for Holmeja, Kopparås 1 and Stordalen are shown in Figure 2. In terms of CO_2 fluxes and carbon balances the monoliths represent different growth states. The south Swedish

Holmeja monolith (Figure 2a) showed very strong rates of CO_2 exchange due to the dense vegetation, which resulted in CO_2 limitation of the photosynthesis rate (CO_2 concentration in outflowing air was 180 ppm). This can be seen from the almost flat level of net carbon uptake during the day (Figure 2a).

The Kopparås 1 monolith (Figure 2b) showed stable rates of photosynthesis and dark respiration yielding a slightly negative carbon balance during the experiment. The Stordalen monolith (Figure 2c) clearly had a negative carbon balance but productivity increased slowly during the experiment, as indicated by the increasing rate of photosynthesis seen from the increasing amplitude of the day-night cycles

In all cases, CH_4 emission had a stable "background" (Figure 3) with episodic substantial CH_4 release by ebullition. In the case of the presented experiments the bubble contribution varied between 17 and 50% (Figure 3, Table 2) before the manipulations shown below.

Closed flow CO_2 drawdown experiments.

As mentioned above, the experimental system may also be used in a closed set-up where it is possible to follow the flux behaviour over a few hours as the CO_2 is being assimilated by the plants and CH_4 emitted. This type of experiment was conducted in a series of measurements to investigate the influence of vascular plants on the total CH_4 emission. Thus, the vascular plants (including main roots) were incrementally removed from a third Kopparås mire core and the impact on the CH_4 emission studied. Figure 4a shows how incremental removal of the vascular plants decreased the overall CH_4 emission, but that emission was still affected by ebullition.

In Figure 4a we can see that every withdrawal induces transient gas dynamics with jumps and falls (this is not actual gas flux, but a reflection of air mixing inside the chamber), but a steady decline in emission is also observed, which sometimes is interrupted by ebullition. In Figure 4b the mean long-term flux from Kopparås 1 and 2 and 20 observations from Kopparås 3 of *se* from each of the declining emission "steps" are averaged and plotted against the residual biomass of *Eriophorum angustifolium* shoots.

Labeling using $^{14}CO_2$ pulse injection techniques.

In the surface fluxes the emitted $^{14}CO_2$ shows an expected exponential decline following each labelling as a result of the dilution of ^{14}C in the aerobic respiration (both plant and microbial). The data show variable dynamics of the formation and emission of $^{14}CH_4$ from labelled photosynthate (Figure 5). In all experiments emission of labelled ^{14}C started almost immediately but in the experiments on the Kopparås 1 as a relative small fraction (4%) of the total gaseous C emission. In the labelling on the Kopparås 2 monolith (Figure 5), which, as mentioned above, had a greater amount of vascular plants (77 g dw m^{-2} versus 38 g dw m^{-2}), a clear peak in the $^{14}CH_4$ was seen a few days after the labelling.

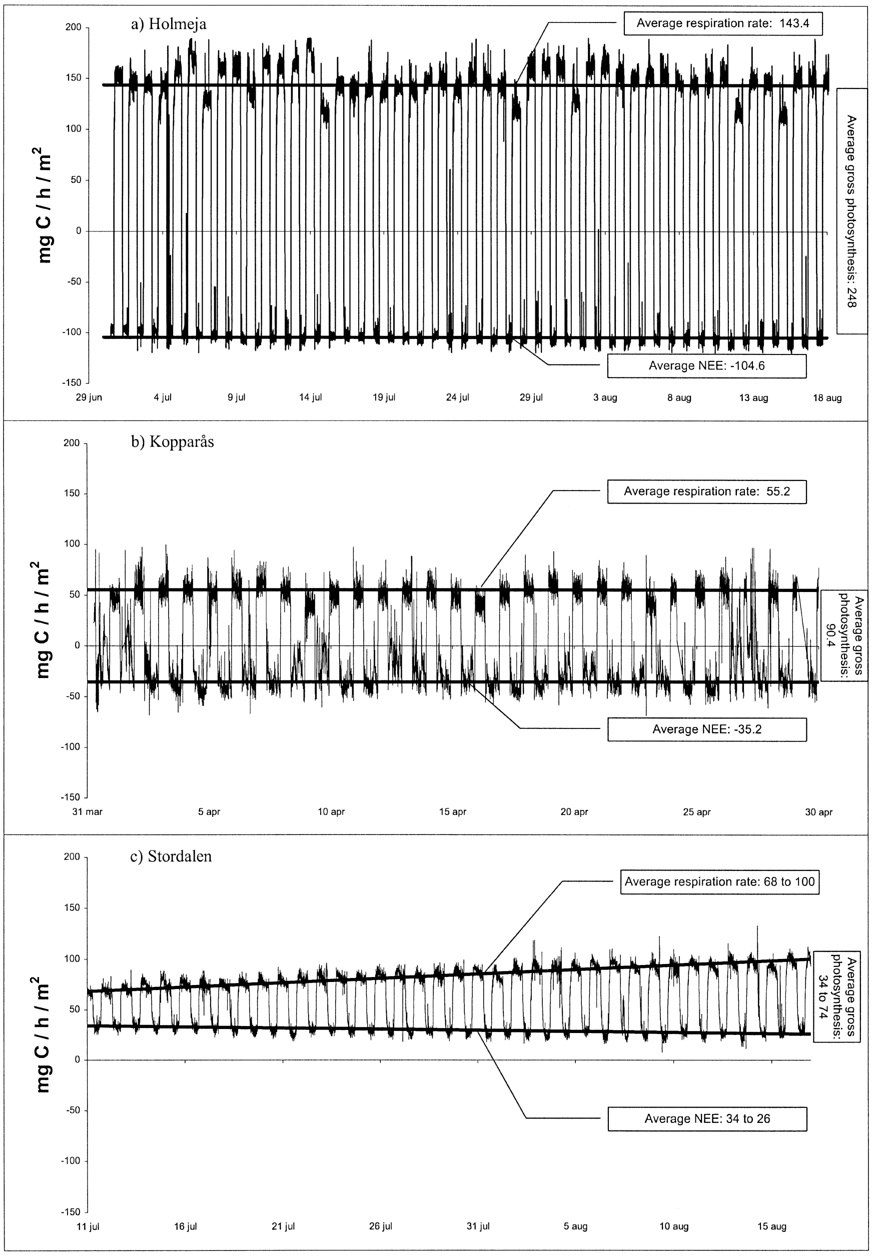

Figure 2. The CO_2 fluxes of three vegetated peat monoliths over > 30 day periods under constant conditions (19 °C, water table 4 cm below soil surface) continuously monitored with high time resolution (30 measurements/hr). High positive values on the CO_2 flux means nighttime loss of C to the atmosphere. a) Holmeja mire b) Kopparås 1 mire c) Stordalen. See Table 1 for site characteristics.

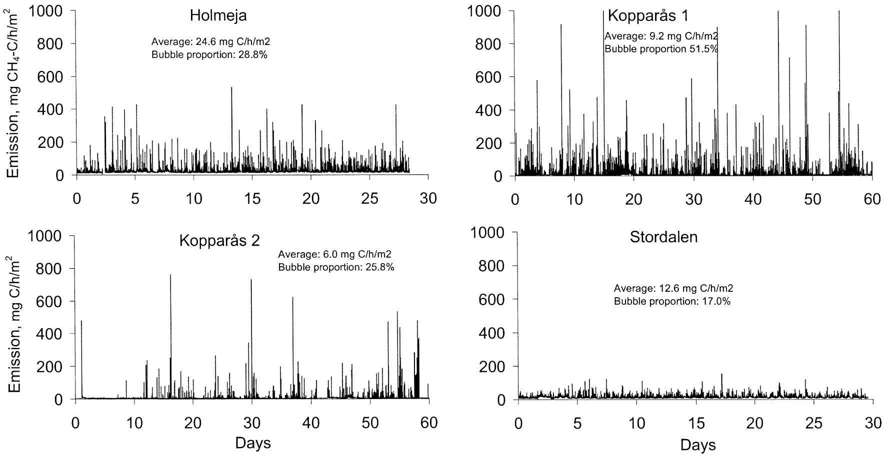

Figure 3. The CH_4 flux patterns in the four monoliths over a > 30 day period. All monoliths were exposed to the same air and soil climatic conditions. The contribution of ebullition to the total CH_4 flux is estimated using the methods described in the text.

Table 2. Contribution of ebullition to total methane transport: summary of calculations.

	Unit	Holmeja	Kopparås 1	Kopparås 2	Stordalen
Average total emission	mg C/h/m^2	24.6	9.2	5.9	12.6
Median		18.6	4.5	4.4	10.2
Standard deviation		23.9	30.8	16.4	8.3
Average background	mg C/h/m^2	17.5	4.5	4.4	10.4
Median		17.0	4.3	4.4	9.6
Standard deviation		3.2	1.4	1.8	3.5
Average background	%	71.2	48.5	74.2	83.1
Bubbles	mg C/h/m^2	7.1	4.7	1.5	2.1
Bubbles	%	28.8	51.5	25.8	17.0

The total recovery of ^{14}C (Table 3) was 100%. Of the ^{14}C fixed during the labelling, 69% remained in the living above and belowground biomass after a four-month period. Dead belowground tissue accounted for 10%, microbial biomass 8.5% and the amounts respired as CO_2 and CH_4 were 12 and 0.5% respectively.

Discussion

The overall carbon fluxes of all monoliths are showing negative carbon balances. This is most likely due to the artificial laboratory conditions chosen for comparative reasons where the low light levels, high temperatures and relatively short "day lengths" all causes more limitation on the photosynthesis rates that on the total respiratory activity.

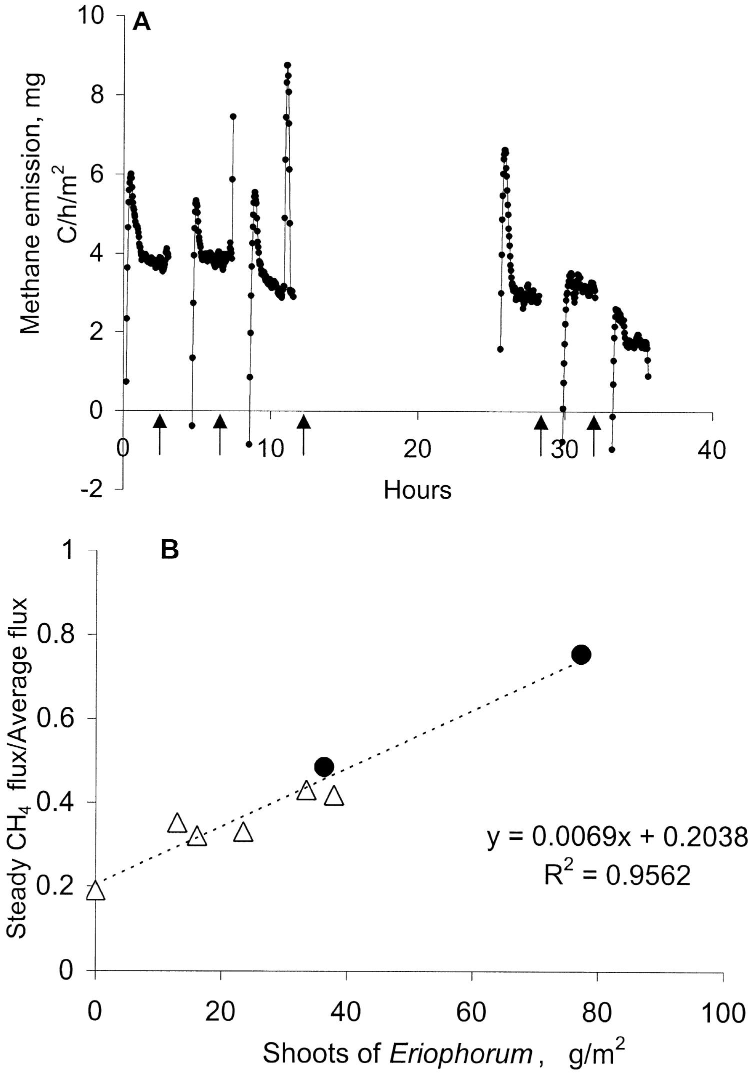

Figure 4. a) CH_4 emissions as responding to five gradual removals of the vascular plant biomass to an ultimate full removal. The arrows along the x-axis indicate the individual removals of plant tillers + roots. b) Steady specific flux, *se* (see text for definition) plotted against residual vascular plant (*Eriophorum angustifolium*) shoots. Black dots indicate the long term average fluxes for Kopparås 1 and 2 (the latter being with the higher biomass) and the open triangles the mean fluxes following plant removal as illustrated in a).

It may be argued that the calculation of *se* and hence quantification of the frequency and contribution to the total flux of episodic extreme events depend critically on the arbitrary choice of "baseline". In Figure 6 we show calculations of the sensitivity of the *se* calculation of the baseline choice. It can be seen that the Ko-

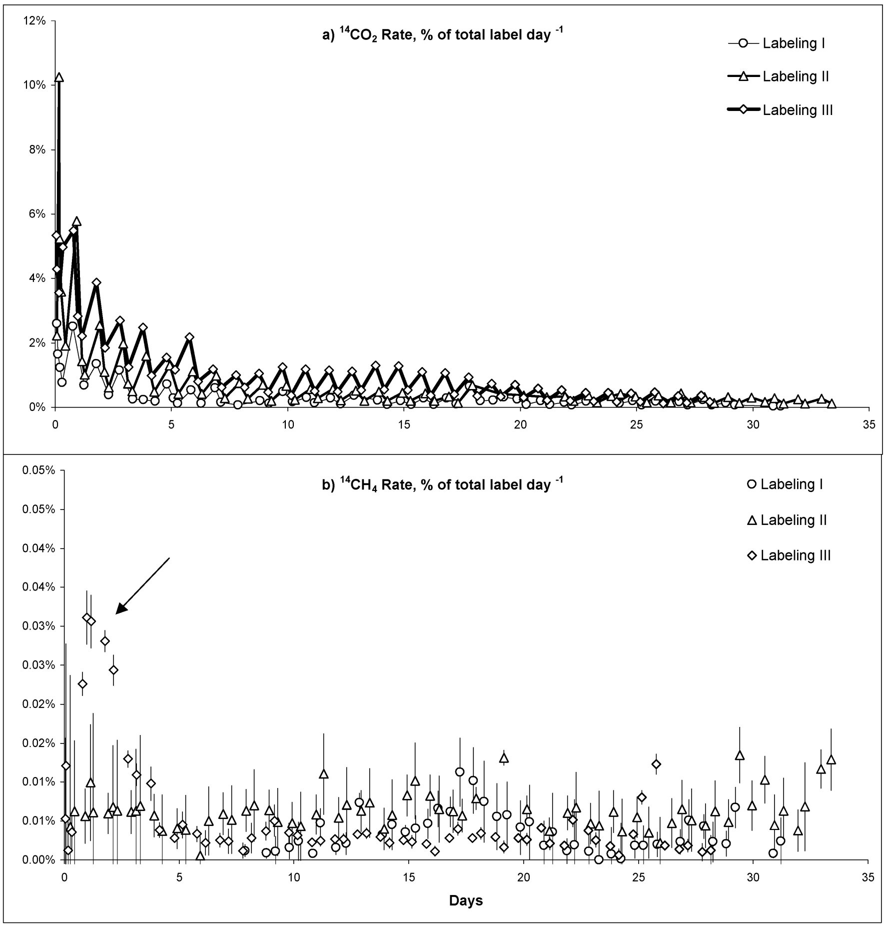

Figure 5. The return of ^{14}C labelled CO_2 and CH_4 in three labelings on the Kopparås 1 and 2 monoliths with different amounts of vascular plants. Labelings 1 and 2 were on Kopparås 1 that had 38 g dw/m^2 of *Eriophorum* biomass while labeling 3 was on Kopparås 2 which had 77 g dw/m^2. The arrow indicates the peak in $^{14}CH_4$ in the third labelling discussed in the text.

pparås monoliths are a lot less sensitive to the arbitrary choice than the Holmeja and Stordalen monoliths. This also indicates that the baselines were rather more disctinct and reliably quantified in the Kopparås monoliths compared to the Holmeja and Stordalen monoliths.

The CH_4 flux measurement technique we have developed in this study allows potentially for a detailed comparison of the emission patterns and how they differ between different vegetation types. In this study we present examples of results that may be obtained using this system but to achieve a full comparison of vegetation types replication of the monoliths would be required. We did see, however, even in identical vegetation compositions sampled only a few metres apart, that a difference in the density of vascular plants may cause significant differences in the flux

Table 3. Total recovery at the end of ^{14}C labeling experiment running from 1 April – 9 Aug. 1999 on Kopparås 1.

	^{14}C, MDPM	%
Living green plant tissue	643.1	60
Living roots	100.5	9
Total living plant	743.6	69
Dead belowground plant tissue	103.6	10
Peat without roots (presumably mostly microbes)	92.0	8.5
CO_2 evolved	133.2	12
CH_4 evolved	5.4	0.5
Sum	**1077.7**	**100**

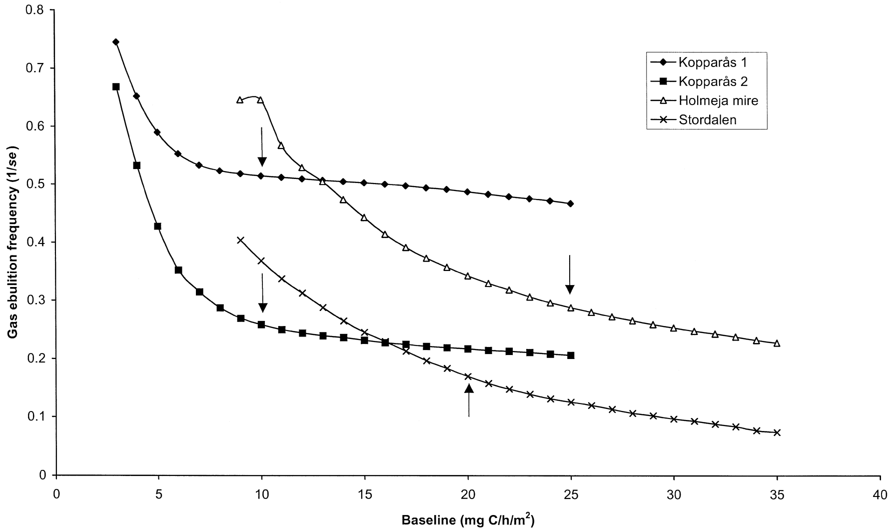

Figure 6. The dependency of the estimated relative proportion of ebullition or episodic extreme flux events to the total flux as a function of the choice of "baseline". Arrows indicate the baseline values chosen for the calculations of steady and gas ebullition fluxes presented in Table 2.

pattern. Comparing Kopparås 1 and Kopparås 2 in Table 2 we observe that, in the first case, there is a considerable divergence between mean (average) and median. Hence, there is a very strong deviation from normal Gauss distribution which tends to be log-normal. This means that episodic events of ebullition and extreme flux rates with a longer time between them contribute significantly to the total emission. In the Kopparås 2 monolith, mean and median are closer, indicating smoother dynamics with smaller contributions of rare extreme events to the overall flux. This is also reflected in a much higher standard deviation (Table 2) in the first monolith. Two conclusions can be drawn from this comparison: a) the Kopparås 2 monolith, which had twice the population density of vascular plants (*Eriophorum angustifolium*) as Kopparås 1, was characterised by much smoother methane emission dynamics; b) Kopparås 2 was a weaker methane source when compared with Kopparås 1 under identical environmental conditions. This may be be explained by a predominant process of rhizospheric oxidation decreasing methane emissions in the presence of the vascular plant species. The difference between Kopparås 1 and 2 may also be explained by natural spatial variation in the rates of methanogenesis that in turn could be caused by differences in peat quality or other factors. In short, the exact spot where Kopparås 2 was excavated may simply have contained a lower population of methanogenic bacteria or a higher rhizospheric oxidising capacity than Kopparås 1.

It is a unique asset of this experimental system that we obtain a very clear picture of the relative proportion of ebullition to the total flux at the chamber scale. Under the conditions in this controlled study up to half the fluxes was as bubbles or episodic fluxes. The relative bubble contribution may increase with temperature and therefore the rates may decline when moving to colder wetland habitats (Beckmann and Lloyd 2001). This could lead to an overestimation of the bubble contribution in the current experiment (Christensen 1994). However, with the isothermal and very stable laboratory conditions our current measurements were made under we are probably seeing fewer bubbles than what could be expected under field conditions where wind stirring effects may increase the bubble contribution (Friborg et al. 1997).

The effect on CH_4 fluxes of the gradual removal of *Eriophorum* tillers and roots from a third monolith is seen in Figure 4a and the relationship between *se* and the amount of vascular plants is shown in Figure 4b. It shows correspondence with respect to flux sizes between long-term and short-tem plant removal data across three independent cores with a very high correlation coefficient. The intercept of the regression line (i.e. supposedly where no vascular plant associated transport is happening) could indicate as much as 20% of steady emission is attributed to gas diffusion about non-vascular plants (mosses) or through peat material. However, there are uncertainties associated with such an interpretation of this very rapid diffusion rate, as it contradicts an estimation of molecular diffusion through water-saturated peat, which is estimated at no more than 0.02 mg C h^{-1} m^{-2} (Panikov et al. 2001). More detailed studies are required to accurately identify the ratio between vascular transport and molecular diffusion.

The data from the ^{14}C labelling represents an example of a specific "closed budget" for the carbon flow in a particular whole ecosystem monolith (Kopparås 1) over a period of four months (Table 3). The relatively small amount of ^{14}C recovered as $^{14}CH_4$ indicates a slow decomposition pathway to the formation of methanogenic substrates is the dominating source of methanogenic substrate in this system although further replication is needed to verify this pattern (Figure 7).

The data from the ^{14}C labelling indicates a limitation to the hypothesised coupling between productivity of vascular plants and CH_4 emission (Whiting and Chanton 1992; Bubier and Moore 1994; King et al. 1998). For this boreal bog the low but maintained contribution from recently fixed carbon to CH_4 formation indicates that the use of NEP and/or NEE as an indicator of CH_4 flux will be best applied on a seasonal/annual scale. This finding is in accordance with other studies

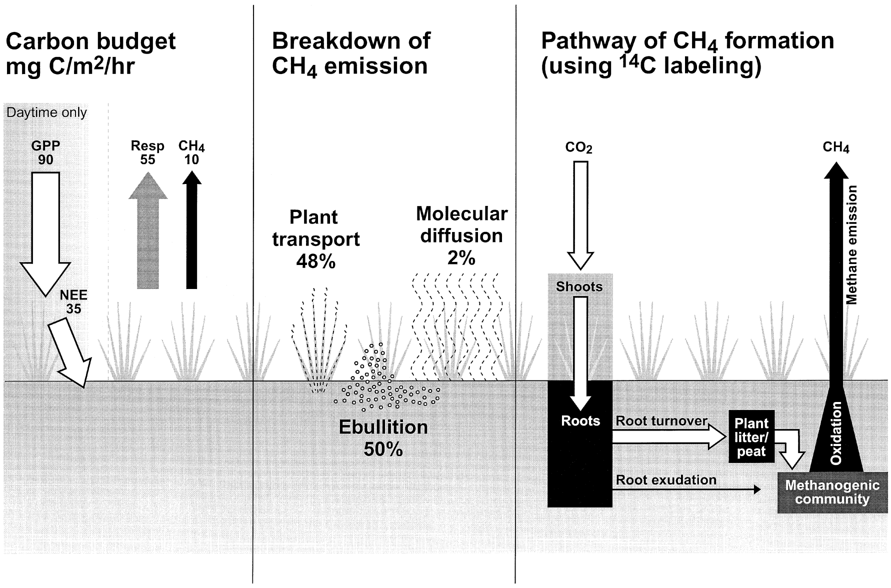

Figure 7. Summary of the C cycling and pathways of CH_4 emission as shown for the Kopparås 1 core under the specific conditions incubated under using the different techniques presented. Some uncertainty are associated with the low diffusion value of 2% as it is estimated based on a study of other peatland systems than the one studied here (Panikov et al. 2001).

(Bubier et al. 1995) but not necessarily applicable to all peatland and wet tundra ecosystems. Using indirect measures (flux rates of CO_2 and CH_4) field studies have shown correlations indicating more intimate linkages between net carbon flux and CH_4 emissions in comparable wetland ecosystems (Whiting and Chanton 1992; Waddington et al. 1996; Christensen et al. 2000). Additionally, recent results from comparable ^{14}C labelling experiments in Alaskan tundra systems indicate a closer coupling (King and Reeburgh 2002). The system presented in this paper may prove a useful tool for elucidating these relationships in more detail. The results presented here are short of replications but still indicate that caution should be applied in a wider extrapolation across different wetland systems as the intimate coupling of NEE and CH_4 emission seems highly dependent on vascular species composition and density.

The results from the comparison of the ^{14}C labelling of Kopparås 1 and Kopparås 2 may indicate that a close NEP/CH_4 flux relationship is valid when there is many vascular plants present. Kopparås 2, however, with the closer relationship and more vascular plants still had a significantly lower overall flux rate (Table 2) probably due to a lower methanogenic population, higher rhizospheric oxidation rates and/or a different peat quality. More experiments on monoliths from a variety of peatland ecosystems should be performed to elucidate how different vascular species composition and chemical composition of the peat influences the relationship between primary productivity and CH_4 formation and emission.

Figure 7 summarises what we have shown as a specific picture of the C turnover and CH_4 flux in the Kopparås 1 monolith under controlled conditions. The breakdown of the CH_4 flux is indicated and also the dominance of the slower peat/root turnover associated decomposition over a fast release of root exudates as the pathway of substrate production for the methanogens.

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