Gross photosynthesis explains the ‘artificial bias’ of methane fluxes by static chamber (opaque versus transparent) at the hummocks in a boreal peatland

Junwei Luan and Jianghua Wu

Sustainable Resource Management, Grenfell Campus, Memorial University of Newfoundland, 20 University Drive, Corner Brook, NL A2H 5G4, Canada

E-mail: Jwu@grenfell.mun.ca

Received 6 June 2014, revised 29 August 2014
Accepted for publication 4 September 2014
Published 10 October 2014

Abstract

The closed chamber technique has been widely employed to detect methane emissions, despite little being known about whether the absence or presence of light will impact the flux estimation. Here, we employed a laser greenhouse gas analyzer with an opaque—transparent chamber pair to measure the methane emission rate in a boreal peatland complex. Microtopography (i.e., hummocks and hollows) in natural and drained peatlands, and plant communities (i.e., grasses and shrubs) in a pasture converted from natural peatlands, were considered to cover the local heterogeneity. Our results indicated that opaque chambers (0.58–0.78 g CH\textsubscript{4} m\textsuperscript{-2} during the growing season) measured a significantly higher (∼2–3 times) methane emission at the hummocks than transparent chambers (∼0.24 g CH\textsubscript{4} m\textsuperscript{-2}); however, a similar phenomenon was not found at the hollows or at other measurement plots. Gross photosynthesis explained 44%–47% of the temporal variation of the ‘artificial bias’ (the difference in methane flux obtained by the opaque versus transparent chambers) at the hummocks. Additionally, both water table depth and surface soil moisture significantly explained spatial variations of methane emissions. Our study suggests that microtopography has a significant influence on the artificial bias in methane emission estimation and the artificial properties of a chamber (transparency/opacity) method can be vitally important in some cases (i.e., hummocks), and negligible in others (i.e., hollows). The observed connection between the photosynthesis process and the ‘artificial bias’ of closed chambers (opaque versus transparent) can be used to improve methane flux modeling. Separate parameterization schemes are needed for methane transportation under the presence or absence of light.

Keywords: methane oxidation, Sphagnum moss, microtopography, oxygen recycling, transparent chambers, opaque chambers, boreal peatlands

1. Introduction

Understanding the dynamics of methane (CH\textsubscript{4}) emissions is of paramount importance because CH\textsubscript{4} has 34 times the global warming potential of carbon dioxide (CO\textsubscript{2}) (IPCC 2013) and is currently the second most important anthropogenic greenhouse gas (Bridgham et al 2013). Global wetlands are the largest single atmospheric source of natural methane, and they were estimated to emit ∼100–200 Tg yr\textsuperscript{-1} CH\textsubscript{4} into the atmosphere (Neef et al 2010, Dlugokencky et al 2011). Further, it was found that freshwater methane emissions can even offset the continental carbon sink (Bastviken et al 2011). Wetland emissions dominated the inter-
annual variability of atmospheric methane sources between 1984 and 2003 (Bousquet et al. 2006). Therefore, it is critically important to accurately estimate methane emission from natural wetlands.

A variety of approaches have been employed to detect the methane exchanges between the biosphere and the atmosphere (Wang et al. 2012), such as chamber enclosure techniques (Moore & Roulet 1991, Altar & Mitsch 2008, Mastepanov et al. 2008, Christiansen et al. 2011, Strack & Zuback 2013, Sabrekov et al. 2014), eddy covariance techniques (Rinne et al. 2007, Wille et al. 2008, Kroon et al. 2010, Wang et al. 2012), flux-gradient techniques (Edwards et al. 2001), and CH$_4$ mixing ratio measurements (e.g., Dlugokencky et al. 2009). Among them, chamber enclosure techniques have been widely employed to measure the CH$_4$ flux of a variety of ecosystems in the field because of the simplicity and relatively inexpensive nature of the method (Cao et al. 2008, Davidson et al. 2008, Mastepanov et al. 2008, Guckland et al. 2009). Data from chamber based measurements have been taken as an important source of examining spatial variability and environmental controls of methane emission from various ecosystems, including wetland ecosystems. However, either opaque (Davidson et al. 2008, Guckland et al. 2009) or transparent (Cao et al. 2008, Mastepanov et al. 2008) chambers were employed to conduct the chamber enclosure measurement, even though clear plastic chambers can lead to high temperatures as a result of a long covering period (Chanton & Whiting 1995), while an opaque chamber might impact CH$_4$ emission estimation over 30 min coverage since stomata started to close after 30 min (Morrissey et al. 1993).

Many studies mentioned the potential artifacts (Silvola et al. 2003, Hirota et al. 2004) of the opaque chamber. The opaque chamber will apparently block the light from the chamber and thus may stop the light or slow ecosystem processes, such as photosynthesis, transpiration, and evaporation. As a result, the blockage of light under opaque chambers potentially impacts the production, transportation, or emission process of CH$_4$. For example, plants take up and transpire water containing dissolved methane (Nisbet et al. 2009), while light levels are tightly connected to stomata openness and thus transpiration rates (Shimazaki et al. 2007). The absence of photosynthesis will slow the transport of the substrate to the rhizosphere, and thus reduce the substrate supply to the methanogenesis process. As a result, the reduction in the substrate supply will impact the methane production, because the production of CH$_4$ is highly constrained by the substrate availability (Kankaala & Bergström 2004). Methane oxidation activated by the light (Graetzel et al. 1989), and methane emissions from wetlands regulated by the light (King 1990) were also reported. Sphagnum moss was also reported to consume CH$_4$ through symbiosis with partly endophytic methanotrophic bacteria, providing carbon for photosynthesis in the peat bogs (Raghoebarings et al. 2005, Kip et al. 2010). However, the heating effects of the transparent chamber might cause a faster or slower emission rate of CH$_4$, as both production and consumption of CH$_4$ are regulated by temperature (Frolking & Crill 1994, Bergman et al. 1998, Segers 1998). On the basis of previous research, the main artificial effects of either opaque or transparent chambers come from the ‘long coverage period’ (Morrisey et al. 1993, Chanton & Whiting 1995). Here, we employed a portable greenhouse gas analyzer with a 1 Hz response rate, which allowed covering for a significantly shorter period (three minutes, compared to 30 min or longer for gas sampling and the Gas Chromatography method). We hypothesized that there could be a significant difference in CH$_4$ flux between opaque and transparent chambers as a result of the absence or presence of the photosynthesis process.

A group of opaque—transparent chamber pair measurements were conducted in a boreal peatland complex (including natural peatlands, drained peatlands, and discontinued pasture peatlands with drainage) throughout the growing season (May–October) of 2013. To cover as many vegetation or microtopography types as possible, different communities in the discontinued pasture (i.e., shrub dominated, grass dominated, and ditch) and microtopography (i.e., hummock, hollow, ditch, and pool) in the drained or undisturbed peatlands were covered separately and measured. Our specific objectives were: (1) to investigate the difference between opaque and transparent chambers for measuring CH$_4$ fluxes within a short covering period (three minutes); and (2) to identify if a similar phenomenon exists among different communities or hummocks and hollows in boreal peatlands.

2. Research sites and methods

2.1. Site description and experimental design

Our research sites are located in Robinsons pasture, western Newfoundland, 100 km southwest of Conner Brook, Newfoundland and Labrador (48° 15.842’N, 58° 39.91’W). It is an oceanic temperate climate with an annual rainfall of 1340 mm and yearly average temperatures of 5°C, average January and July temperature of −9 to −2 °C and 13 to 20 °C respectively (1981–2010) (data from the nearest weather station in Stephenville, ~50 km away from our site). Our site is a peatland complex, comprising of a discontinued pasture, drained peatlands, and natural peatlands. The discontinued pasture was converted from drained peatland 35 years ago, and was abandoned after 10 years of active pasture. It is composed of patches of different dominant species, including reed canary grass (Phalaris arundinacea) dominated patches, various lower herbaceous and graminoid species (Carex spp., Ranunculus acris, Ranunculus repens, Hieracium sp.) dominated patches, and clumps of low shrubs overtopped by the tall grass, including sweet gale (Myrica gale), labrador tea (Rhododendron groenlandicum), mountain fly honeysuckle (Lonicera villosa), rhodora (Rhododendron canadense), and chokeberry (Photinia sp.), with a serious decline of ericaceous shrubs, such as huckleberries (Gaylussacia spp.), several species of lichens (Cladina spp.).
are interspersed with a variety of other shrubs \((R.\ groenlandicum)\) and herbs \((Trichophorum\ cespitosum)\) typical of this type of peatland on the island of Newfoundland. The natural peatlands are wetter than the drained peatlands and include some wet depressions and peatland pools (permanently inundated with about 40–60 cm of standing water depth, from about 10–200 m² in area). The same \(Sphagnum\) moss covers the drier hummocks and many of the same ericaceous shrubs and herbs are also seen on the hummocks and hollows, but with more lush and vigorous growth. Microtopography, comprising of hummocks and hollows (dominated by sedges, with saturated surface peat as a result of the high water table level), exists in the natural peatlands and drained peatlands, but it disappeared in the discontinued pasture peatlands.

In the discontinued pasture, three plots were established, and in each plot four subplots were established to cover four communities, each of which has its dominated species, such as reed canary grass dominated, lower herbaceous and graminoid dominated, sweet gale and labrador tea dominated. One drainage ditch subplot was also established in each plot. Three plots were also established in the drained peatlands, and in each plot three subplots were established to cover one hummock, hollow, and drainage ditch. In the natural peatlands, three plots were set up, and in each plot three subplots were set up to cover one hummock, hollow, and pool.

2.2. Measurement of \(\text{CO}_2\) and \(\text{CH}_4\) fluxes

Boardwalks were constructed to prevent any disturbance to peat gas storage and emission during our measurements and to prevent any damage to the vegetation when regularly visiting the site. The PVC (polyvinyl chloride polymer) collars (26 cm in inner diameter) were permanently inserted into the peat to a depth of 10–15 cm of each subplot in early May, 2013 before the start of our measurements. The upper part of the collars had a groove for the water seal needed for the chamber measurements. Adjacent to each of the collars, perforated ABS (acrylonitrile butadiene styrene) pipes with sealed bottoms were inserted into the peat to measure water table depth. One permanent floating chamber frame with four ABS pipes was established in each pool, where a collar was not employed due to the self-seal characteristic of water. Our measurements were conducted biweekly or monthly from May to October in 2013.

\(\text{CH}_4\) emissions and \(\text{CO}_2\) exchange rates of each subplot were measured by an Ultra-Portable Greenhouse Gas Analyzer (Los Gatos Research, CA, USA) connected to a transparent chamber (made by a clear acrylic tube, which allows ~90% light transmission) or an opaque chamber (made by PVC tube covered by aluminum foil). All the measurements were made between 10:00 and 16:00 of the day. Both chambers were 50 cm in height and 26.3 cm in diameter. Air from the chambers passed through 4 m of tubing with an internal diameter of 3 mm to the analytical box. After the non-destructive analysis, it went back to the chambers. Concentrations of \(\text{CH}_4\), \(\text{H}_2\text{O}\), and \(\text{CO}_2\) as well as the air temperature inside the chambers were recorded. There was a battery-operated fan in the chambers to help mix the air while doing the measurement. The chambers were equipped with a capillary tube to retain atmospheric pressure inside the chambers when sampling.

The gas concentration data were collected at 1 Hz rate and the data acquisition lasted for three minutes for both chambers. There was one to two minutes for the equilibrium between the opaque and transparent chamber measurements. We randomly chose either the transparent or the opaque chamber measurement as the first measurement for each subplot. All fluxes were adjusted for field sampling temperature, headspace volume, and chamber area (Holland et al. 1999), and calculated from the slope of concentration change in the closed chamber (Mastepanov et al. 2008). To remove the influence of increasing \(\text{H}_2\text{O}\) in the chamber, the dry mixing ratio of \(\text{CH}_4\) was calculated before calculating the slope of concentration change. The net ecosystem \(\text{CO}_2\) exchange (NEE) and methane emission rate with light (CH4 Transparent) were obtained by the transparent chamber measurements, and the total release of \(\text{CO}_2\) (R\_ECO) and methane emission rate without light (CH4 Opaque) were obtained by the opaque chamber measurements. Soil temperatures were measured near the collars with a temperature probe at the depths of 5 cm and 20 cm when the gas flux measurement was taken. The water table was measured from the perforated pipes with a ruler. Soil moisture at 0–5 cm was measured with a GS3 probe connected to a ProCheck reader (Decagon Devices).

2.3. Gross photosynthesis rate and the difference in \(\text{CH}_4\) emission between the opaque and transparent chambers

Negative NEE values were used when the \(\text{CO}_2\) fixation by the vegetation exceeded the total respiration of the vegetation and the soil. With this approach, respiration had positive values. Similarly, the \(\text{CH}_4\) emissions were positive, and an uptake from the atmosphere to the soil had negative values. The gross photosynthesis (\(P_G\)) is the result of subtracting R\_ECO from NEE, i.e., \(P_G = \text{NEE} - \text{R\_ECO}\). The R\_ECO was the sum of \(\text{CO}_2\) produced by plant dark respiration, and by respiration of microbes and soil fauna (Nykanen et al. 2003). We defined the artificial bias in the \(\text{CH}_4\) emission rate of the transparent chamber compared with the opaque chamber as the difference in \(\text{CH}_4\) fluxes obtained by the opaque versus the transparent chamber, i.e., \(\text{CH}_4\) Diff = \(\text{CH}_4\) Opaque − \(\text{CH}_4\) Transparent. The accumulated \(\text{CH}_4\) emissions across the growing season were simply calculated by the integration on the emission rate and the growing season period.

2.4. Data analysis

Repeated measures of GLMs (generalized linear model) were used to evaluate the effects of the chamber (opaque versus transparent) on \(\text{CH}_4\) flux, air temperature inside the chamber across the growing season. Linear regressions were conducted to investigate the correlations between the \(P_G\) and \(\text{CH}_4\) Diff rate, the \(\text{CO}_2\) and \(\text{CH}_4\) flux, and to examine the correlations between soil water content, water table depth, and the \(\text{CH}_4\) emission rate. Data analysis was conducted by IBM SPSS 20.
3. Results

Significantly higher CH$_4$ fluxes were measured with the opaque chambers compared to the transparent ones at the hummocks of both natural and drained peatlands (figure 1). At the hummocks of drained peatlands, the opaque chambers estimated a net emission of 0.58 ± 0.16 (SE) g CH$_4$ m$^{-2}$ across the growing season, while the transparent chambers showed a net emission of 0.24 ± 0.10 g CH$_4$ m$^{-2}$ (table 1). At the hummocks of the natural peatlands, the opaque chambers estimated 0.78 ± 0.23 g CH$_4$ m$^{-2}$, which was a 3.25 times higher methane emission compared with the transparent chambers (0.24 ± 0.07 g m$^{-2}$) across the growing season (table 1). No significant difference in CH$_4$ fluxes between the opaque and transparent chambers was found for other sites (figure 1 and table 1).

We did not find any significant difference in air temperature between the transparent and opaque chambers during the three minutes of measurement period ($P > 0.05$) across the growing season (figure 5). Significantly positive relationships between $P_G$ and the difference in CH$_4$ obtained between the opaque versus transparent chambers were found at the hummocks of both natural and drained peatlands (figures 2(a), (b)). The $P_G$ accounted for approximately 44–47% seasonal variation in ‘artificial bias’ between opaque versus transparent chambers (figures 2(a), (b)). No correlation was found between the difference in air temperature and CH$_4$ flux obtained by opaque versus transparent chambers (figures 2(c), (d)). Significantly negative correlations between NEE and CH$_4$ Transparent (figures 3(a), (c)), while positive correlations between $R_{ECO}$ and CH$_4$ Opaque (figures 3(b), (d)), were found at hummocks for both drained and natural peatlands. Both soil

![Figure 1. Emission patterns of the CH$_4$ fluxes estimated with the opaque and transparent chambers in different sites, error bars denote standard errors of the mean (n = 3). a The $P$ values are the result of ANOVA analysis.](image-url)
moisture and water table depth accounted for the spatial variations of the CH$_4$ fluxes among sites across the growing season (table 2).

4. Discussion

Significantly higher methane fluxes were found by the opaque chambers compared with the transparent chambers at the hummocks in both the drained and the natural peatlands (figure 1, table 1). However, no significant difference was found in CH$_4$ fluxes between the transparent and opaque chambers at other subplots. Livingston and Hutchinson (1995) recommended a minimization of the headspace heating as a precautionary measure against the unknown bias because the temperature in the chamber headspace may increase significantly during the closed chamber measurements at high irradiances (Günther et al 2013). However, we did not find any significant difference in the air temperature between the chambers (figure 5), because we only closed the chambers for three minutes during our measurements. This evidence makes us speculate that any difference in CH$_4$ emission rate between the opaque and transparent chambers, if detected, was not attributed to the temperature difference. No correlation between the difference in air temperature and the difference in CH$_4$ flux obtained by the opaque versus transparent chambers (CH$_4$ Diff.) at the hummocks in drained (a) and natural (b) peatlands. Relationships between air temperature difference ($T_{\text{Diff}} = T_{\text{Transparent}} - T_{\text{Opaque}}$) inside the chamber and the CH$_4$ Diff. at the hummocks in drained (c) and natural (d) peatlands.

Table 1. Estimated growing season (May–October 2013) CH$_4$ emissions with the transparent and opaque chambers.

| Types                  | Transparent chamber (g CH$_4$ m$^{-2}$) | Opaque chamber (g CH$_4$ m$^{-2}$) |
|------------------------|-----------------------------------------|------------------------------------|
| Natural peatlands      | ---                                     | ---                                |
| Hollows                | 1.93 (1.32)                             | 2.51 (1.95)                        |
| Hummocks               | 0.24 (0.07)                             | 0.78 (0.23)$^a$                    |
| Pools                  | 0.63 (0.19)                             | 1.43 (0.98)                        |
| Drained peatlands      | ---                                     | ---                                |
| Hollows                | 1.67 (0.66)                             | 1.36 (0.51)                        |
| Hummocks               | 0.24 (0.10)                             | 0.58 (0.16)$^b$                    |
| Ditches                | 2.95 (2.31)                             | 18.48 (9.23)                       |
| Discontinued pasture   | ---                                     | ---                                |
| Reed canary grass      | 0.46 (0.13)                             | 0.26 (0.06)                        |
| Lower herbaceous and graminoid | 0.56 (0.25) | 0.66 (0.25) |
| Shrub a (Labrador tea) | 1.40 (0.84)                             | 1.13 (0.83)                        |
| Shrub b (Sweet gale)   | 0.36 (0.24)                             | 0.47 (0.24)                        |
| Ditches                | 7.41 (4.17)                             | 9.03 (6.95)                        |

$^a$ Denote paired $t$-test (2-tailed) $P=0.08$.

$^b$ Denote paired $t$-test (2-tailed) $P=0.047$. 

5 Environ. Res. Lett. 9 (2014) 105005 J Luan and J Wu
transparent chambers (figures 2(c), (d)) confirmed our speculation. However, our regression analysis, where the gross photosynthesis rate positively correlated with the difference in CH$_4$ flux obtained by the opaque versus transparent chambers at the hummocks in both the drained and the natural peatlands (figures 2(a), (b)), implied that the photosynthesis process can explain the ‘artificial bias’ (the opaque versus transparent, explained 44–47% of this ‘artificial bias’, figures 2(a), (b)) in CH$_4$ estimation based on the enclosure method on the hummocks. In our study sites, water table depths were lower than 10 cm below ground (excluding ditches and pools) (figure 4). We can consider the 0–10 cm depth of peat as the potential oxidation layer because the aerobic layer is defined by the water table position (Bubier & Moore 1994, Frolking et al 2002). With water tables being at or near the surface, the Sphagnum moss layer represents most of the aerobic environment where CH$_4$ oxidation can occur (Basiliko et al 2004), particularly at the hummocks, where CH$_4$ has to transport through it before being released into the atmosphere. Thus, oxygen derived from photosynthesis can be more important

Figure 3. Relationships between the net ecosystem CO$_2$ exchange (NEE, negative value means net uptake of CO$_2$) and the methane flux obtained by the transparent chamber (CH$_4$ Transparent) at the hummocks in drained (a) and natural (c) peatlands. Relationships between ecosystem respiration ($R_{ECO}$) and the methane flux obtained by the opaque chamber (CH$_4$ Opaque) at the hummocks in drained (b) and natural (d) peatlands.

Table 2. Correlations between the CH$_4$ emission rate (estimated with the transparent chamber) and soil moisture at 0–5 cm, or water table depth throughout our sites during each measurement campaign.

| Date            | Soil moisture of 0–5 cm | Water table depth |
|-----------------|-------------------------|-------------------|
|                 | R          | P value | n | R          | P value | n |
| 27 May          | 0.57       | 0.006   | 22 | 0.46       | 0.021   | 25 |
| 10 June         | 0.45       | 0.03    | 23 | 0.44       | 0.021   | 26 |
| 24 June         | 0.513      | 0.006   | 27 | 0.637      | <0.001  | 27 |
| 9 July          | 0.59       | 0.002   | 25 | 0.63       | 0.001   | 25 |
| 12 August       | N          | N       | N | 0.56       | 0.002   | 29 |
| 20 August       | N          | N       | N | 0.56       | 0.016   | 18 |
| 6 September     | 0.509      | 0.005   | 29 | 0.474      | 0.009   | 29 |
| 11 October      | 0.553      | 0.002   | 29 | 0.399      | 0.032   | 29 |

* Data from the pools and ditches of drained peatlands were excluded in our analysis because soil moisture was not determined. N: not determined (soil moisture sensor failed).
for CH4 oxidation in this layer. On the other hand, the symbiotic relationship between methanotrophs and Sphagnum mosses, which was reported to facilitate recycling of the oxygen produced from photosynthesis and CH4 derived from decaying plants (Raghoebarsing et al 2005, Kip et al 2010), might also be contributing to the connection between photosynthesis and ‘artificial bias’. The significantly negative relationships between NEE and CH4 Transparent (figures 3(a), (c)), as well as the significantly positive relationships between R_ECO and CH4 Opaque (figures 3(b), (d)), both imply the connections between CO2 and CH4 fluxes, and partly support our speculation on the connection between photosynthesis process and the CH4 oxidation. Apparently, the mechanisms underlying the photosynthesis process and the ‘artificial bias’ of CH4 flux estimation, however, need to be further elucidated through a process-based research, such as the stable isotope (e.g., 13C) labeling.

The significant differences in CH4 emission rate between the transparent and opaque chambers were only found at the hummocks rather than the hollows. One of the reasons might be that the high moisture content in the surface soil at the hollows, as a result of high water table levels, significantly reduces the ability of the oxidation potential. Larmola et al (2009) found that water level was the key environmental factor regulating methanotrophy in Sphagnum moss layer. Therefore, the CH4 will bypass the oxidation process and become released directly to the atmosphere, which leads to no significant differences in the CH4 emission between the transparent and opaque chambers. Another reason might be the dominance of sedges at the hollows in our study sites, because sedges can help emit more CH4 (Dorodnikov et al 2011, Olefeldt et al 2013), especially during the presence of light when the stomata are open. It was also reported that stomata significantly controlled methane release from wetlands (Morrissette et al 1993). Thus, CH4 emission facilitated by plants offset the lowered CH4 emission due to oxidation and did not result in significantly lower CH4 flux measured by transparent chambers at hollows. No significant difference here in the pasture might be simply attributed to the serious decline of Sphagnum moss in these sites. A closed chamber method has a number of well-known limitations and artifacts in estimating the CH4 flux (Morrissette et al 1993, Frolking & Crill 1994, Chanton & Whiting 1995). Our results suggest that the artificial properties of a chamber (transparency/opacity) can be vitally important in some cases (i.e., hummocks), but negligible in others, even during a significantly shorter closure period (three minutes).

We found that not only the water table depths, but also the soil moisture of the 0–5 cm, showed a significant correlation with the CH4 emission rates across our sites (table 2). This result indicates that the potential oxidation layer plays an important role in regulating the CH4 transportation in our sites. Our results might be able to help explain the recent study that reported greater nighttime CH4 emissions than those recorded during the daytime in a fen with a hummock-hollow microtopography (Godwin et al 2013). Clearly, our results indicate that the opaque chambers estimated a higher CH4 flux than the transparent ones at the hummocks, which is a typical setting of microtopography in boreal peatlands (Bubier et al 1993). In contrast, Günther et al (2013) found that the fluxes measured by the transparent chamber almost doubled those measured by the opaque chambers in the convective transporting Phragmites stand as a result of internal convective gas transport responding quickly to changes in irradiation. Shrubs and sedges apparently play a significantly different role than Sphagnum moss in regulating the CH4 emissions under the ambient light. Our findings suggest that the difference in the chamber method will possibly give us significantly different CH4 flux, and thus increase the uncertainties in the CH4 flux estimation. We propose that the differences in the microtopography (Wu et al 2011) and the corresponding vegetation need to be

Figure 4. Seasonal patterns of water table depth at different sites.
considered when modeling the methane transportation in a peatland. Our results also suggest that the surface soil water content plays an important role in regulating the methane emissions in these peatlands, and therefore not only water table depth but also the surface soil moisture needs to be monitored to assist in interpreting the CH$_4$ flux. The magnitude of our fluxes is consistent with what is presented in the literature (Waddington & Roulet 1996, Bubier et al 2005, Forbrich et al 2011) where the hummocks are at the lower end of the methane flux range, where the hollows and minerotrophic peatlands are the main source of CH$_4$ to the atmosphere at the ecosystem scale. It is critical to address that the larger fluxes measured with the opaque chamber are still relatively low compared to the fluxes from the other microforms in this study (figure 1). Therefore, the variability of CH$_4$ fluxes observed between the two chamber types would not have a significant impact on the ecosystem-scale estimation of the CH$_4$ budget.

Acknowledgements

Special thanks to Dr Henry Mann for his help in vegetation identification. We would like to thank Sarah Scott, Krystal Pye, and Nicholas J Andrews for their help in field sampling. This study was made possible by the following sources of funding: Canada Foundation for Innovation-Leaders Opportunity Fund (CFI-LOF); the Ignite R&D, Leverage R&D of Research & Development Corporation, NL; Agricultural Research Initiative of NL; Humber River Basin Research

Figure 5. Seasonal patterns of the air temperatures (°C) inside the opaque and transparent chambers in different sites; error bars denote standard errors of the mean (n = 3).
References

Altor A E and Mitsch W J 2008 Methane and carbon dioxide dynamics in wetland mesocosms: effects of hydrology and soils Ecol. Appl. 18 1307–20

Basiliko N, Knowles R and Moore T 2004 Roles of moss species and habitat in methane consumption potential in a northern peatland Wetlands 24 178–85

Bastviken D, Tranvik L J, Downing J A, Crill P M and Enrich-Prast A 2011 Freshwater methane emissions offset the continental carbon sink Science 331 50

Bergman I, Svensson B H and Nilsson M 1998 Regulation of methane emissions from northern wetlands, northern Ontario, Canada Can. J. Bot. 76 1056–63

Bubier J L and Moore T R 1994 An ecological perspective on methane emissions from wetlands: biochemical, microbial, and modeling perspectives from local to global scales Glob. Change Biol. 19 1325–46

Bubier J, Costello A, Moore T R, Roulet N T and Savage K 1993 Microtopography and methane flux in boreal peatlands, northern Ontario, Canada Can. J. Bot. 71 1056–63

Bubier J, Mose C, Savage K and Crill P 2005 A comparison of methane flux in a boreal landscape between a dry and a wet year Glob. Biogeochem. Cycles 19 GB1023

Bubier J L and Moore T R 1994 An ecological perspective on methane emissions from northern wetlands Trends Ecol. Evol. 9 460–4

Cao G, Xu X, Long R, Wang Q, Wang C, Du Y and Zhao X 2008 Methane emissions by alpine plant communities in the Qinghai-Tibet Plateau Biol. Lett. 4 681–4

Chanton J P and Whiting G J 1995 Trace gas exchange in freshwater and coastal marine environments: ebullition and transport by plants Biogenic Trace Gases: Measuring Emissions From Soil and Water ed P A Matson and R C Harriss (Oxford: Blackwell) pp 98–125

Christiansen J, Korhonen J J, Juszczyk R, Giebels M and Pihlatie M 2011 Assessing the effects of chamber placement, manual sampling and headspace mixing on CH4 fluxes in a laboratory experiment Plant Soil 343 171–85

Davidson E A, Nepstad D C, Ishida F Y and Brando P M 2008 Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest Glob. Change Biol. 14 2582–90

Dlugokencky E J et al 2009 Observational constraints on recent increases in the atmospheric CH4 burden Geophys. Res. Lett. 36 L18803

Dlugokencky E J, Nisbet E G, Fisher R and Lowry D 2011 Global atmospheric methane: budget, changes and dangers Phil. Trans. R. Soc. A 369 2058–72

Dorodnikov M, Knorr K H, Kuzyakov Y and Wilming K 2011 Plant-mediated CH4 transport and contribution of photosynthates to methanogenesis at a boreal mire: a 13C pulse-labeling study Biogeochemistry 8 2365–75

Edwards G C, Dias G M, Thurtell G W, Kidd G E, Roulet N T, Kelly C A, Rudd J W M, Moore A and Halfenny-Mitchell L 2001 Methane fluxes from a wetland using the flux-gradient technique the measurement of methane flux from a natural wetland pond and adjacent vegetated wetlands using a TDL-based flux-gradient technique Water Air Soil Pollut.: Focus 1 447–54

Forbrich I, Kutzbach L, Wille C, Becker T, Wu J and Wilming K 2011 Cross-evaluation of measurements of peatland methane emissions on microform and ecosystem scales using high-resolution landcover classification and source weight modelling Agric. Forest Meteorol. 151 864–74

Frolking S and Crill P 1994 Climate controls on temporal variability of methane flux from a poor fen in southeastern New Hampshire: measurement and modeling Glob. Biogeochem. Cycles 8 385–97

Frolking S, Roulet N T, Moore T R, Lafleur P M, Bubier J L and Crill P M 2002 Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada Glob. Biogeochem. Cycles 16 1–4

Godwin C M, McNamara P J and Markfort C D 2013 Evening methane emission pulses from a boreal wetland correspond to convective mixing in hollows J. Geophys. Res.: Biogeosci. 118 994–1005

Graetzl M, Thampi K R and Kiwi J 1989 Methane oxidation at room temperature and atmospheric pressure activated by light via polytungstate dispersed on titania J. Phys. Chem. 93 4128–32

Gucklhorn A, Flessa H and Prenzel J 2009 Controls of temporal and spatial variability of methane uptake in soils of a temperate deciduous forest with different abundance of European beech (Fagus sylvatica L.) Soil Biol. Biochem. 41 1659–67

Günther A, Jurasinski G, Huth V and Glatzel S 2013 Opaque closed chambers underestimate methane fluxes of Phragmites australis (Cav.) trim. ex Steud Environ. Monit. Assess. 1–8

Hirota M, Tang Y, Hu Q, Hirata S, Kato T, Mo W, Cao G and Mariko S 2004 Methane emissions from different vegetation zones in a Qinghai-Tibetan Plateau wetland soil Biol. Biochem. 36 737–48

Holland E A, Robertson G P, Greenberg J, Groffman P M, Boone R D and Gosz J R 1999 Soil CO2, N2O, and CH4 exchange Standard Soil Methods for Long-Term Ecological Research (Oxford: Oxford University Press) pp 185–201

IPCC 2013 Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change ed T F Stocker, D Qin, G-K Plattner, M Tignor, S K Allen, J Boschung, A Nauels, Y Xia, V Bex and P M Midgley (Cambridge: Cambridge University Press) p 1535

Kankaala P and Bergström I 2004 Emission and oxidation of methane in equisetum fluviatile stands growing on organic sediment and sand bottoms Biogeochemistry 67 21–37

King G M 1990 Regulation by light of methane emissions from a wetland Nature 345 513–5

Kip N, van Winden J F, Pan Y, Bodrossy L, Reichart G-J, Smolders A J P, Jetten M S M, Damste J S S and Op den Camp H J M 2010 Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems Nature Geosci. 3 617–21

Kroon P S, Hensen A, Jonker H J J, Ouweloos H G, Vermeulen A T and Bosveld F C 2010 Uncertainties in eddy covariance flux measurements assessed from CH4 and NOx observations Agric. Forest Meteorol. 150 806–16

Larmola T, Tuittila E-S, Tiirola M, Nykanen H, Martikainen P J, Yrjälä K, Tuomivirta T and Fritze H 2009 The role of Sphagnum mosses in the methane cycling of a boreal mire Ecology 91 2356–65

Livingston G P and Hutchinson G 1995 Enclosure-based measurement of trace gas exchange: applications and sources of error Biogenic Trace Gases: Measuring Emissions From Soil and Water ed P A Matson and R C Harriss (Oxford: Blackwell) pp 98–125

Mastepanov M, Sigsgaard C, Dlugokencky E J, Houweling S, Strom L, Tamstorf M P and Christensen T R 2008 Large tundra methane burst during onset of freezing Nature 456 628–30

Environ. Res. Lett. 9 (2014) 100505 J Luan & J Wu
Moore T R and Roulet N T 1991 A comparison of dynamic and static chambers for methane emission measurements from subarctic fens Atmos.-Ocean 29 102–9
Morrissey L A, Zobel D B and Livingston G P 1993 Significance of stomatal control on methane release from Carex-dominated wetlands Chemosphere 26 339–55
Neef L, van Weele M and van Velthoven P 2010 Optimal estimation of the present-day global methane budget Glob. Biogeochem. Cycles 24 GB4024
Nisbet R E R et al 2009 Emission of methane from plants Proc. R. Soc. B 276 1347–54
Nykänen H, Heikkinen J E P, Pirinen L, Tiilikainen K and Martikainen P J 2003 Annual CO2 exchange and CH4 fluxes on a subarctic palsa mire during climatically different years Glob. Biogeochem. Cycles 17 1018
Olefeldt D, Turetsky M R, Crill P M and McGuire A D 2013 Environmental and physical controls on northern terrestrial methane emissions across permafrost zones Glob. Change Biol. 19 589–603
Raghoebarsing A A et al 2005 Methanotrophic symbionts provide carbon for photosynthesis in peat bogs Nature 436 1153–6
Rinne J, Riutta T, Pihlatie M, Aurela M, Haapanala S, Tuovinen J-P, Tuittila E-S and Vesala T 2007 Annual cycle of methane emission from a boreal fen measured by the eddy covariance technique Tellus B 59 449–57
Sabrekov A F, Runkle B R K, Glagolev M V, Kleptsova I E and Maksyutov S S 2014 Seasonal variability as a source of uncertainty in the West Siberian regional CH4 flux upscaling Environ. Res. Lett. 9 045008
Segers R 1998 Methane production and methane consumption: a review of processes underlying wetland methane fluxes Biogeochemistry 41 23–51
Shimazaki K.-I., Doi M, Assmann S M and Kinoshita T 2007 Light regulation of stomatal movement Annu. Rev. Plant Biol. 58 219–47
Silvola J, Saarnio S, Foot J, Sundh I, Greenup A, Heijmans M, Ekberg A, Mitchell E and van Breemen N 2003 Effects of elevated CO2 and N deposition on CH4 emissions from European mires Glob. Biogeochem. Cycles 17 1068
Strack M and Zebabdi Y C A 2013 Annual carbon balance of a peatland 10 yr following restoration Biogeosciences 10 2885–96
Waddington J M and Roulet N T 1996 Atmosphere-wetland carbon exchanges: Scale dependency of CO2 and CH4 exchange on the developmental topography of a peatland Glob. Biogeochem. Cycles 10 233–45
Wang J M, Murphy J G, Geddes J A, Winsborough C L, Basiliko N and Thomas S C 2012 Methane fluxes measured by eddy covariance and static chamber techniques at a temperate forest in central Ontario, Canada Biogeosci. Discuss. 9 17743–74
Wille C, Kutzbach L, Sachs T, Wagner D and Pfeiffer E-M 2008 Methane emission from Siberian arctic polygonal tundra: eddy covariance measurements and modeling Glob. Change Biol. 14 1395–408
Wu J, Roulet N T, Moore T R, Lafleur P and Humphreys E 2011 Dealing with microtopography of an ombrotrophic bog for simulating ecosystem-level CO2 exchanges Ecol. Modelling 222 1038–47