Spatial and Temporal Variations of Carbon Dioxide and Methane Fluxes Measured by Autochambers at the Mer Bleue Bog

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Abstract

The net ecosystem carbon (C) balance and radiative forcing impact of northern peatlands are largely governed by the exchange of carbon dioxide (CO_2) and methane (CH_4) gases with the atmosphere. To predict the effects of perturbations on peatland C exchange, the relationships between gas fluxes and environmental correlates should be established at the plant community and microtopographic level to capture the spatial heterogeneity of peatlands. In this research, I use an autochamber system to quantify CO_2 and CH_4 fluxes at a sub-daily time scale among three vascular plant communities at the Mer Bleue ombrotrophic bog, and examine how gas exchange is related to environmental and biotic factors across time and space.

In highly turbulent conditions, CH_4 and nighttime CO_2 effluxes measured by autochambers with a short deployment period were underestimated by 9-57% and 13-21%, respectively, due to wind flushing the dry and porous surface peat as shown by a reduction in pore space CO_2 concentration gradient. In contrast, CH_4 and nighttime CO_2 effluxes measured in calm conditions were overestimated by ~100%. These problems were resolved by extending the deployment period and discarding data in the initial 13 minutes when calculating fluxes. *Eriophorum* and *Maianthemum/Ledum* communities contributed to over half of the total CH_4 emissions from the bog, although they covered only 30% of the total area. The temporal variability of CH_4 flux was correlated ($r > 0.4$) with peat temperature, only when water table was less than 20, 30, and 40 cm below the peat surface for *Maianthemum/Ledum*, *Chamaedaphne*, and *Eriophorum* communities, respectively. Significant differences in the overall photosynthesis and respiration models existed among all three plant communities. Maximum net ecosystem CO_2 exchange explained well the variations in seasonal mean CH_4 flux among *Eriophorum* and lawn sites, but the relationship was weakened after including hummock sites. Cross-correlation results show a lag of 9-12 hours of CH_4 flux behind photosynthetic activity for the *Eriophorum* community, but a much longer

lag of 18-26 days for the *Maianthemum/Ledum* community. My findings highlight the importance of considering separately the functionally different plant communities dominated by distinct growth forms in the modelling of C gas exchange in ombrotrophic bogs.

Résumé

L'équilibre du carbone (C) net de l'écosystème et l'impact du forçage radiatif des tourbières dans le Nord sont largement régis par les échanges de dioxyde de carbone (CO_2) et du méthane (CH_4) entre l'atmosphère. Pour prédire les effets des perturbations sur les échanges C à la tourbière, les relations entre les flux de gaz et les corrélats environnementaux devraient être établies au niveau de la communauté végétale et microtopographique afin de saisir l'hétérogénéité spatiale de la tourbière. Dans cette recherche, un système de chambre de automatique est utilisé pour quantifier les flux de CO_2 et de CH_4 à une échelle de temps sous-quotidienne entre les trois communautés de plantes vasculaires à la tourbière ombrotrophe Mer Bleue. Les liens entre les échanges gazeux et les facteurs environnementaux et biotiques sont examinés dans le temps et l'espace.

Dans des conditions très turbulentes, l'écoulement du CH_4 et celui du CO_2 de la nuit mesurés par les chambres automatiques avec une courte durée de déploiement ont été sous-estimés par 9-57% et 13-21% respectivement, en raison du vent soufflant sur la surface de la tourbe sèche et poreuse tel que témoigné par une réduction dans le gradient de concentration du CO_2 dans l'espace poreux. En revanche, l'écoulement du CH_4 et celui du CO_2 de la nuit mesurés dans les conditions calmes ont été surestimées par environ 100%. Ces problèmes ont été résolus par allonger la durée de déploiement et par supprimer les données dans les 13 premières minutes lors du calcul des flux. Les communautés *Eriophorum* et *Maianthemum/Ledum* ont contribué à plus de la moitié des émissions totales du CH_4 provenant de la tourbière, bien qu'ils ne couvrent que 30% de la superficie totale. La variabilité temporelle des flux du CH_4 est corrélée ($r > 0.4$) avec la température de la tourbe, seulement si le niveau hydrostatique est inférieur à 20, 30 et 40 centimètres sous la surface de la tourbe respectivement pour les communautés *Maianthemum/Ledum, Chamaedaphne* et *Eriophorum*. Il existe des différences significatives entre les modèles globaux de photosynthèse et de respiration pour les trois communautés végétales. L'échange maximal net du CO_2

dans l'écosystème explique bien les variations dans les moyennes saisonnières du flux CH_4 pour l'*Eriophorum* et les sites de pelouse. La relation est plus faible si les sites buttes sont inclus. Les résultats de la corrélation croisée montrent un décalage de 9 à 12 heures entre le flux du CH_4 et l'activité photosynthétique pour la communauté *Eriophorum*, mais un décalage beaucoup plus long, de 18 à 26 jours, pour la communauté *Maianthemum/Ledum*. Mes résultats soulignent l'importance de considérer séparément les communautés de plantes, qui ont des fonctionnalités différentes et sont dominées par des formes de croissance distinctes, dans la modélisation de l'échange du gaz carbonique (C) dans les tourbières ombrotrophes.

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Contribution of Authors

This thesis contains four chapters (Chapters 3 to 6) that are written as manuscripts in a format suitable for publication in scientific journals. For all four manuscripts, I developed the research questions and research design, collected the data, did the analysis and interpretation of results, and wrote the manuscripts as lead author. Nigel T. Roulet and Tim R. Moore, both as my Ph.D. co-supervisors, provided advice on the development of my research questions, research planning, and data analysis, and have read and provided comments and criticisms on my manuscripts. The roles of other co-authors are described below:

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Chapter 1
Introduction

1.1 Research Context

Although constituting only less than 3% of the global total land area (~3.4 x 10^6 km^2) (Rydin and Jeglum, 2006), northern peatlands play an important role in the global carbon (C) cycle. Peatlands are typically net sink of carbon dioxide (CO_2), owing to the dominance of low temperature, anoxic conditions, small microbial populations and high refractory content of plant litter that contribute to low decomposition rates (Moore and Basiliko, 2006). The boreal and subarctic peatlands store 270 to 370 Pg C in peat (Turunen *et al.*, 2002), which is equivalent to 18-25% of the total C stored globally in the top 1 m of soils (Jobbágy and Jackson, 2000). However, recent studies suggest that the C stored in northern soils is even higher if peatlands containing permafrost and at higher latitudes are included (McGuire *et al.*, 2009; Tarnocai *et al.*, 2009). Meanwhile, natural and anthropogenic disturbances could increase the release of C stored in peat as CO_2 gas and weaken the C sink function of northern peatlands (Tarnocai, 2006; Turetsky *et al.*, 2002). In addition, northern peatlands are one of the world's major natural sources of methane (CH_4) gas because of the presence of anaerobic conditions (Spahni *et al.*, 2011; Wuebbles and Hayhoe, 2002). Assessing the balance between CO_2 and CH_4 exchange is essential to determine the carbon sequestration ability as well as the net atmospheric radiative forcing impact of northern peatlands (Frolking *et al.*, 2006).

The net ecosystem exchange of CO_2 (NEE) in peatlands comprises two main processes that operate in opposite directions, namely gross primary production (GPP) where plants fix atmospheric CO_2 through photosynthesis, and ecosystem respiration (ER) where vegetation and microbes release CO_2 into the atmosphere (Chapin *et al.*, 2006). On the other hand, net CH_4 emissions in northern peatlands are governed by the magnitude of CH_4 production, oxidation, and transport processes (Bubier and Moore, 1994). These biogeochemical

processes are controlled to varying extents by environmental and biotic factors including, for example, light, temperature, water table, leaf area, and plant species composition (Dorodnikov *et al.*, 2011; Frolking *et al.*, 1998; Lund *et al.*, 2010; Moore *et al.*, 2011). Given the spatial heterogeneity of northern peatlands, establishing quantitative relationships between gas fluxes and their controlling variables at the plant community level is needed for accurately predicting the effects of perturbations on peatland CO_2 and CH_4 exchange. However, there is currently a limited understanding of the interactions between numerous factors affecting the overall peatland-atmosphere CO_2 and CH_4 exchange, the consistency of the relationships between fluxes and environmental variables across time, as well as the functional similarities or differences among peatland vascular plant communities with respect to the response of gas exchange to changing environmental variables.

Micrometeorological techniques can be used to measure gas fluxes at the ecosystem level quasi-continuously over time, but they do not shed light at the process level on how gas exchanges from vegetation communities react to environmental change (Griffis *et al.*, 2000). While manual chambers can be deployed to measure community level fluxes, their capability of quantifying temporal changes in the flux-environment relationship is limited by infrequent sampling. In contrast, automatic chambers (or autochambers) have the advantage of being able to collect high temporal resolution flux data from different plant communities. Recently, autochambers have been used to quantify CO_2 exchange in two minerotrophic fens (Bubier *et al.*, 2003b; Cai *et al.*, 2010), and CH_4 emissions in temperate and boreal fens (Goodrich *et al.*, 2011; Kettunen *et al.*, 2000), as well as an Arctic tundra (Mastepanov *et al.*, 2008). Yet, no attempts have thus far been made to investigate community level CO_2 and CH_4 fluxes in an ombrotrophic bog using high frequency data from autochambers.

1.2 Research Objectives

In view of the above knowledge gaps, the overarching objectives of my

doctoral research are to quantify CO_2 and CH_4 fluxes at a sub-daily scale among three vascular plant communities in an ombrotrophic bog, and examine the relationships between gas fluxes and environmental correlates across time and space. Since no prior studies have deployed autochambers in a dry bog with porous substrate, I further investigate a methodological issue regarding the use of autochambers for flux measurements in this unique ecosystem. The specific objectives of my research are to:

1) Examine the effects of atmospheric turbulence and chamber deployment period on CO_2 and CH_4 fluxes measured by autochambers in an ombrotrophic bog;
2) Determine the temporal variability, as well as the environmental and biotic controls of CH_4 flux over the season in three vascular plant communities in a bog;
3) Investigate the temporal controls of CO_2 exchange, and compare the photosynthetic and respiratory responses to changing environmental and biotic conditions among three vascular plant communities; and
4) Assess the linkage between CO_2 and CH_4 exchange across space, and the correlation and time lag between photosynthesis and CH_4 flux at different temporal scales in three vascular plant communities.

This research was conducted at the Mer Bleue ombrotrophic raised bog in eastern Canada. An autochamber system was established within a 15-m radius area about 50 m south of the eddy covariance tower, with replicate chambers covering three vascular plant communities dominated by different growth forms. Fluxes of CO_2 and CH_4 were measured quasi-continuously from each autochamber every 0.5 to 3 hours during the snow-free period in 2009 and 2010. This bog has one of the longest running records of NEE from eddy covariance measurements in a peatland beginning in 1998 (Roulet *et al.*, 2007). A profile system is also in place to monitor CO_2 concentrations half-hourly at 7 different heights in the air column and 4 depths in the peat profile of a hummock. Manual

chamber measurements had been previously made in this bog to investigate the variability of community level NEE (Bubier *et al.*, 2003a) and CH_4 flux (Moore *et al.*, 2011).

1.3 Thesis Structure

This thesis consists of 7 chapters. Chapter 1 puts my Ph.D. research into the context of peatland biogeochemistry. Chapter 2 provides a comprehensive review of the existing literature on various aspects of carbon cycling in northern peatlands that are pertinent to my Ph.D. work. Chapters 3 to 6 present the main results of my doctoral research, in a series of four individual manuscripts that are accepted or in preparation for publication in peer-reviewed scientific journals. Chapter 3 examines the influence of atmospheric turbulence and chamber deployment period on autochamber CO_2 and CH_4 fluxes and suggests ways to obtain more reliable estimates of net biological gas fluxes in a dry bog. Chapter 4 presents the measured CH_4 fluxes and discusses the relationships between fluxes and environmental correlates over time in three plant communities. Chapter 5 assesses the functional similarities of three vascular plant communities by comparing their photosynthetic and respiratory responses to variations in environmental parameters. Chapter 6 explores the spatial and temporal relationships between CO_2 and CH_4 exchange at the Mer Bleue bog. Chapter 7 then concludes this thesis by summarizing the major findings of my Ph.D. research, highlighting the original contributions to knowledge, and proposing directions for further research based on my results.

Chapter 2
Literature Review

This literature review presents a general overview of the current understanding of carbon cycling in northern peatland ecosystems. It begins with a brief description of the classification and characteristics of northern peatlands. This is followed by a discussion of the role of northern peatlands in the global C cycle, and the importance of CO_2 and CH_4 fluxes in determining the net peatland C balance. I then introduce the commonly used techniques in quantifying gas exchange, and review the biogeochemical processes involved in, as well as the effects of environmental and biotic factors on, C gas exchange in peatlands. Further, I address the spatial and temporal variability of peatland CO_2 and CH_4 fluxes. Lastly, I identify the knowledge gaps regarding C gas exchange in northern peatlands at the plant community level.

2.1 Northern Peatlands

2.1.1 Classification of Northern Peatlands

Peatlands are ecosystems characterized by the accumulation of thick layers (generally > 30 cm) of peat that is partially decomposed plant remains with over 65% organic matter on a dry weight basis (Charman, 2002). The world's peatlands cover an area of 3.99 x 10^6 km^2, with northern peatlands comprising 87-89% (3.46-3.56 x 10^6 km^2) of this global coverage (Joosten and Clarke, 2002; Tarnocai *et al.*, 2009). Boreal and subarctic peatlands are almost entirely found in Russia, Canada, the USA, and Fennoscandia countries (Gorham, 1991). In Canada, peatland covers 12% of the country's land area and hence is an integral component of the overall landscape (Tarnocai, 2006).

Northern peatlands can be broadly classified into two categories, namely bogs and fens, according to their hydrology, acidity, nutrient status, and vegetation composition (Rydin and Jeglum, 2006; Vitt, 2006; Wheeler and Proctor, 2000). Bogs are typically ombrotrophic systems, receiving water inputs

from rain and snow only. They are characterized by strong acidity in surface water (pH < 5.0), extremely low nutrient availability, a relatively deep water table, and the dominance of *Sphagnum* moss and ericaceous shrubs. In contrast, fens are minerotrophic systems that are nourished by surface water and groundwater. They can be further differentiated into poor fens and rich fens depending on their trophic status. Fens in general are highly alkaline (water pH > 6.0), rich in base cations, have water table close to or above the peat surface, and are dominated by sedges, forbs, and brown moss.

2.1.2 Role of Northern Peatlands in the Global Carbon Cycle

Northern peatlands are known to store a considerable amount of C in peat, but the total C stock reported vary among different studies depending on the bulk density, peat depth, peat C concentration, and peatland area used in the estimation (Turunen *et al.*, 2002). Previous studies have estimated a total C stock of 273-455 Pg in northern peatlands (Gorham, 1991; Turunen *et al.*, 2002), with Canadian peatlands contributing to 147 Pg of C (Tarnocai, 2006). The amount of soil C stored in the northern circumpolar permafrost region is estimated to be even higher, in the range of 1672-1850 Pg, when Siberian frozen loess deposits, deep alluvial sediments, and soils in the top 3 m are included (McGuire *et al.*, 2009; Tarnocai *et al.*, 2009). These numbers are substantial considering the amounts of C stored globally in the atmosphere and in the top 3 m of soils are 762 and 2344 Pg, respectively (Denman *et al.*, 2007; Jobbágy and Jackson, 2000).

Northern peatlands have been a persistent net sink of CO_2 for millennia (Frolking and Roulet, 2007). Based on measurements of carbon content in radiocarbon dated peat cores, northern peatlands are reported to have a long-term apparent rate of carbon accumulation of 14-29 g C m^{-2} yr^{-1} (Gorham, 1991; Roulet *et al.*, 2007; Turunen *et al.*, 2002; Vitt *et al.*, 2000), which translates to a global C uptake rate of ~0.1 Pg C yr^{-1}. However, peatland ecosystems can switch rapidly between a net sink and source of C from one year to another as shown by contemporary flux measurements (Roulet *et al.*, 2007). Climate change may also

increase or decrease the C sequestration rate of peatlands depending on peatland type (Moore *et al.*, 1998), but overall the direct impacts of climate change on peatland CO_2 exchange are probably too small to cause a major influence on the global C budget (Frolking *et al.*, 2011). Other disturbances like permafrost thaw, peat harvesting, and energy development can lead to considerable loss of C from peatlands (Roulet, 2000; Schuur *et al.*, 2008). Turetsky *et al.* (2002) estimated a total release of 6.46 Tg C yr^{-1} from western boreal peatlands into the atmosphere owing to fire-dominated disturbances, leading to a weakening of the peatland C sink function.

Natural wetlands are the single largest CH_4 source globally, with estimated annual emissions of 100-231 Tg CH_4 yr^{-1} (Denman *et al.*, 2007). Methane flux from northern peatlands contributes about 30% of the global wetland emissions (Chen and Prinn, 2006), and 5% of the global CH_4 budget (Spahni *et al.*, 2011). Top-down approaches using atmospheric inverse modelling estimate that northern peatlands emit 12-37 Tg of CH_4 gas annually into the atmosphere (Chen and Prinn, 2006; Fung *et al.*, 1991; Mikaloff Fletcher *et al.*, 2004; Spahni *et al.*, 2011). Wetland emissions play a key role in governing the interannual global CH_4 flux anomalies, with boreal wetlands contributing to about 80% of the positive anomaly (Bousquet *et al.*, 2006; Ringeval *et al.*, 2010). Moreover, CH_4 emissions from northern ecosystems can cause strong feedbacks in atmospheric chemistry that substantially enhance climate warming (Isaksen *et al.*, 2011). Quantifying the relative magnitudes of CO_2 uptake and CH_4 emissions in northern peatlands is crucial for assessing their net radiative forcing impacts over time (Frolking and Roulet, 2007; Frolking *et al.*, 2006).

2.2 Carbon Cycling in Northern Peatlands

2.2.1 Net Ecosystem Carbon Balance

The net rate of C accumulation of an ecosystem is equivalent to its net ecosystem carbon balance (NECB), determined as the balance between net biosphere-atmosphere exchange of CO_2, CH_4, carbon monoxide (CO), and

volatile organic C (VOC), in addition to the net lateral transfer of particulate C, dissolved organic and inorganic C (DOC and DIC, respectively) (Chapin *et al.*, 2006).

Only a few studies have measured all or most of the C flux components for quantifying the NECB of northern peatlands. Based on 6-year measurements at the Mer Bleue ombrotrophic bog, Roulet *et al.* (2007) found mean NEE-C (negative denotes an uptake), CH_4-C release, and net DOC export of -40.2, 3.7 and 14.9 g m^{-2} yr^{-1}, respectively. In addition, evasion of CO_2 and CH_4 from beaver ponds and streams contributes to the loss of another ~3.1-4.0 g C m^{-2} yr^{-1} from this bog (Billett and Moore, 2008). In a Swedish nutrient-poor fen, Nilsson *et al.* (2008) reported annual net CO_2 uptake rates of 48-55 g C m^{-2} yr^{-1}, of which 16-29% was lost through CH_4 emissions and another 31-37% exported in runoff mainly as TOC and DIC. In an Atlantic blanket bog, CH_4 flux and DOC export offset 8.6 and 29.3%, respectively, of the annual CO_2 uptake of 47.8 g C m^{-2} yr^{-1} over 6 years (Koehler *et al.*, 2011). Oldfeldt *et al.* (2012) recently estimated that 4.3-6.9% of NEE-C fixed was lost due to total hydrocarbon (including CH_4) emissions in a palsa mire, although these measurements were not concurrently made in the same years. Results from these studies show that the contribution of CH_4 emissions and DOC export to the overall NECB of northern peatlands should not be overlooked.

2.2.2 Carbon Dioxide Exchange

The net ecosystem exchange of CO_2 (NEE) in northern peatlands is determined as the difference between the amount of CO_2 fixed by plant photosynthesis (i.e. GPP) and that released into the atmosphere through ecosystem respiration, assuming negligible inorganic sinks and sources for CO_2 (Lovett *et al.*, 2006). Because of the difficulty in directly measuring GPP, GPP is usually estimated as measured ER - NEE. In this thesis, we treat gross ecosystem production (GEP), estimated on the extrapolation of night-time chamber ER measurements, as the equivalent of GPP, assuming that the re-assimilation of CO_2

from dark respiration within the leaf is small (Stoy *et al.*, 2006). Also throughout this thesis, we adopt the atmospheric sign convention for NEE, with a positive value indicating a net CO_2 release from peatland to the atmosphere, while we use positive values to represent the individual exchange processes of GEP and ER.

Total ecosystem respiration in northern peatlands comprises autotrophic respiration from vegetation, and heterotrophic respiration from decomposition of litter and soil organic matter. The total CO_2 efflux from belowground is contributed by three components, namely root respiration, rhizospheric respiration due to root exudation, and heterotrophic microbial respiration (Crow and Wieder, 2005). Pulse labelling of intact peat cores in a boreal bog shows that aboveground autotrophic respiration, root and rhizospheric respiration, and heterotrophic respiration accounts for 16-25%, 19-32% and 37-57% of total ER, respectively (Crow and Wieder, 2005). Stewart (2006) found that 59% of total CO_2 efflux at the Mer Bleue bog is from belowground respiration, of which 63% is derived from respiration of soil organic matter. Moreover, over 99% of ER in this bog occurs in the aerobic zone above the water table (Blodau *et al.*, 2007). Although heterotrophic respiration is an integral component of ER in northern peatlands, both surface litter decomposition rate (exponential decay constants of 0.05-0.37 yr^{-1}) (Moore *et al.*, 2007) and annual oxic peat decomposition rate (0.016-0.060 yr^{-1}) were generally low (Blodau *et al.*, 2007; Scanlon and Moore, 2000).

Numerous studies have quantified multi-year NEE at the ecosystem level in northern peatlands. Using eddy covariance data from seven northern peatlands with 24 site years, Lund *et al.* (2010) found a mean annual NEE of -103 g C m^{-2} yr^{-1}, with especially strong uptake of over -200 g C m^{-2} yr^{-1} in a boreal treed fen and a temperate rich fen. Mean annual NEE was moderate in the Degerö Stormyr poor fen in Sweden with -55 g C m^{-2} yr^{-1} (Sagerfors *et al.*, 2008). The same annual NEE was observed in an Irish blanket bog, probably due to a higher mean annual temperature and herbaceous plant cover that compensated for the lower nutrient status at this site (Sottocornola and Kiely, 2010). The Mer Bleue bog had

a smaller magnitude of annual NEE with -40 g C m^{-2} yr^{-1} (Roulet *et al.*, 2007), while the weakest CO_2 uptake (-22 g C m^{-2} yr^{-1}) was in the subarctic Kaamanen mesotrophic fen because of the shortest growing season (Aurela *et al.*, 2004). These results show that northern peatlands are a contemporary C sink on average, even though the magnitude of uptake varies among different peatland types.

2.2.3 Methane Exchange

The net biosphere-atmosphere exchange of CH_4 in northern peatlands is influenced by the rates of CH_4 production, CH_4 oxidation, and physically or biologically mediated CH_4 transport processes (Bubier and Moore, 1994). CH_4 gas is produced by methanogenic archaea in anoxic, thermodynamically favourable environments with low concentrations of sulphate, nitrate, ferric, and Mn(IV) ions (Thauer *et al.*, 2008). There are two physiological groups of methanogens depending on the substrates they use for methanogenesis, namely acetoclastic methanogens that convert acetate to CH_4, and hydrogenotrophic methanogens that oxidize H_2 and reduce CO_2 to produce CH_4 (Conrad, 2007). Contrasting results have been reported regarding the dominant pathway of methanogenesis in northern peatlands. Chasar *et al.* (2000) found that H_2/CO_2 and acetate are the major precursors of CH_4 produced in a bog and fen, respectively. Acetate is found to accumulate in a northern bog as an end product of anaerobic decomposition (Duddleston *et al.*, 2002), but Avery *et al.* (1999) observed an active acetoclastic CH_4 production during late spring in a Michigan bog.

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Some of the CH_4 produced is subsequently consumed by methanotrophic bacteria, usually in an aerobic environment as oxygen is needed for enzymatic catalysis and serving as the terminal electron acceptor in CH_4 oxidation (Whalen, 2005). As a result, methanotrophic activity in northern peatlands is mostly concentrated in the narrow zone around the seasonal mean water table with high availability of both CH_4 and oxygen (Kettunen *et al.*, 1999). Meanwhile, recent findings suggest that considerable methanotrophic activity could also occur in association with submerged *Sphagnum* moss in peatlands, providing an additional

source of C for moss photosynthesis (Kip *et al.*, 2010; Larmola *et al.*, 2010; Parmentier *et al.*, 2011a). Methanotrophs play a key role in the overall CH_4 cycling in peatlands, being able to oxidize 20-90% of CH_4 produced in the rhizosphere (Ström *et al.*, 2005).

The rate of CH_4 emission is also partly determined by how rapid the CH_4 gas produced in the deeper anaerobic peat is being transported to the atmosphere. Molecular diffusion through the peat profile is the slowest CH_4 transport pathway but plays a key role in enabling methanotrophic activity to take place in the upper peat layers (Whalen, 2005). Ebullition occurs when CH_4 gas bubbles accumulated in waterlogged peat are being released suddenly due to the build-up of pressure exceeding a threshold level (Kellner *et al.*, 2004). Strack *et al.* (2005) hypothesized the occurrence of constant bubbling in a poor fen, as the high CH_4 flux measured by static chambers could not be explained by diffusive flux alone. Moreover, some vascular plants possess aerenchymatous tissues that provide a conduit with minimal resistance for the transport of gases between the peat and the atmosphere. CH_4 gas generated in the anoxic peat layers could escape into the atmosphere rapidly by diffusion or pressure-driven bulk flow via the aerenchyma, while bypassing the CH_4 oxidation zone (Joabsson *et al.*, 1999a). Using a shoot isolation experiment, plant-mediated CH_4 transport was found to account for 31-51% of the total CH_4 flux from a boreal poor fen (Dorodnikov *et al.*, 2011).

Owing to recent advances in sensor technology, ecosystem level measurements of CH_4 flux in northern peatlands are rapidly growing. Previous studies have reported annual CH_4 emissions of 3.2 g m^{-2} yr^{-1} in an arctic tundra (Wille *et al.*, 2008), 9.4-12.6 g m^{-2} yr^{-1} in two boreal poor fens (Forbrich *et al.*, 2011; Rinne *et al.*, 2007), and 24.5-29.5 g m^{-2} yr^{-1} in a subarctic palsa mire containing a lake component in the footprint (Jackowicz-Korczyski *et al.*, 2010). In addition, mean growing season CH_4 fluxes ranging between 25 and 98 mg CH_4 m^{-2} d^{-1} have been observed over a range of boreal and arctic peatlands (Friborg *et al.*, 2000; Long *et al.*, 2010; Parmentier *et al.*, 2011b; Shurpali and Verma, 1998).

All these measurements demonstrate the role of northern peatlands as a net source of CH_4 at the ecosystem level, yet cannot address the spatial heterogeneity of CH_4 fluxes within a peatland.

2.3 Measurement of Peatland-Atmosphere Gas Exchange

Measurement of gas exchange across the peatland-atmosphere interface is usually made using either the micrometeorological technique or the chamber method, which both have their own pros and cons. The micrometeorological technique (e.g. eddy covariance method) has the advantage of enabling *in situ*, non-invasive, and continuous measurements of spatially-integrated surface-atmosphere gas exchanges over a large footprint area (~10^4-10^5 m^2) (Baldocchi *et al.*, 1988). This has led to an increasing number of long-term flux data sets being made available for studying C cycling in various ecosystems. However, there are numerous uncertainties involved in employing the eddy covariance method, including the unreliable night-time fluxes measured in calm conditions, and the occurrence of horizontal advection below the measurement level (Loescher *et al.*, 2006). Moreover, the ecosystem level fluxes obtained by eddy covariance can only be related to some master environmental variables while providing no mechanistic details about the flux-environment relationships for individual plant communities (Griffis *et al.*, 2000).

On the other hand, chambers can be used to measure gas fluxes at the plant community level by enclosing a small, well-defined source area (~0.01-10 m^2). Depending on the mode of operation, chambers can be classified into automatic and manual types. Manual chambers are portable and can easily be used to capture the spatial heterogeneity of a site, but their sampling frequency is limited owing to time and labour constraints in chamber deployment (Savage and Davidson, 2003). Moreover, manual chamber measurements of NEE are often not made at naturally low light levels, leading to possible bias in the parameter estimation of photosynthetic models (Burrows *et al.*, 2005). In contrast, autochambers have a poorer spatial resolution as they require a huge input of

money and infrastructure to operate. Yet, they can be deployed to measure gas fluxes continuously over time, hence providing a huge data set with a high temporal resolution for modelling and statistical analysis of fluxes at different temporal scales (Savage *et al.*, 2008). While some researchers have measured gas fluxes with autochambers in northern fens and tundra (e.g. Bubier *et al.*, 2003b; Mastepanov *et al.*, 2008), there is still a dearth of information on the temporal variations and controls of CO_2 and CH_4 fluxes in northern peatlands, especially in ombrotrophic bogs, based on simultaneous, high frequency measurements by autochambers.

Chambers can also be classified into steady state (or open) and non-steady state (or closed) systems on the basis of their operating conditions. An open chamber maintains a constant gas concentration gradient across the soil-atmosphere interface by continual flushing of headspace with external air, while the concentration gradient reduces in a closed chamber over time due to gas accumulation in the headspace (Livingston and Hutchinson, 1995). Davidson *et al.* (2002) suggested that closed chambers be deployed for a period as short as possible to minimize the artefact of a persistent decrease in diffusion gradient. On the other hand, closed chamber measurements using a short deployment period may underestimate fluxes in a turbulent environment as the diffusive transport rate is not yet in equilibrium with the biological production rate (Rayment and Jarvis, 2000). Determining an appropriate deployment period is thus important for obtaining reliable estimates of gas fluxes using the chamber method.

2.4 Factors Governing Peatland Carbon Gas Exchange

The spatial and temporal variability of CO_2 and CH_4 fluxes in northern peatlands is influenced by a number of environmental and biotic variables. In this section, I will focus on discussing the effects of some of the key factors on peatland C gas exchange.

2.4.1 Light

The presence of light, or specifically photosynthetically active radiation (PAR), is a pre-requisite for photosynthetic activity by green plants. It drives the circadian rhythm of CO_2 exchange in vegetation, with a net uptake during the day and a net release into the atmosphere at night. The response of GEP to changing PAR levels is often described by a rectangular hyperbolic function, where GEP has a near-linear increase at low PAR levels and then reaches an asymptotic maximum (Frolking *et al.*, 1998). Below is one commonly used Michaelis-Menten rectangular hyperbola for modelling GEP (Ruimy *et al.*, 1995):

$$GEP = \left(\frac{\alpha * PAR * P_{\max}}{\alpha * PAR + P_{\max}} \right) \tag{2.1}$$

where α is the apparent quantum yield and P_{max} is maximum gross photosynthesis.

Apparent quantum yield is the initial slope of the hyperbola and indicates the rate at which GEP increases with PAR at low light levels. Compared to upland grassland, cropland, and forest ecosystems, northern peatlands exhibit lower α values (0.02 *vs.* 0.04 mol CO_2 mol^{-1} PAR) and hence are less efficient in fixing CO_2 at the lower range of PAR (Frolking *et al.*, 1998). Similarly, maximum gross photosynthesis is considerably lower in northern peatlands than in other upland ecosystems (9.2 *vs.* 43.4 μmol m^{-2} s^{-1}) (Frolking *et al.*, 1998). Moreover, previous studies have reported lower mid-summer P_{max} values in bogs than in fens (Bubier *et al.*, 1998; Frolking *et al.*, 1998), as well as lower P_{max} in northern open fens with smaller biomass than in wooded fens (Humphreys *et al.*, 2006).

Seasonal variability of α and P_{max} values has been observed in northern peatlands, with generally higher values in the mid-growing season than the early and late growing seasons (Adkinson *et al.*, 2011; Glenn *et al.*, 2006; Lindroth *et al.*, 2007). The spatial difference in photosynthetic model parameters among peatland sites can also vary over the growing season. Owing to a shorter growing period, rich fen dominated by deciduous shrubs has a higher P_{max} than evergreen-dominated bog and sedge-dominated intermediate fen in summer, but lower P_{max} than the other two sites in the early and late seasons (Bubier *et al.*, 1998).

2.4.2 Temperature

Temperature is known to be positively correlated with soil respiration rate, with the relationship often described by either an exponential or Arrhenius function (Lloyd and Taylor, 1994). Based on nighttime eddy covariance measurements, Lafleur *et al.* (2005) found that surface peat temperature could explain 58-62% of the temporal variations in ER at the Mer Bleue bog. Results from laboratory incubation of peat soil columns demonstrate a mean increase of CO_2 efflux rate by 2.4 times at 23 ºC compared to 10 ºC (Moore and Dalva, 1993). A long-term warming experiment in a subarctic bog further shows that a ~1 ºC increase in temperature could cause a 52-60% increase in ER, with respiration from deep peat layers contributing to almost 70% of the rate increase (Dorrepaal *et al.*, 2009). Temperature sensitivity of ER in northern peatlands is high compared to other sites with mineral soils, with Q_{10} values (relative increase in ER per 10 ºC rise in temperature) of 3.0-4.1 and 5.0-6.4 for ER (Bubier *et al.*, 1998) and aerobic heterotrophic respiration, respectively (Blodau *et al.*, 2007). On the other hand, Lund *et al.* (2010) found a strong correlation between summer mean air temperature and GPP across 12 northern peatland and tundra sites, while the effect of temperature on peatland NEE is in general poorly known (Frolking *et al.*, 2011).

Peat temperature is a major control of CH_4 flux variability in northern peatlands over the growing season (Laine *et al.*, 2007b; Long *et al.*, 2010), and over space across some wetter sites (Christensen *et al.*, 2003a). Peat temperature measured at the mean water table position has the strongest relationship with CH_4 flux, since the variable combines the influences from both temperature and moisture (Bubier *et al.*, 1995a; Pelletier *et al.*, 2007). Since CH_4 production has a higher temperature sensitivity than CH_4 oxidation (Q_{10} of 5.3-16 *vs.* 1.4-2.1) (Dunfield *et al.*, 1993), a rise in temperature often leads to a corresponding increase in net CH_4 emissions. Moreover, a temperature rise can enhance CH_4 ebullition in peatlands by increasing the repartitioning of CH_4 to gas phase and hence bubble volume (Fechner-Levy and Hemond, 1996; Waddington *et al.*,

2009). Plant-mediated transport of CH_4 can also increase with temperature as the enhanced thermal gradient between plant interior and exterior leads to greater ventilation and bulk flow of CH_4 from the peat to atmosphere *via* aerenchyma (Große, 1996; Joabsson *et al.*, 1999a).

2.4.3 Water Table

Changes in water table position can affect the aeration status and moisture availability in the peat profile non-linearly (Lafleur *et al.*, 2005; Strack and Price, 2009), which have implications to the biogeochemical processes in peatlands. Previous studies reported a unimodal photosynthetic response to *Sphagnum* water content or median water table of sampling plots, since CO_2 diffusion and plant metabolic activity are reduced when moisture content is above and below an optimal level, respectively (Laine *et al.*, 2007a; Williams and Flanagan, 1996). Strack & Price (2009) further observed a cessation of photosynthesis by *Sphagnum rubellum* in a bog when mean water table dropped to more than 55 cm below the peat surface. Ecosystem respiration in peatlands is also influenced by changes in water table position. Results from field measurements and laboratory core incubation have demonstrated an increase in ER with water table depth owing to a more rapid microbial decomposition in aerobic conditions (Moore and Dalva, 1993; Silvola *et al.*, 1996), although Lafleur *et al.* (2005) only observed a weak relationship between ER and water table depth in the relatively dry Mer Bleue bog. Moreover, Tuittila *et al.* (2004) partitioned the ER components and obtained good fits ($r^2 > 0.9$) when respiration rates from peat and *Sphagnum* moss were modelled as a function of water table depth separately using a sigmoidal and a Gaussian relationship, respectively.

Numerous studies have found a decrease in CH_4 emissions from northern peatlands as water table drops below the peat surface (Laine *et al.*, 2007b; Moore *et al.*, 2011), due to the presence of a thicker oxic peat layer for CH_4 oxidation and a thinner anaerobic layer for methanogenesis (Waddington *et al.*, 1996). However, some studies observed an increase in CH_4 flux with a lower water table

position, which might be partly related to increasing CH_4 ebullition as a result of a reduction in hydrostatic pressure, or increasing CH_4 production in response to a warming that is associated with increasing dryness (Bellisario *et al.*, 1999; Moore and Dalva, 1993; Treat *et al.*, 2007). In some peatlands with a water table close to or above the peat surface, no clear relationships between CH_4 flux and water table depth were seen, since the ratio of oxic to anoxic peat depth remained relatively constant (Jackowicz-Korczyski *et al.*, 2010; Sachs *et al.*, 2010; Wille *et al.*, 2008). Nevertheless, CH_4 emissions from these sites could decrease drastically when water table further drops below a certain depth, with this threshold reported to range between 10 and 20 cm below the peat surface (Christensen *et al.*, 2003a; Moore and Roulet, 1993; Shannon and White, 1994). There is a need for a better understanding of the threshold of water table depth above which other variables are more dominant temporal controls of CH_4 flux, and whether such threshold is a function of plant community composition.

2.4.4 Photosynthetic Area/Biomass

The amount of photosynthetic materials in green plants strongly governs the community level CO_2 exchange rate. Summer mean NEE and GPP were shown to relate strongly with leaf area index (LAI) across a range of northern peatlands (Lund *et al.*, 2010). In an Arctic tundra in Sweden, GPP at 600 μmol PAR m^{-2} s^{-1} was shown to increase linearly with LAI across some heterogeneous plots (Street *et al.*, 2007). On the other hand, both maximum net CO_2 uptake and ER rates increased with the amount of foliar biomass in the fen plant communities (Bubier *et al.*, 2003b). Laine *et al.* (2012) also found that the green biomass of dominant plant functional type best explained the variations in peak growing season NEE among northern peatlands. As such, modelling or upscaling NEE without taking into account differences in photosynthetic area or biomass could lead to considerable bias (Riutta *et al.*, 2007a).

CH_4 emissions from northern peatlands have been found to correlate positively with the number of shoots of sedges (Christensen *et al.*, 2003b; Öquist

and Svensson, 2002) and the sedge biomass (Bellisario *et al.*, 1999; Joabsson and Christensen, 2001; Marinier *et al.*, 2004). This positive relationship is mainly driven by a higher substrate supply from plant productivity, as well as a greater plant-mediated transport via the aerenchymatous tissues of sedges (Joabsson and Christensen, 2001). Strong relationships between seasonal mean CO_2 uptake (including NEE and GPP) and CH_4 emissions have also been reported across a range of flooded wetlands (Whiting and Chanton, 1993) and in a number of northern peatlands (Alm *et al.*, 1997; Ström and Christensen, 2007; Ström *et al.*, 2012), though Waddington *et al.* (1996) found that this relation only held at wetter lawns but not drier ridges of a boreal peatland. Pulse labelling of ^{14}C in intact cores have revealed a fast (from hours to days) turnover of recent photosynthate from sedges to the rhizosphere for CH_4 production (King *et al.*, 2002). Strom *et al.* (2012) suggested that the presence of a continuous supply of organic acids from sedges is needed to sustain the level of CH_4 flux obtained in the arctic fen. Yet, it is not clear whether a substrate-based coupling of plant production and CH_4 emissions exists for peatland plant communities dominated by different growth forms, and if so, the time lag and correlations based on time series analysis of high temporal resolution flux measurements made in the field.

2.4.5 Plant Species Composition

Different plant growth forms in northern ecosystems have different plant traits and effects on growth, production and decomposition, thus leading to variations in overall C exchange (Dorrepaal, 2007). Photosynthetic rate per unit green area of peatland plant functional groups is found to decrease in the order of graminoids > evergreen shrubs > deciduous shrubs > *Sphagnum* moss > herbs (Leppälä *et al.*, 2008), while maximum NEE per unit foliar biomass at a poor fen follows the descending order of sedge/herb > deciduous shrub > evergreen shrub (Bubier *et al.*, 2003b). Moore *et al.* (2007) found that the litter decomposition rate at peatland surface decreased in the order of sedge and shrub leaves > shrub stems > *Sphagnum*.

Peatland CH_4 emissions are strongly influenced by species-specific factors. While graminoids generally have a high translocation rate of recent photosynthate (Ward *et al.*, 2009), acetate production rate in the rhizosphere is substantially higher in the *Eriophorum* microcosms compared to the *Carex* and *Juncus* counterparts (Ström *et al.*, 2005). Moreover, ^{14}C pulse labelling of mesocosms shows that the contribution of recent photosynthate to methanogenesis is lower in *Eriophorum vaginatum* than in *Scheuchzenia palustris* in a boreal poor fen (Dorodnikov *et al.*, 2011). Rhizospheric CH_4 oxidation rate also varies depending on vascular plant species, with over 90% of CH_4 being consumed in *Eriophorum* and *Juncus* monoliths but only 20-40% in *Carex* (Ström *et al.*, 2005). Joabsson & Christensen (2001) found positive relationships between mean seasonal CH_4 flux and foliar biomass of *Eriophorum* and *Carex* but not *Dupontia* across the plots in an arctic tundra, attributing this difference to the proportion of coarse roots and hence the ability to transport gases among these species. In view of the above findings, the exchange of CO_2 and CH_4 from peatland vascular plant communities dominated by different growth forms or species deserves more detailed investigation.

2.4.6 Atmospheric Turbulence

Atmospheric turbulence plays a role in affecting gas exchange dynamics in peatlands. Strong atmospheric turbulence is observed to relate to high ecosystem level CH_4 emissions from the arctic polygonal tundra, probably due to an enhanced gas transport from the open water surfaces at the site, and mechanically-induced release of gas bubbles adhered to surfaces under water (Sachs *et al.*, 2008; Wille *et al.*, 2008). Also, turbulent conditions are shown to cause a reduction in the surface CO_2 concentration gradient in the high-porosity litter layer of a boreal forest floor dominated by *Sphagnum* moss due to wind flushing of CO_2 stored in pore spaces (Hirsch *et al.*, 2004). Since closed chambers essentially eliminate the direct influence of atmospheric turbulence, the measurements might not be reliable in representing the actual gas exchange rate (Sachs *et al.*, 2008) or biological gas production rate (Rayment and Jarvis, 2000).

Atmospheric turbulence also has some influence on the gas fluxes measured by the chamber method. Strong turbulence has been found to enhance gas fluxes from soils measured by open chambers in a spruce forest owing to pressure pumping effects (Subke *et al.*, 2003), as well as by vented, closed chambers in a deciduous forest because of Venturi effects induced by winds blowing over the vent tube (Bain *et al.*, 2005). Meanwhile, nighttime respiration measured by closed chambers was found to be overestimated under calm conditions in a boreal peatland (Schneider *et al.*, 2009). Understanding the influence of atmospheric turbulence on pore space gas dynamics and measured fluxes from chambers is important to obtain reliable flux estimates particularly in the *Sphagnum*-dominated ombrotrophic bogs with a high air-filled peat porosity.

2.5 Variability of Carbon Gas Exchange in Northern Peatlands

2.5.1 Spatial Variability

Northern peatlands are complex adaptive systems that have a high degree of spatial heterogeneity and strong nonlinearity in ecosystem functions (Belyea and Baird, 2006). Baird *et al.* (2009) proposed three spatial scale levels (SL) that can be used to characterize peatland C dynamics, including SL1 with a length of 1-10 m that represents fundamental functional units, e.g. hummocks, SL2 with a length of 10-10^2 m that represents aggregation of SL1 units, e.g. ridges, and SL3 with a length of 10^2-10^4 m that can be features like the dome of a bog. Peatland structure can vary considerably at the finest scale of SL1. Microtopography is a feature commonly seen in northern peatlands, with hummocks being elevated mounds about 20-40 cm above the surface of hollows that are wetter, flatter depressions spaced ~1-3 m apart (Nungesser, 2003). The difference in water table depth between microtopographic forms leads to a large variability in the dominant moss and vascular plant species, as well as the allocation of above- and below-ground biomass at these locations (Bubier *et al.*, 1995b; Bubier *et al.*, 2006; Murphy *et al.*, 2009).

The exchange of C gas from peatlands also varies across SL1 units as a

result of the spatial variations in environmental and biotic parameters. Riutta *et al.* (2007a) observed significantly lower GEP, ER, and NEE rates in hollows than hummocks in a Finnish poor fen, owing to a smaller leaf area and a water table above the peat surface that were unfavourable for both photosynthesis and respiration. Submerged hollows of a boreal bog in Sweden were even a net CO_2 source in contrast to a net CO_2 sink in hummocks (Waddington and Roulet, 1996). Yet, Bubier *et al.* (2003a) found no significant difference in maximum NEE, GEP and ER between hummocks and hollows at the Mer Bleue bog probably due to the small variations in foliar biomass across sites. Variations in seasonal mean peatland CH_4 emissions at the SL1 unit are fairly consistent, with exponentially higher fluxes at hollows than at hummocks following the water table gradient (Bubier *et al.*, 1993a; Pelletier *et al.*, 2007). Meanwhile, the presence of aerenchymatous plants, e.g. *Eriophorum vaginatum* and *Maianthemum trifolium*, can create some local CH_4 emission hotspots within a peatland (Moore *et al.*, 2011). As discussed in Section 2.4.5, differences in species composition of plant communities can contribute to additional spatial variations in CO_2 and CH_4 fluxes.

Modelling of ecosystem level C gas exchange in northern peatlands should incorporate the spatial variations at the plant community level, as the area coverage of plant communities is dynamic over time and the response of different communities to changing environmental conditions is not necessarily the same (Laine *et al.*, 2009). If plant communities in a peatland are very different in their C exchange dynamics, the upscaled fluxes will be highly sensitive to the areal proportion of communities (Riutta *et al.*, 2007a). While flux upscaling has been done by establishing C flux models for individual plant communities or mosaic elements (e.g. Fox *et al.*, 2008; Riutta *et al.*, 2007a), few have examined explicitly whether these scaling units are functionally different with respect to C gas exchange. Williams *et al.* (2006) found in an arctic catchment that only 7 generic parameter sets were needed to model the response of NEE to light and temperature across 23 heterogeneous locations in a toposequence. In the Kaamanen aapa mire in Finland, Maanavilja *et al.* (2011) reported that CO_2

exchange from the four plant community types could be modelled based on two functional components, namely ombrotrophic and minerotrophic. However, the similarity of CO_2 exchange function of different plant communities dominated by shrubs, sedges and herbs in an ombrotrophic peatland is yet to be tested.

2.5.2 Temporal Variability

The exchange of CO_2 and CH_4 in northern peatlands exhibits considerable variations at different temporal scales in response to environmental changes. The diel cycle of NEE in peatlands is widely known, with a net CO_2 uptake in daytime due to plant photosynthesis and a net CO_2 release at night as a result of respiratory activities (e.g. Aurela *et al.*, 1998; Humphreys *et al.*, 2006). On an annual basis, northern peatlands begin to photosynthesize quickly after snowmelt (Moore *et al.*, 2006), with net CO_2 uptake increasing towards a maximum in mid-summer, and then decreasing to eventually become a net CO_2 source in late fall (Lafleur *et al.*, 2001). The length of growing season decreases with the latitudinal position of northern peatlands, such that sites located closer to the arctic region have a shorter duration of net C uptake (Lindroth *et al.*, 2007). Roehm & Roulet (2003) estimated that CO_2 efflux during the non-growing-season could offset 33-40% of the amount of C fixed in summer. Northern peatlands also demonstrate considerable interannual variability in CO_2 exchange. Sulman *et al.* (2010) found lower ecosystem level GEP and ER associated with a higher growing season mean water table at fens, but opposite relationships at the bogs. On the other hand, Bubier *et al.* (2003a) observed in the drier year a lower GEP at the fen community due to early senescence of sedges in drought conditions, but no significant changes at the shrub-dominated bog sites based on manual chamber measurements.

Previous studies have reported very different diel patterns of CH_4 flux from northern peatlands, ranging from peak emissions during daytime (Long *et al.*, 2010), peak emissions at nighttime (Baldocchi *et al.*, 2012), to no significant variations over the day (Jackowicz-Korczyski *et al.*, 2010). This is indicative of

the complexity of physical and biological controls on the production, consumption and transport of CH_4. A single seasonal peak of peatland CH_4 flux is generally seen in summer with the highest temperature and plant production for methanogenesis, while winter CH_4 flux contributes to 6-15% of annual emissions (Jackowicz-Korczyski *et al.*, 2010; Rinne *et al.*, 2007). Meanwhile, Mastepanov *et al.* (2008) detected a large release of CH_4 gas from an Arctic tundra into the atmosphere in late autumn when soils above the permafrost layer began to freeze up. Moreover, ebullition events were identified in over 15% of autochamber flux measurements made between April and December in a temperate poor fen, leading to episodic release of CH_4 into the atmosphere (Goodrich *et al.*, 2011). Also, large interannual variations in CH_4 emissions have been shown in boreal peatlands, with a mean increase of 60% in the wetter and warmer year (Bubier *et al.*, 2005).

2.6 Conclusions

Northern peatlands play an important role in the global C cycle and the relative magnitude of CO_2 and CH_4 exchange largely determines the radiative forcing impacts of peatlands. Fluxes of CO2 and CH4 show large variability over space and time, and are influenced by environmental and biotic factors, e.g. light, temperature, water table, photosynthetic area, and plant species composition. A thorough understanding of the relationships between gas fluxes and environmental correlates at the plant community level is needed to accurately estimate peatland gas exchange at the ecosystem scale. The use of autochambers provides a unique opportunity to explore the temporal variations of C gas exchange in ombrotrophic peatlands with the generation of a huge, continuous flux data set. In my Ph.D. research, I address the following questions to fill the knowledge gaps:

1) What is the effect of atmospheric turbulence on CO_2 dynamics in the peat pore space of an ombrotrophic bog with a high air-filled porosity? What are the relationships between atmospheric turbulence and CH_4 and nighttime CO_2 fluxes measured by autochambers using different deployment periods?

2) How do CH_4 emissions vary across seasons and years from different vascular plant communities at a bog? What are the relationships between CH_4 flux and environmental and biotic correlates over the season? Do the dominant temporal controls of CH_4 flux vary among plant communities and during the season?
3) What are the magnitudes and controls of seasonal mean CO_2 exchange (NEE, GEP and ER) across vascular plant communities dominated by different growth forms in a bog? Are the photosynthetic and respiratory responses to changing environmental and biotic conditions similar among peatland plant communities?
4) How does seasonal mean CO_2 exchange relate with CH_4 emissions across a range of sites in a bog? What are the temporal correlation and time lag between photosynthetic activity and CH_4 flux at different time scales in distinct plant communities?

Chapter 3

The Effect of Atmospheric Turbulence and Chamber Deployment Period on Autochamber CO_2 and CH_4 Flux Measurements in an Ombrotrophic Peatland

Context within Thesis

This chapter investigates the effect of atmosphere turbulence and chamber deployment period on autochamber flux measurements at the Mer Bleue bog, driven by the question of whether the observed diel CH_4 flux pattern is a result of natural processes or measurement artefact. Results in this chapter demonstrate the presence of a turbulence-induced measurement artefact in the initial 13 minutes after chamber closure. Based on the findings of this study, I extended the chamber deployment period to 15 minutes in the summer of 2010 and developed turbulence-based protocols for filtering or correcting fluxes measured with a short deployment period to obtain reliable estimates of net biological gas fluxes for further analysis in subsequent chapters.

3.1 Abstract

Accurate quantification of soil-atmosphere gas exchange is essential for understanding the magnitude and controls of greenhouse gas emissions. We used an automatic closed dynamic chamber system to measure the fluxes of CO_2 and CH_4 for several years at the ombrotrophic Mer Bleue peatland near Ottawa, Canada and found that atmospheric turbulence and chamber deployment period had a considerable influence on the observed flux rates. With a short deployment period of 2.5 minutes, CH_4 flux exhibited strong diel patterns and both CH_4 and nighttime CO_2 effluxes were highly and negatively correlated with friction velocity as were the CO_2 concentration gradients in the top 20 cm of peat. This suggests winds were flushing the very porous and relatively dry near surface peat layers, altering the concentration gradient and resulting in a 9 to 57% underestimate of CH_4 flux at any time of day and a 13 to 21% underestimate of nighttime CO_2 fluxes in highly turbulent conditions. Conversely, there was evidence of an overestimation of ~100% of CH_4 and nighttime CO_2 effluxes in calm atmospheric conditions possibly due to enhanced near-surface gas concentration gradient by mixing of chamber headspace air by fans. These problems were resolved by extending the deployment period to 30 minutes. After 13 minutes of chamber closure, the flux rate of CH_4 and nighttime CO_2 became constant and were not affected by turbulence thereafter, yielding a reliable estimate of the net biological fluxes. The measurement biases we observed likely exist to some extent in all chamber flux measurements made on porous and aerated substrate, such as peatlands, organic soils in tundra and forests, and snow-covered surfaces, but would be difficult to detect unless high frequency, semi-continuous observations are made.

3.2 Introduction

Northern peatlands in the boreal and subarctic regions play an important role in the global carbon cycle. They store a total of 270 to 370 Pg of carbon (C) as peat (Turunen *et al.*, 2002), which is equivalent to 18-25 % of the C held globally in the top 1 m of soil (Jobbágy and Jackson, 2000), though these estimates are considered low when the peatlands containing permafrost and at higher latitudes are included (McGuire *et al.*, 2009; Tarnocai *et al.*, 2009). While northern peatlands have been net sinks of C for millennia, natural and anthropogenic disturbances could lead to substantial release of C to the atmosphere (Turetsky *et al.*, 2002). The land-atmosphere exchange of carbon dioxide (CO_2) and methane (CH_4) gases largely governs the overall peatland carbon balance (Roulet *et al.*, 2007) as well as the net radiative forcing impacts of peatlands over time (Frolking *et al.*, 2006). Accurate measurement of land-atmosphere gas fluxes is needed to quantify peatland gas exchange at different spatial-temporal scales, understand the environmental controls on gas fluxes, and parameterize peatland and global carbon models (Limpens *et al.*, 2008).

Flux measurement in peatlands is often done using chamber enclosures and/or micrometeorological methods, e.g. eddy covariance. Eddy covariance gives continuous, spatially-averaged gas fluxes over an ecosystem at scales of 10^4-10^5 m^2 (Scanlon and Kiely, 2003), but it does not provide any mechanistic detail about the flux components at a finer spatial scale (Griffis *et al.*, 2000). In contrast, chamber methods measure gas concentration changes in a headspace resulting from small, well-defined areas (0.01-10 m^2). Most studies on small-scale peatland C dynamics have employed manual chambers (e.g. Carroll and Crill, 1997; Moore *et al.*, 2002; Pelletier *et al.*, 2007), which are relatively easy and inexpensive to use, but difficult to sample more frequently than weekly because of labour constraints. Automated chambers thus far have not been used extensively for flux measurements owing to the high cost and infrastructure requirements for installation and operation (Savage and Davidson, 2003), yet they offer great opportunity to collect flux data with a much higher temporal resolution than

manual chambers.

The use of chamber enclosures is known to create some artefacts and bias in flux measurements. One artefact associated with the deployment of closed chambers is the accumulation of gases in the chamber headspace and the subsequent decrease in diffusive concentration gradient and measured flux over time (Davidson *et al.*, 2002). This suggests that chamber deployment period should be kept short to minimize the build-up of gases inside the chamber. On the other hand, a short chamber deployment period increases the uncertainty of flux calculation and the difficulty in obtaining a detectable flux (Khalil *et al.*, 1998). There are also potential errors in flux measurement at the beginning of deployment period, since chamber placement on the soil surface can cause a disturbance of the atmospheric interfacial layer (Hutchinson *et al.*, 2000). The duration and timing of chamber deployment is therefore important to obtaining accurate flux estimates.

Atmospheric turbulence has been shown to exert considerable influence on gas transport in soils (Kimball and Lemon, 1971). Numerous studies have observed the effects of atmospheric turbulence on gas dynamics in soil pore space in grassland (Flechard *et al.*, 2007), pine forest (Maier *et al.*, 2010) and black spruce boreal forest (Hirsch *et al.*, 2004). Moreover, highly turbulent atmospheric conditions were found to enhance soil gas fluxes measured by both open chambers in a spruce forest (Subke *et al.*, 2003) and closed chambers in an aggrading deciduous forest (Bain *et al.*, 2005), while Schneider *et al.* (2009) observed an overestimation of nighttime respiration under calm conditions in a boreal peatland by closed chambers. Atmospheric turbulence has a more pronounced effect on gas exchange from soils with large pore size and low moisture content owing to significantly greater air permeability (Conen and Smith, 1998; Kimball and Lemon, 1971). In light of these findings, there is a need to better understand how headspace gas concentration is affected by turbulence and pressure disturbances arising from chamber deployment (Kutzbach *et al.*, 2007).

Autochambers have the advantage of providing a large empirical dataset covering a range of turbulence conditions that occur naturally in the field for statistically robust analysis.

The exchange of CO_2 and CH_4 at the Mer Bleue bog, a peatland with very porous and aerated peat, was measured using a closed dynamic autochamber system with a short deployment period of 2.5 minutes. We found strong diel variations in CH_4 flux with significantly larger nighttime emissions. Diel patterns in CH_4 flux are not as clearly prescribed as those of CO_2 that typically show net uptake during the day and emissions at night on vegetated terrain (e.g. Cai *et al.*, 2010). Recent studies using the eddy covariance technique, a method which is not subject to chamber-specific artefacts, have reported very different diel CH_4 flux patterns in peatlands. Higher CH_4 flux during the daytime was observed in a boreal treed fen (Long *et al.*, 2010) as well as a Dutch peat meadow (Hendriks *et al.*, 2010), attributable to greater temperature and vapour pressure gradients that enhanced both plant-mediated convective flow as well as transpiration loss of dissolved CH_4 in soil water. On the other hand, Baldocchi *et al.* (2012) reported higher CH_4 emissions at night in a peatland pasture, owing to collapse of the nocturnal boundary layer and elongation of flux footprint to elevated CH_4 source areas in calm conditions. In a subarctic peatland dominated by tall graminoids, no diel cycle in CH_4 flux was seen throughout the year (Jackowicz-Korczyski *et al.*, 2010). Some studies that used autochambers on wetlands have reported CH_4 or total hydrocarbon fluxes for time periods of a day or more (Bäckstrand *et al.*, 2010; Mastepanov *et al.*, 2008), making it hard to deduce the variability over shorter time periods from their results. Our central research question is whether the diel CH_4 flux pattern at Mer Bleue is a result of natural processes or measurement artefacts. If it is the former, then biological and biogeochemical reasons for the repetitive pattern of variability need to be studied to provide an explanation. If the latter, modifications to the chamber methodology may be needed to eliminate or at least greatly reduce the measurement artefacts.

We hypothesize that the diel variability of CH_4 flux at the Mer Bleue bog is largely governed by physical processes associated with atmospheric turbulence and chamber deployment. Turbulence-driven pressure fluctuations can induce mass flow of gas from soil pore space to the atmosphere, reducing gas concentration and storage in soils (Maier *et al.*, 2010). We expect that during daytime when turbulent conditions are dominant, the reduction in diffusive concentration gradient in surface peat before chamber lid closure will lead to a lower transient CH_4 flux measured by autochambers when the deployment period is short. For the same reason, nighttime CO_2 efflux will be lower when measured in highly turbulent conditions. In calm conditions, mechanical mixing of headspace air by fans can increase the near-surface concentration gradient and lead to an immediate enhancement of gas fluxes following chamber deployment (Hutchinson *et al.*, 2000). For example, Schneider *et al.* (2009) observed non-linear increases in headspace CO_2 concentration when the closed manual chamber was deployed during calm nights at three microsites of a boreal peatland. We hypothesize that in the calm conditions that occur during some nights, chamber-induced turbulence enhances both soil CO_2 and CH_4 effluxes measured during the initial period after autochamber closure, before an equilibrium is reached between the net rates of gas production in peat and gas exchange across the peat surface.

The objectives of our study are to: (1) investigate the relationship between atmospheric turbulence and autochamber CH_4 and nighttime CO_2 fluxes; (2) examine the influence of atmospheric turbulence on the surface peat CO_2 concentration gradient; and (3) determine the effects of chamber deployment period on gas fluxes measured by autochambers.

3.3 Methods

3.3.1 Site Description

Mer Bleue peatland is a 28 km^2 ombrotrophic bog located near Ottawa, Canada (45.41ºN, 75.52ºW). This region has a cool continental climate, with a mean annual temperature of 6.0±0.8 ºC and mean annual precipitation of 943.5

mm (1971-2000 climate normals) (Environment Canada, 2011). Field measurements were made at a dome-shaped bog in the northwest part of this peatland. Peat depth reaches about 5 to 6 m near the centre of the bog, and is shallower (<0.3 m) near the beaver pond margin (Roulet *et al.*, 2007). The surface of this peatland is completely covered by *Sphagnum* moss (*Sphagnum angustifolium*, *Sphagnum capillifolium*, *Sphagnum fallax*, *Sphagnum magellanicum*) and the vascular plant cover is dominated by low growing ericaceous evergreen shrubs (*Chamaedaphne calyculata*, *Ledum groenlandicum*, *Kalmia angustifolia*), with an occasional mix of deciduous shrub (*Vaccinium myrtilloides*), sedge (*Eriophorum vaginatum*) and forb (*Maianthemum trifolium*).

This bog is relatively dry, with a mean growing season (May to October) water table depth of 42.7 cm from the top of hummock over 1998-2008 (Teklemariam *et al.*, 2010). It has a hummock-lawn-hollow microtopography, with a mean difference of 17 cm in elevation between the hummock and hollow surfaces (Wilson, 2012). Depending on the microtopographic location, the top 10-30 cm peat at Mer Bleue is fibric and has a total porosity and macroporosity of greater than 0.9 and 0.8, respectively (Dimitrov *et al.*, 2010). Air-filled porosity of surface peat in the unsaturated zone of this bog is between 0.82 and 0.92 (Deppe *et al.*, 2010).

3.3.2 Autochamber System

We set up 10 autochambers at the Mer Bleue bog within a 15-m radius about 50 m south of the eddy covariance tower. Chamber locations were chosen to represent the major plant communities, while covering a range of water table and leaf area (Table 3.1). Wooden boardwalks were constructed to minimize disturbance during access to the chambers. The dynamic, closed autochamber system established at this bog was identical to the one used in a moderately rich treed fen (Cai *et al.*, 2010), a temperate Douglas-fir forest (Drewitt *et al.*, 2002), a boreal aspen forest (Griffis *et al.*, 2004) and two boreal black spruce forests (Bergeron *et al.*, 2009; Gaumont-Guay *et al.*, 2008). The autochamber consisted

of a transparent Plexiglas dome fitted to a PVC cylinder with a hinged aluminum frame. The near semi-spherical dome had a height of 20.5 cm and the PVC cylinder had an internal diameter of 52 cm, a thickness of 1 cm and a height of 38.5 cm. Hence each autochamber covered a surface area of 0.21 m^2. The PVC cylinders were inserted 16 to 31 cm deep into the peat, leaving about 7 to 22 cm above the peat surface, but below the height of the top of the shrubs. After insertion, any gaps between the outside of the cylinder and surrounding peat were filled with surface peat taken from elsewhere at the site. A partially inflated bicycle tube sealed to the top of the cylinder and a foam gasket on the aluminum flange at the dome base ensured a good seal when the chamber was closed. A small brushless fan within the dome mixed the air in the chamber headspace and a coiled 50-cm long open-ended vent tube on the dome top ensured equilibration of pressure between the inside and outside of chamber during flux measurements.

Control of the autochamber system, including chamber selection, measurement timing and data acquisition, was controlled by a datalogger (CR23X, Campbell Scientific, UT, USA). A pneumatic cylinder assembly (Model BFT-173-DB, Bimba Manufacturing, IL, USA) connected to an oil-free air compressor (Model CPFAC2600P, Porter Cable, TN, USA) opened and closed the chamber dome. Sampling tubes (Synflex 1300, 4.3 mm i.d., Saint-Gobain Performance Plastics, NJ, USA) connected to the gas inlet and outlet located at the top of chamber dome led to a sampling manifold controlled by solenoid valves. Concentrations of CO_2 and CH_4 were measured by a closed-path infrared gas analyzer (LI-6262, LI-COR, NE, USA) and a fast methane analyzer based on off-axis integrated cavity output spectroscopy (DLT-100, Los Gatos Research, CA, USA), respectively. The LI-6262 was manually calibrated weekly using ultra-high purity nitrogen gas containing no CO_2 (for zero) and 356 μmol mol^{-1} of CO_2 (for span), and the fast methane analyzer was calibrated with CH_4 standard gas (1.8 and 5.01 μmol mol^{-1}) once at the beginning of measurement season. Air was circulated to the LI-6262 and back to the chambers at a flow rate of 3.5 L min^{-1} by an AC linear pump (Model DDL, Gast Manufacturing, MI, USA). The internal

pump on the fast methane analyzer sub-sampled the air stream at approximately 0.5 L min^{-1}. The datalogger, pump, and gas analyzers were all placed inside temperature-controlled housings.

The autochamber system was in operation between 22 May and 7 December in 2009 and between 26 March and 5 December in 2010. Prior to 6 July 2010, the autochambers were programmed to close sequentially to measure gas fluxes for 2.5 minutes to provide one measured flux for each chamber every 30 minutes. Fluxes were continuously measured between 0200 and 2400 h daily. Between midnight and 0200 h, the system was used to estimate the effective volume of the chamber (Drewitt *et al.*, 2002). From 6 July 2010 onwards, the chamber deployment period was increased from 2.5 to 15 minutes, and one flux measurement was made for each chamber every three hours. To investigate the effect of chamber deployment period on measured fluxes, we operated only two autochambers using extended deployment periods of 15 minutes for three days (23-26 June) and 30 minutes for four days (26-30 June 2010). Analog outputs from the gas analyzers were sampled at 1 Hz by the datalogger, averaged every 5 seconds, and downloaded automatically to a PC located in a hut on site. All high frequency data were retained for flux processing.

3.3.3 CO_2 Concentration Profile System

A profile system was set up within 25 m of the autochambers to monitor CO_2 and water vapour concentrations in the air at seven different levels, namely 255, 120, 20 and 10 cm above the peat surface, in the *Chamaedaphne* canopy (5 cm above peat surface), and on the *Sphagnum* peat surface of both a hummock and hollow (5 and 25 cm below the *Chamaedaphne* canopy respectively). Air samples were drawn through sampling tubes (Synflex 1300, 4.3 mm i.d. and Bev-A-Line IV, 3.2 mm i.d.) into an infrared gas analyzer (LI-6262, LI-COR, NE, USA) by an AC linear pump (Model SPP-15EBS-101, Gast Manufacturing, MI, USA). The seven different levels were sampled sequentially for two minutes each using solenoid valves (Model 701N13A5P, Honeywell, CT, USA), with air being

flushed through the system in the first minute and CO_2 and water vapour concentrations measured every two seconds and then averaged in the second minute. Operation of this system was controlled by a datalogger (CR10X, Campbell Scientific, UT, USA).

We also measured CO_2 concentrations in the peat profile by non-dispersive infrared CO_2 sensors (Model CARBOCAP GMM220, Vaisala, Finland) that were enclosed by an expanded polytetrafluoroethylene (PTFE) membrane permeable to gas but not water. A few meters away from the air profile system, we cut out peat blocks, and inserted the sensors horizontally in the pit face at 5, 10, 20 and 40 cm depth at a hummock, and 5 and 10 cm depth at a hollow. Thermocouples were also installed next to the sensors to monitor peat temperature. The peat blocks were carefully returned to the pits. Peat pore space CO_2 concentration and temperature were measured at 5-minute intervals and averaged every half hour on a datalogger (CR21X, Campbell Scientific, UT, USA).

3.3.4 Ancillary Field Measurements

We installed thermocouples into the peat at 10 cm depth inside each of the chamber cylinders to monitor peat temperature at 1 Hz for the calculation of half-hourly averages. Continuous 30-minute records of water table position were obtained with a capacitance water level probe (Model Odyssey, Dataflow Systems, New Zealand) placed inside a perforated ABS tube (3.8 cm i.d.) in the peat besides each chamber. A perforated PVC tube (1.25 cm i.d.) was installed next to each ABS tube to manually measure water table position at weekly intervals in order to calibrate the capacitance probe records.

Friction velocity (u_*), a generalized velocity defined as the square root of shear stress divided by density, was computed every 30 minutes as:

$$u_* = \left[\left(\overline{u'w'}\right)^2 + \left(\overline{v'w'}\right)^2\right]^{1/4} \quad (3.1)$$

from 20 Hz measurements of wind velocity in three dimensions (u, v, and w) with a sonic anemometer (Model R3-50, Gill Instruments, UK) and rotated to a natural

wind coordinate system (Foken, 2008). The sonic anemometer was mounted on an instrument tower at a height of 3 m and was also used to compute cup wind speed. In addition, we measured air temperature (Model HMP35CF, Campbell Scientific Inc., UT, USA) 2 m above the surface, incoming photosynthetically active radiation (PAR, Model LI-190SA, LI-COR, NE, USA), and barometric pressure (Model CS105, Campbell Scientific Inc., UT, USA) at the site every 5 seconds and averaged them half-hourly (Lafleur *et al.*, 2003).

3.3.5 Data Analysis

Concentrations of CO_2 and CH_4 measured in the autochamber headspace were first corrected for water vapour dilution effects using water vapour concentration data from the LI-6262. Methane flux (μmol CH_4 m^{-2} hr^{-1}) and nighttime CO_2 efflux (mmol CO_2 m^{-2} hr^{-1}) were then calculated from:

$$F_{gas} = PVS / RTA \quad (3.2)$$

where F_{gas} is gas flux, P is barometric pressure (Pa), V is chamber geometric volume (m^3), S is rate of change in headspace gas concentration (expressed as μmol mol^{-1} hr^{-1} for CH_4 and mmol mol^{-1} hr^{-1} for CO_2), R is universal gas constant (8.3144 Pa m^3 mol^{-1} K^{-1}), T is air temperature (K), and A is surface area of autochamber (m^2). S is determined by linear regression of gas concentration in chamber headspace against time over a period of 1.5 minutes, after discarding the data in the initial 45 seconds following chamber closure. Fluxes were accepted only if $r^2 > 0.9$ ($p < 0.01$, N=19), except when CH_4 flux measured with a 15-min deployment period was ≤ 39 μmol m^{-2} hr^{-1} then a r^2 threshold of 0.7 was used due to both lower flux magnitude and sensitivity of analyzer signal output. The use of r^2 as a filtering criterion might underestimate the contribution of near-zero fluxes, yet the number of near-zero fluxes (±0.36 mmol CO_2 m^{-2} hr^{-1} and ±26 μmol CH_4 m^{-2} hr^{-1}) removed due to low r^2 was small (<5% of the whole data set for most chambers). Moreover, the u_* levels at which these rejected fluxes were measured had a similar distribution as for all the half-hourly u_* measured at the Mer Bleue site over a full year, indicating that the rejection of these small number of near-zero fluxes did not bias the analysis towards certain turbulence conditions. Poor

quality flux data obtained during periods of equipment failure (e.g. broken tubing) and system maintenance were also removed from analysis. All these quality control procedures led to the removal of 3 to 17% of all CO_2 fluxes and 2 to 28% of all CH_4 fluxes collected for a given chamber. Nighttime CO_2 respiration was calculated only when the half-hour PAR value was zero.

We also accounted for the water dilution effects in the air profile CO_2 concentration data and expressed these as μmol CO_2 mol^{-1} dry air. CO_2 concentrations measured by sensors in the peat profile were adjusted for temperature and pressure (Vaisala Inc., 2011). Half-hour CO_2 concentration gradient in the top 20 cm surface peat of hummock was then estimated as the slope of the linear regression between pore space CO_2 concentration (measured at 0, 5, 10 and 20 cm below peat surface) and peat depth. Pearson correlation analyses were conducted to establish relationships between gas fluxes, concentration gradient, and environmental variables. All the data filtering and statistical analyses were conducted in MATLAB R2009a (MathWorks, MA, USA).

3.4 Results

3.4.1 Atmospheric Turbulence and Autochamber Gas Fluxes

Figure 3.1 shows the diel variability of monthly mean CH_4 flux as measured using a 2.5 min deployment period in 2009 from three autochambers located at a sedge-dominated hollow, a shrub-dominated hollow, and a shrub-dominated hummock. These three chambers represented the range of the microtopography and plant communities commonly found in the Mer Bleue peatland. A distinct diel CH_4 flux pattern was observed throughout the year for all chambers, with lower emissions during the day than at night. The difference in minimum daytime and maximum nighttime CH_4 flux (see Figure 3.1) was greatest in the mid to late growing season between July and September. For instance, the difference was 703 μmol m^{-2} hr^{-1} at the sedge-dominated hollow in August but only 232 μmol m^{-2} hr^{-1} in November. Among the various collar locations, the diel

variation in CH_4 flux was smallest at the shrub-dominated hollow. For example, mean CH_4 flux in September decreased from a nighttime maximum to a daytime minimum by 41.1% at the shrub hollow, compared to 55.3% and 74.6% at the sedge hollow and shrub hummock, respectively (Figure 3.1).

Time series plot of half-hourly CH_4 flux and u_*, which characterizes the strength of atmospheric turbulence, shows that the two variables were tightly and inversely related (Figure 3.2). CH_4 fluxes were higher at night for most of the days over this two-week period when u_* was low. However, on DOY 206 when u_* increased throughout the 24-hour period without dropping at night, CH_4 flux decreased consistently over the same period without exhibiting the usual diel CH_4 flux pattern. It is also interesting to note that the response of one variable to the change in the other was very quick. For instance on DOY 204, a sharp drop in u_* in the middle of the day was followed by an immediate increase in CH_4 flux rate measured by the autochamber in the same half hour.

We further investigated the relationship between u_* and autochamber CH_4 flux by correlation analysis using the half-hourly data collected between June and September 2009. The data set was first stratified by air temperature in 5 °C classes to control for the effects of temperature on flux rate. Table 3.2 shows that CH_4 fluxes from all the autochambers were significantly and negatively correlated with u_* when air temperature was between 5 and 25 °C, while some of the autochambers did not have significant correlations for the 0-5 °C and 25-30 °C classes with smaller sample sizes. The relationships were stronger in the sedge-dominated chambers, with correlation coefficients ranging from -0.18 to -0.55. Apart from using the instantaneous CH_4 fluxes, we also rank ordered and binned the flux data by u_* into 20 groups (u_* range: 0-0.72 m s^{-1}, N=188-218 for each group) to examine the relationship between u_* and CH_4 flux. Negative relationships between the two are clearly seen from all the three differently located chambers (Figure 3.3). As mean u_* increased from 0.01 to 0.47 m s^{-1}, mean CH_4 flux decreased by 76.5% from 204 to 48 μmol m^{-2} hr^{-1} from the shrub

hummock chamber, by 71.0% from 967 to 280 μmol m^{-2} hr^{-1} from the sedge hollow chamber, but only by 32.1% from 523 to 355 μmol m^{-2} hr^{-1} from the shrub hollow chamber.

We also conducted correlation analysis to determine whether u_* had a significant relationship with autochamber CO_2 efflux, as was the case with CH_4 flux. We used nighttime CO_2 efflux measurements for this analysis to avoid the confounding effects of simultaneous CO_2 uptake and release. Nighttime CO_2 effluxes measured in all the autochambers were significantly and negatively correlated with u_*, with even stronger relationships than CH_4 fluxes (Table 3.3). Correlation coefficients obtained from sedge-dominated chambers were between -0.40 and -0.80, while those from shrub-dominated chambers were between -0.29 and -0.78. Moreover, the rank ordered and binned autochamber CO_2 effluxes (u_* range: 0-0.50 m s^{-1}, N=82-107 for each of the 15 groups) showed a decreasing trend at all three locations as u_* increased (Figure 3.4). Similar to CH_4 flux, we found that the extent of decrease in nighttime CO_2 efflux with u_* was smallest at the shrub hollow, with only a drop of 40.4% from 9.9 to 5.9 mmol m^{-2} hr^{-1}, compared to a reduction of 54.2% from 14.4 to 6.6 mmol m^{-2} hr^{-1}, and of 58.9% from 14.1 to 5.8 mmol m^{-2} hr^{-1} at the shrub hummock and sedge hollow respectively, as u_* rose from 0.01 to 0.31-0.33 m s^{-1}. The range of u_* was smaller for CO_2 than CH_4 effluxes because highly turbulent conditions were dominant during the daytime and largely excluded from the nighttime CO_2 efflux data set.

3.4.2 Atmospheric Turbulence and Surface Peat CO_2 Concentration Gradient

Ideally we would have liked to analyze the influence of atmospheric turbulence on the concentrations of CH_4 in the peat profile but it is very difficult to obtain non-destructive high frequency samples. It is possible that a membrane probe like those of Mastepanov and Christensen (2008) would be capable of continuous monitoring of subsurface CH_4 concentrations but we are unaware of this kind of probe being tested and subsequently used in peatlands. Instead, we investigated the influence of turbulence on gas dynamics in peat pore space by

examining the relationship between half-hourly u_* and pore space CO_2 concentration gradient in the top 20 cm of peat measured between June and September 2009. Figure 3.5 shows a general negative relationship between u_* and the rank ordered and binned (u_* range: 0-0.72 m s^{-1}, N=224-234 for each of the 20 groups) surface peat CO_2 concentration gradient. As u_* increased slightly under calm condition from 0.01 to 0.06 m s^{-1}, the mean CO_2 concentration gradient increased correspondingly from 21.3 to 26.4 μmol mol^{-1} cm^{-1}. Yet, as u_* further increased from 0.06 to 0.47 m s^{-1}, we observed a consistent and substantial decrease in mean CO_2 concentration gradient from 26.4 to 3.0 μmol mol^{-1} cm^{-1}. Moreover, the half-hourly surface peat CO_2 concentration gradient was strongly and negatively correlated with u_* (r = -0.56, $p < 0.01$, N=4490).

3.4.3 Effects of Chamber Deployment Period on Measured Fluxes

We operated two autochambers with an extended deployment period of 30 minutes (i.e. 24 lid closures/chamber/day) for four days and investigated how the fluxes derived from the rate of change in chamber headspace gas concentrations varied over 19 successive 1.5-minute periods. Figures 3.6a and 3.6c show that autochamber CH_4 fluxes from the sedge- and shrub-dominated lawns became relatively constant starting from the 9th and 7th 1.5-minute periods respectively, regardless of whether the flux increased or decreased during the initial period after chamber closure. Nighttime CO_2 efflux rates from both the sedge- and shrub-dominated chambers decreased consistently at the beginning of the measurement and then generally reached a stable level at approximately the 9th 1.5-minute period (Figs. 3.6b and 3.6d). Relative to the difference in flux between the 1st and 2nd periods, the mean absolute difference in CH_4 flux and nighttime CO_2 flux between the 8th and 9th periods was only 8-16% and 16-23%, respectively for a given chamber.

Figure 3.7 shows the time series of friction velocity and CH_4 flux from the sedge-dominated chamber calculated during various 1.5-minute periods over the 30 minutes of chamber deployment between DOY 177 and 181 (u_* range: 0.01-

0.51 m s^{-1}). Fluxes determined in the first 1.5-minute period, equivalent to those obtained with the original protocol using a 2.5-minute deployment period, still exhibited a diel pattern that was negatively correlated with u_*. However, for CH_4 fluxes determined in the 9th 1.5-minute period and beyond, diel variability and correlation with u_* disappeared. We found that in calm conditions, fluxes determined in the first 1.5-minute period were considerably higher than those in the later periods. In contrast, during times of strong turbulence, CH_4 fluxes obtained in the first 1.5-minute period were much lower than those obtained in the 9th 1.5-minute period and beyond.

Based on the above results, we assumed that fluxes determined in the 9th 1.5-minute period were no longer influenced by the atmospheric turbulence experienced prior to chamber closure and hence were more realistic. We then estimated the degree of flux over- or underestimation associated with a short deployment period of 2.5 minutes, by calculating the difference in fluxes determined in the 1st and 9th 1.5-minute periods when all the chambers were operated with a 15-minute deployment period between 6 July and 15 September 2010. The relationships between u_* and the overestimation of CH_4 and nighttime CO_2 flux at hollow sites were well described by quadratic equations with r^2 values between 0.44 and 0.74 (Figs. 3.8a to 3.8d). We found on average an overestimation of autochamber CH_4 flux of about 100% in calm conditions. The degree of flux overestimation gradually decreased towards zero as u_* increased up to 0.2 and 0.4 m s^{-1} at the sedge-dominated and shrub-dominated hollows respectively (Figs. 3.8a and 3.8c). When u_* increased even further, we observed a relatively constant underestimation of CH_4 fluxes. Flux underestimation when atmospheric turbulence was high was more pronounced at the sedge-dominated hollow (-57%) than the shrub-dominated counterpart (-9%). Similarly, nighttime CO_2 fluxes were overestimated at hollows by about 100% in calm conditions (Figs. 3.8b and 3.8d). As u_* increased to more than 0.5 m s^{-1}, we found a 13-21% underestimation of nighttime CO_2 flux based on the limited number of measurements made in windy nights. Meanwhile, at the shrub hummock site, the

overestimation of CH_4 and nighttime CO_2 fluxes varied greatly for a given u_* such that relationships with u_* were poorly described by quadratic equations with low r^2 values of 0.07 and 0.02 respectively.

We calculated the average overestimation of CH_4 flux for groups of u_* with a range of 0.1 m s^{-1} increasing at 0.05 m s^{-1} intervals based on the results in Figure 3.8. When u_* was within a range associated with an average flux overestimation or underestimation of less than 20%, CH_4 fluxes collected with a 2.5-minute deployment period were retained in the data set. The u_* threshold for accepting fluxes was smaller in both magnitude and range for a sedge-dominated (0.15-0.3 m s^{-1}) than a shrub-dominated hollow (0.25-0.6 m s^{-1}). This filtering resulted in a data set of 596 to 3887 CH_4 fluxes per chamber through the 2009 measurement period after removing 51.3 to 92.5% of the flux measurements per chamber. Figure 3.9 shows the diel variability of monthly mean CH_4 flux in 2009 from autochambers at the three sites (also illustrated in Figure 3.1) after filtering with u_* thresholds. After filtering, the monthly variability of CH_4 fluxes from autochambers was still clear, but much of the diel flux patterns shown in Figure 3.1 disappeared.

3.5 Discussion

Friction velocity is commonly used as a measure of atmospheric turbulence and momentum transfer between the atmosphere and plant canopy (Foken, 2008). While we found significant, negative correlations between u_* and autochamber CH_4 and nighttime CO_2 fluxes (Tables 3.2 and 3.3), previous studies have reported a positive effect of turbulence on ecosystem gas fluxes. Using the eddy covariance technique, near-surface turbulence was shown to enhance ecosystem level CH_4 fluxes from a Siberian polygonal tundra with a high surface coverage of water bodies (Wille *et al.*, 2008) and a Russian boreal peatland with a water table above the peat surface during the snowmelt period (Gažovič *et al.*, 2010), due to turbulence-induced gas transfer across the air-water interface and release of gas bubbles that were adhered to the water surface. This mechanism

does not occur at Mer Bleue because of the much lower water table. Measurements with closed dynamic chambers equipped with vents also demonstrated a higher CO_2 efflux from soils of a deciduous forest and a temperate cropland as wind speed increased (Bain *et al.*, 2005; Suleau *et al.*, 2009). As strong winds blow across the chamber vent tube, a pressure deficit develops inside the chamber (a phenomenon known as the Venturi effect) which is compensated for by mass flow of CO_2-enriched air from soils into the chamber headspace (Conen and Smith, 1998). Although we had no available data on chamber pressure to exclude the possibility of a Venturi effect, we did not observe enhanced gas fluxes under windy conditions at the Mer Bleue bog.

Using an open dynamic chamber that enabled changes in atmospheric pressure to be transmitted to the soil surface, Rayment and Jarvis (2000) found that atmospheric turbulence enhanced soil CO_2 efflux from a boreal black spruce forest, with stronger effect at sites with a thicker layer of porous peat. Moreover, Subke *et al.* (2003) observed a positive correlation between the standard deviation of horizontal wind velocity and CO_2 efflux rate from a spruce forest soil by employing the same chamber system. They suggested that the increase in soil CO_2 fluxes was a result of pressure pumping induced by wind actions. When wind passes over an uneven surface or changes in speed and direction, high frequency pressure fluctuations over the soil surface are created. The presence of static horizontal pressure difference can then cause a mass flow of gas horizontally and vertically in the soil and eventually out to the atmosphere along the pressure gradient (Takle *et al.*, 2004). This explains the decrease in the amount of CO_2 stored in the soils of a permanent grassland (Flechard *et al.*, 2007) and pine forest (Maier *et al.*, 2010) with increasing turbulence. Similarly at Mer Bleue, the CO_2 concentration gradient in the top 20 cm of peat was greatly diminished under highly turbulent conditions compared to calm conditions (Figure 3.5). Hirsch *et al.* (2004) also reported a negative relationship between u_* and CO_2 concentration gradient in the top 5 cm litter layer of a boreal forest but attributed this to wind flushing or directly penetrating into the highly porous and air-filled layer near the

moss surface. Since the Mer Bleue bog has a low water table and high surface peat porosity, the large volume of air-filled peat pore space may facilitate wind flushing into the surface peat in addition to turbulence-induced pressure pumping, resulting in depletion of accumulated gases and reduction of the belowground gas concentration gradient.

Although atmospheric turbulence was not expected to alter the closed environment inside the chamber headspace, between measurements (over 90% of time), the chamber was left open and hence the surface peat inside the collar was subject to pressure pumping and wind flushing effects under highly turbulent conditions. With the chamber closed, the diffusive CH_4 and nighttime CO_2 effluxes were small (Figs. 3.3 and 3.4) owing to a reduced concentration gradient caused by turbulence before chamber deployment. Given the short deployment period of 2.5 minutes, there was insufficient time for the diffusive concentration gradient to be re-established and much of the gases produced were stored in peat rather than released into the chamber headspace. Using a longer chamber deployment period of 30 minutes, we show that CH_4 flux rate obtained in turbulent conditions was initially low, but increased over time and reached a stable level ~13 minutes after chamber closure (Figs. 3.6 and 3.7). The attainment of constant flux suggested that at this time, the net rate of gas production (i.e. production minus consumption) in the peat matched that of diffusive flux from the peat into the chamber headspace. Assuming fluxes determined in the 9^{th} 1.5-minute period best represented the net gas production rates, we found underestimations of 13-21% for CO_2 and 9-57% for CH_4 fluxes for a given chamber associated with measurements made during strong turbulence ($u_* > 0.5$ m s^{-1}) with a deployment period of 2.5 minutes (Figure 3.8). Kutzbach *et al.* (2007) observed that for 20-40% of their peatland flux measurements, the curves of headspace concentration evolution over time had a concave-down shape that could not be explained by the exponential model developed based on biophysical theory. Our findings suggest that their measurements showing an increase in CO_2 efflux over time might have been made when atmospheric turbulence was strong

such that belowground concentration gradients were small due to wind flushing and/or pressure pumping before chamber deployment.

On the other hand, we observed substantial overestimation of both CH_4 and nighttime CO_2 effluxes of near 100% in calm conditions when u_* was low (Figure 3.8). Results using an extended deployment period show that measured fluxes were very high immediately after chamber closure and then decreased rapidly over the first 13 minutes before stabilizing (Figure 3.6). It has been suggested that fluxes measured by closed chambers tend to decrease continuously with time, as build-up of gases in the chamber headspace reduces the diffusive concentration gradient, which in turns lowers the diffusive flux as a feedback from the chamber to soil (Livingston *et al.*, 2005). Yet, such chamber feedback was unlikely to be the major cause of flux decrease seen at the beginning of our measurements, since fluxes were maintained at a relatively constant level after the initial period rather than exhibiting a further decreasing trend. We suggest that the large gas flux initially obtained was caused by chamber-induced disturbance. In calm conditions, molecular diffusion dominates gas transport and a thick atmospheric interfacial layer with steep concentration gradient develops near the peat surface. As the chamber closes, the fan equipped on the chamber lid and the air stream circulated through the sample tubing to the gas analyzers facilitate mechanical air mixing in the headspace and disrupts the interfacial layer, thus instantaneously lowering the gas concentration just above the peat surface. This immediately leads to a sharp increase in gas concentration gradient from the peat to the atmosphere and hence the increase in gas flux rate (Hutchinson *et al.*, 2000). Based on manual chamber measurements in a boreal peatland, Schneider *et al.* (2009) found an 18-31% overestimation of cumulative seasonal nighttime ecosystem respiration if CO_2 fluxes measured during calm conditions were included in the dataset. A test of this hypothesis would be to remove the fan and measure fluxes in calm nights, but we have not done this experiment to-date.

The effects of turbulence on chamber flux measurements vary both

spatially and temporally. At hollows, the diel difference in CH_4 flux measured with a short deployment period and the underestimation of fluxes during highly turbulent conditions were both larger at sedge-dominated than shrub-dominated sites. *Eriophorum* sedges at the Mer Bleue bog possess aerenchymatous tissues that act as gas conduits between the soil and atmosphere (Greenup *et al.*, 2000). By generating a pressure gradient, turbulence can induce a plant-mediated convective flow of gases from deep in the root zone to the atmosphere via the aerenchyma (Armstrong *et al.*, 1996). In addition, the large pool of CH_4 stored belowground causes the sedge sites to be highly susceptible to advective transport mechanisms (Forbrich *et al.*, 2010). As a result, the pore space gas concentration gradient and transient diffusive flux measured by autochambers in windy conditions were reduced to a much greater extent at sedge-dominated sites compared to sites dominated by shrubs lacking aerenchymatous tissues. Atmospheric turbulence had the smallest effect on gas fluxes measured at shrub-dominated hollows, owing to the presence of a high water table and absence of plant-mediated transport. The smaller volume of air-filled pore space for the full peat profile implies that effective diffusivity is reduced and only a small amount of gas enriched in CO_2 and CH_4 is released from soil into the atmosphere subsequent to chamber disturbance effects in calm conditions (Schneider *et al.*, 2009). Moreover, the wind flushing/pressure pumping effect is less pronounced at hollows as the air-filled peat layer that stores gas for potential mass flow is thinner. At hummocks, we found a substantial decrease in CH_4 and nighttime CO_2 fluxes in highly turbulent conditions (Figs. 3.3 and 3.4), due to the presence of a thick peat layer with high air-filled porosity. However, flux measurement bias associated with a short chamber deployment period varied considerably at hummocks even under the same u_* (Figure 3.8), possibly because of the inherently high variance of CO_2 flux (Schneider *et al.*, 2009) and small magnitude of CH_4 flux. Temporally, the diel difference in CH_4 flux was largest in the mid-growing season around August and September, because a large amount of CH_4 was produced by active methanogenesis during this period when peat temperature and root exudation were relatively high. Consequently, the amount of CH_4 stored

in peat pore space was large (Blodau *et al.*, 2007), thereby enhancing the effects of wind flushing/pressure pumping and chamber-induced disturbance on flux measurement bias.

Closed chambers are only capable of measuring diffusive and ebullition flux but not mass flow and hence cannot provide a good estimate of the actual rate of peatland-atmosphere gas exchange particularly in times of strong turbulence. Rayment and Jarvis (2000) reported a 2-14% underestimation of soil CO_2 efflux from a boreal forest when the influence of turbulence was not taken into account in flux determination. Some researchers have addressed this issue by correcting the surface gas fluxes measured by chambers with the pore space gas storage fluxes (Hirsch *et al.*, 2004; Maier *et al.*, 2010). Yet, changes in the amount of gas stored in pore space belowground depend on both present and antecedent meteorological conditions, leading to difficulty in using the strength of atmospheric turbulence to estimate the contribution of mass flow to the overall flux (Subke *et al.*, 2003). A brief gust of wind will cause a larger change in gas storage if it follows a calm period than if it follows a prolonged period of strong turbulence which would have already depleted the gas stocks within the pore space. Meanwhile, the reduction in concentration gradient created by the gust of wind in both cases implies that gas fluxes obtained by closed chambers with a short deployment period will likely be low. Instead, we suggest that closed chambers can be used to estimate the net gas production rate when deployed for a long enough time that the initial turbulence-related effects are no longer observed. However, it is likely that the net CH_4 production rate determined will be overestimated if ebullition occurs during a chamber measurement, as gas bubbles containing previously generated CH_4 are released into the atmosphere at a much greater rate than diffusion alone.

Attempts have been made to compare upscaled chamber fluxes to ecosystem level fluxes measured by eddy covariance system in peatlands (e.g. Forbrich *et al.*, 2011; Laine *et al.*, 2006; Riutta *et al.*, 2007a), but such

comparisons should take into account the potential artefacts of both chamber and eddy covariance measurements. In highly turbulent conditions, eddy covariance may measure a higher gas exchange rate than the biological flux due to enhanced gas transport from soil induced by pressure changes (Gu *et al.*, 2005), while closed chambers miss the mass flow component and may measure smaller fluxes when deployed for a short period because of the transient reduction in concentration gradient, or in some cases, may measure larger fluxes due to pressure pumping as winds blow over the vent tube (Conen and Smith, 1998). On the other hand, in calm conditions, the eddy covariance method underestimates gas fluxes because of insufficient turbulent mixing, presence of drainage flows, and errors in estimating the rate of change in gas storage below the height of eddy covariance instrumentation (Aubinet, 2008; Baldocchi, 2003), while chamber deployment perturbs the atmospheric boundary layer and may result in flux overestimation. Using the same autochamber system as ours in a boreal peatland, Cai *et al.* (2010) found higher seasonally integrated respiration rates from chambers than from eddy covariance, which might be partly caused by chamber artefacts that could result in overestimated CO_2 fluxes in calm nights.

Chamber deployment period is an important consideration when making flux measurements. It is preferable to deploy chambers for a period as short as possible to minimize plant stress caused by increasing temperature and build-up of moisture in the headspace over time. Moreover, the use of a short deployment period diminishes chamber feedback effects associated with reducing concentration gradients between the soil and headspace (Davidson *et al.*, 2002), enables a linear increase in headspace gas concentration for flux determination (Kutzbach *et al.*, 2007) and reduces the errors of flux estimates from soils with non-uniform physical properties through the profile (Venterea and Baker, 2008). Furthermore, shortening the deployment period by half in an automated chamber system implies a doubling of the number of measurements that can be made. In spite of all the advantages associated with a short deployment period, we show at the Mer Bleue bog that initial changes in headspace concentration after chamber

closure were greatly affected by turbulence conditions prior to chamber deployment and thus should not be used in flux calculation. This is especially important for the application of non-linear regression in estimating fluxes. Although non-linear regression takes into account the effects of chamber feedback, it is highly sensitive to the initial slope of headspace gas concentration versus time (Forbrich *et al.*, 2010; Kutzbach *et al.*, 2007). It should be noted that the time it takes for the measured flux to reach a stable level unaffected by pre-deployment turbulence conditions is probably a function of peat porosity, water table, plant type and fan speed, and hence should be determined for specific sites and chamber systems.

The calculation of gas fluxes from concentration change in chamber headspace often assumes implicitly that the headspace turbulence is constant and equal to ambient conditions during deployment (Kutzbach *et al.*, 2007). Yet this assumption can hardly be met in the field, as atmospheric turbulence is always changing while the turbulence inside the headspace of a closed chamber is constant. Peatland CH_4 flux is commonly quantified by deploying manual static chambers and withdrawing air samples in the headspace periodically (e.g. every 5 minutes) over the deployment period (e.g. 25 minutes) for subsequent CH_4 analysis in the laboratory (e.g. Moore *et al.*, 2011; Pelletier *et al.*, 2007). Based on an automatic closed dynamic chamber system measuring gas concentrations at 1 Hz, our findings suggest that CH_4 concentration change will be most influenced by turbulence during the initial 5 minutes and then progressively less with time. Such variations in CH_4 flux rates during deployment of manually sampled static chambers are difficult to detect because of the small number of data points. Similarly, the turbulence-related impacts on CO_2 efflux is hardly noticed in measurements with manual dynamic chambers when the duration of deployment is short (~2.5 minutes), although the infrared gas analyzer typically measures CO_2 concentrations with a high temporal resolution (e.g. Bubier *et al.*, 2003a; Pelletier *et al.*, 2011). Further study should be done to investigate the effect of turbulence on gas concentration evolution in the headspace of manual chambers, for example

by sampling air and analyzing for CH_4 concentration every minute for a half hour, and monitoring the change in headspace CO_2 concentration in darkness over a longer deployment period. This will allow us to test the assumption of a constant rate of headspace concentration increase throughout the deployment period used in determining CO_2 and CH_4 effluxes.

Since fluxes are underestimated and overestimated in high and low turbulence conditions respectively, closed chambers when deployed only for a short time are most likely measuring the 'true' biological fluxes at some intermediate atmospheric turbulence levels. The friction velocity thresholds we derived to filter the CH_4 fluxes measured with a 2.5-minute deployment period was successful in eliminating the diel pattern of CH_4 flux and could be potentially used to estimate the biological CH_4 flux. However, since the nighttime CO_2 fluxes were typically measured in calm conditions and hence overestimated, a filtering approach similar to the one used for CH_4 might have removed the bulk of available data. Instead, we suggest estimating the biological CO_2 source strength by correcting all the nighttime CO_2 efflux data based on the empirical relationship between measurement bias (i.e. % overestimation) and friction velocity (Figure 3.8). We do not filter or correct the daytime CO_2 flux data as carbon exchange during this period is dominated by plant uptake. However, as daytime periods are often fairly turbulent, the diffusive soil respiration component of the chamber CO_2 flux is likely underestimated. Based on an aggregated data set from chamber measurements at five sites, Frolking *et al.* (1998) reported a midseason average ecosystem respiration of 2.0 μmol m^{-2} s^{-1} and maximum net ecosystem CO_2 exchange of -2.5 μmol m^{-2} s^{-1} for northern bogs. Using these values, if chamber CO_2 efflux is underestimated by 20% during turbulent conditions, then the magnitude of maximum daytime net ecosystem CO_2 exchange measured by closed chambers at Mer Bleue with a deployment period of 2.5 minutes will be overestimated by 16%.

3.6 Conclusions

We demonstrated that the diel pattern of autochamber CH_4 flux was caused predominantly by a change in the physical processes of gas transport in relation to atmospheric turbulence. CH_4 and nighttime CO_2 effluxes measured with a 2.5-minute deployment period were negatively correlated with u_*. In highly turbulent conditions, underestimation of transient fluxes was caused by reduction of diffusive concentration gradient from wind flushing and/or pressure pumping, as shown by our pore space CO_2 concentration data in surface peat. In calm conditions, chamber-induced disturbance of the atmospheric interfacial layer likely steepened the gas concentration gradient between the peat and atmosphere, which subsequently increased the transient gas flux. This measurement artefact associated with a difference in headspace turbulence before and during chamber deployment created a bias in fluxes measured in the initial 13 minutes after chamber closure. The constant chamber fluxes obtained after this initial period can be used to indicate the strength of biological source of CO_2 and CH_4, as a quasi-equilibrium between the net rates of gas production and gas exchange across the peat surface is likely attained.

We expect turbulence-related measurement bias to be more significant in ombrotrophic bogs than minerotrophic fens, because of the presence of a lower water table and higher air-filled peat porosity that provides an environment more conducive to mass flow of gases from the peat pore space. A pressure pumping effect (or ventilation) has been observed as well in other ecosystems that have porous substrates for gas storage, e.g. boreal forests with moss in the understory (Hirsch *et al.*, 2004), snowpack-covered meadows and forests (Massman and Frank, 2006), and carbonate ecosystems with subterranean pores and cavities (Were *et al.*, 2010). Fluxes from closed chambers in settings like these should be interpreted with caution as they may not quantify the actual rate of gas exchange between soils and the atmosphere. Chamber deployment period should be carefully selected particularly for ecosystems with porous substrates such that headspace concentration data are collected beyond the initial period affected by chamber artefacts. The time required for chamber fluxes to reach a constant level

should be determined for each site and chamber system before actual flux measurement in the field. This bias is not only limited to closed autochambers, but may be more difficult to quantify with a manual closed chamber system owing to the often poorer temporal resolution of headspace concentration data. If the chamber is deployed for a period too short to eliminate this measurement artefact, we suggest filtering the CH_4 data set based on friction velocity thresholds and correcting the nighttime CO_2 data set based on established empirical relationships between measurement bias and u_* to estimate the biological fluxes of these gases.

Figure 3.1. Diel variability of monthly mean autochamber CH_4 flux from (a) sedge-dominated hollow, (b) shrub-dominated hollow, and (c) shrub-dominated hummock in 2009. Error bar indicates ± 1 standard error.

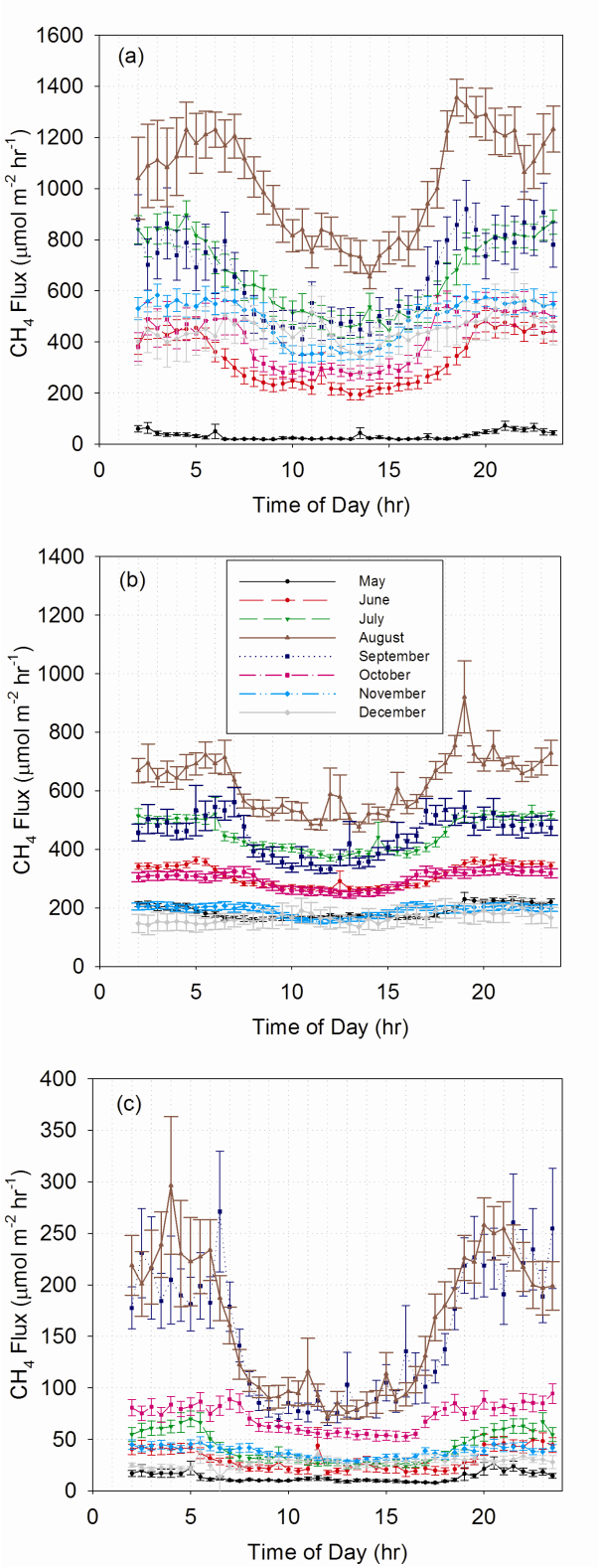


Figure 3.2. Time series of half-hourly friction velocity and CH_4 flux from an autochamber at a sedge-dominated hollow between DOY 200 and 214 in 2009.

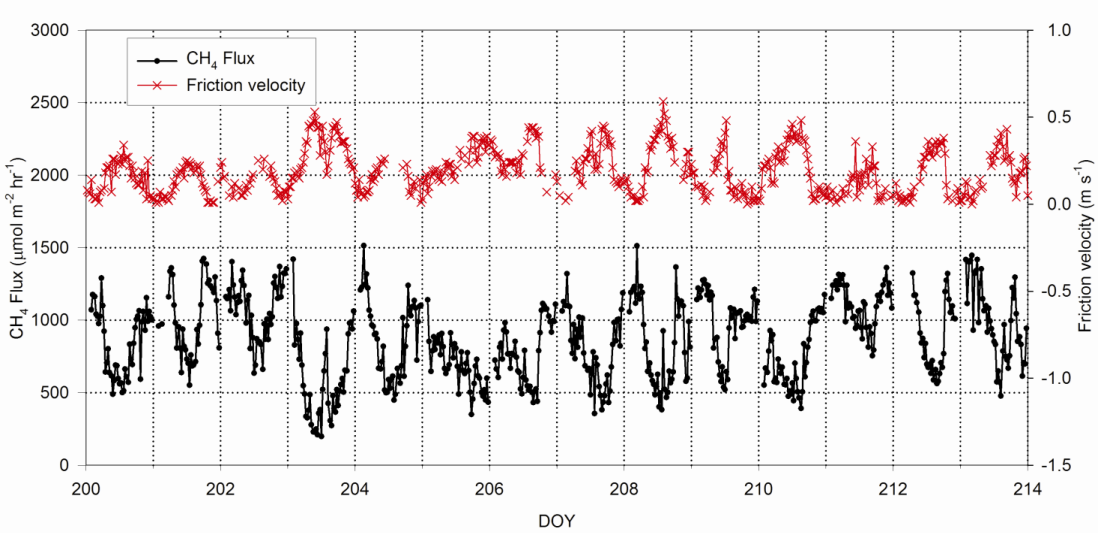


Figure 3.3. Relationship between half-hourly friction velocity and autochamber CH_4 flux from (a) sedge-dominated hollow, (b) shrub-dominated hollow, and (c) shrub-dominated hummock between June and September 2009. Fluxes were rank ordered and binned into 20 groups by friction velocity (N=188-218 for each group). Error bar indicates ± 1 standard error.

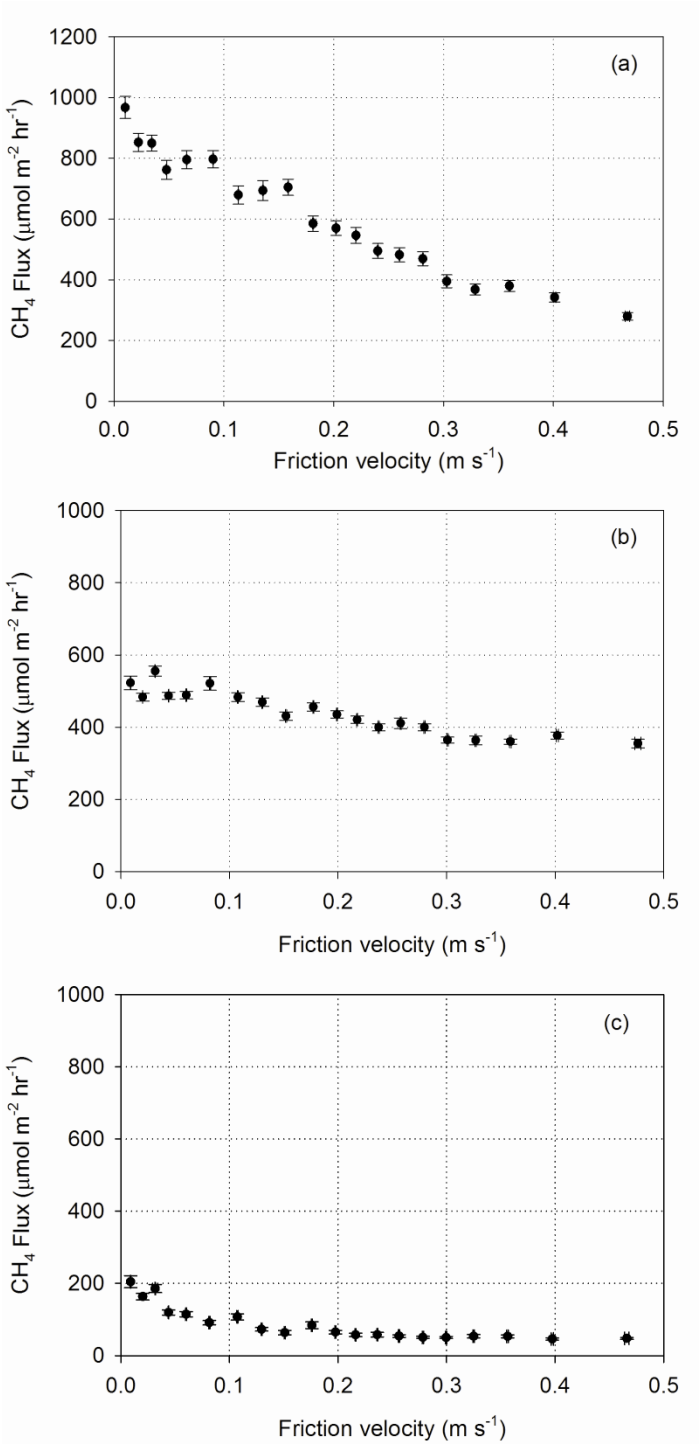


Figure 3.4. Relationship between half-hourly friction velocity and autochamber nighttime CO_2 flux from (a) sedge-dominated hollow, (b) shrub-dominated hollow, and (c) shrub-dominated hummock between June and September 2009. Fluxes were rank ordered and binned into 15 groups by friction velocity (*N*=82-107 for each group). Error bar indicates ± 1 standard error.

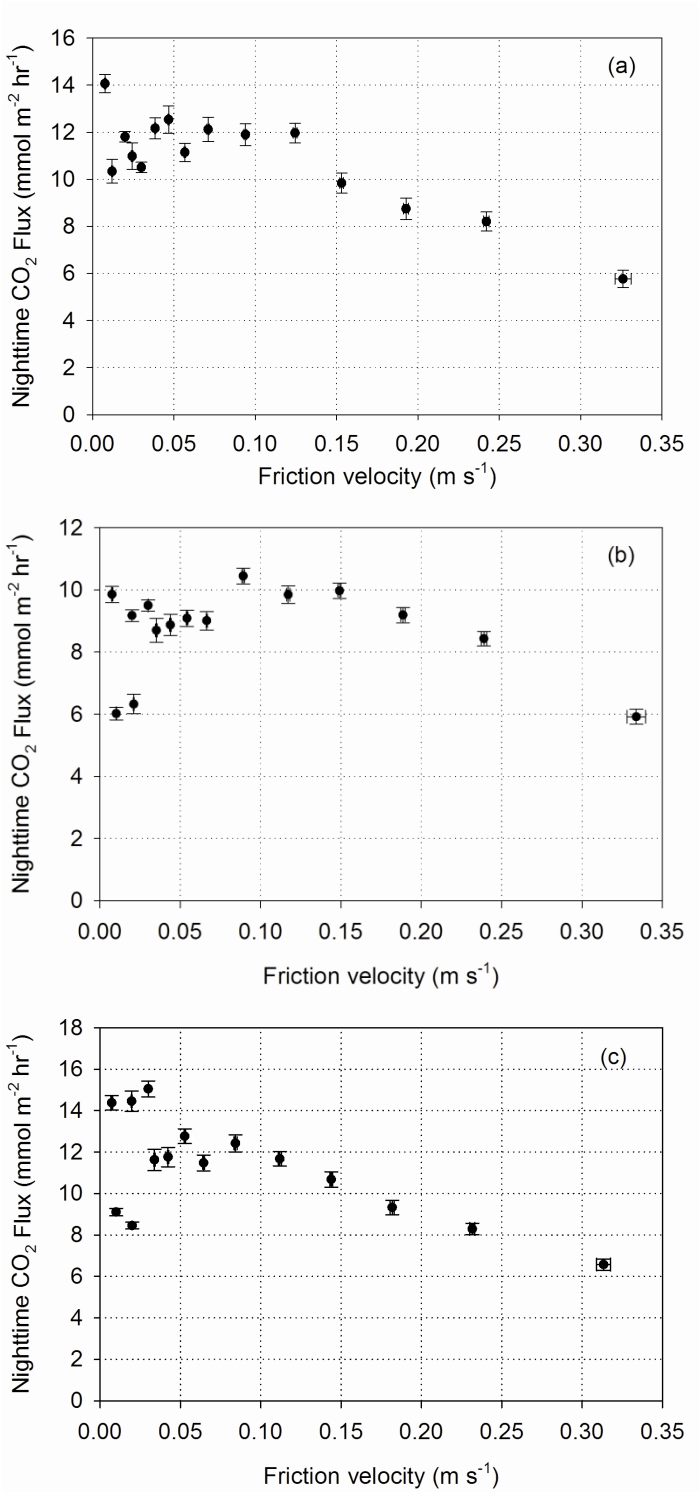


Figure 3.5. Relationship between half-hourly friction velocity and CO_2 concentration gradient in the top 20 cm peat of a hummock between June and September 2009. Gradients were rank ordered and binned into 20 groups by friction velocity (*N*=224-234 for each group). Error bar indicates ± 1 standard error.

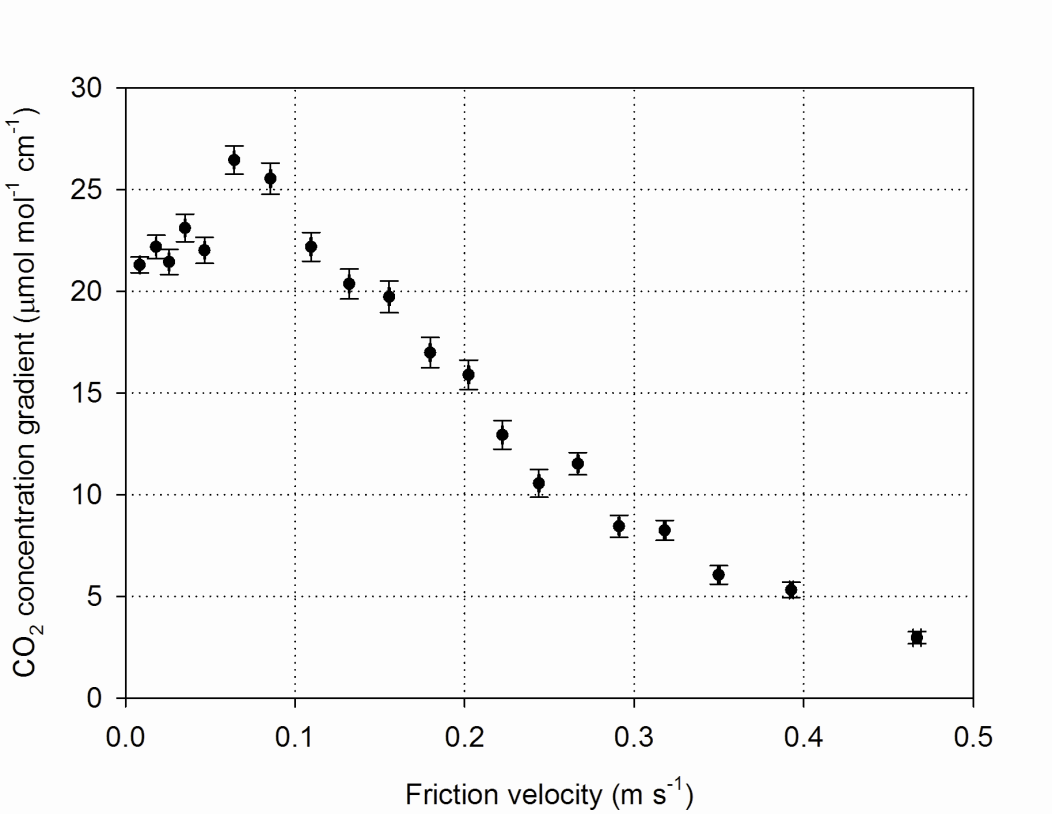
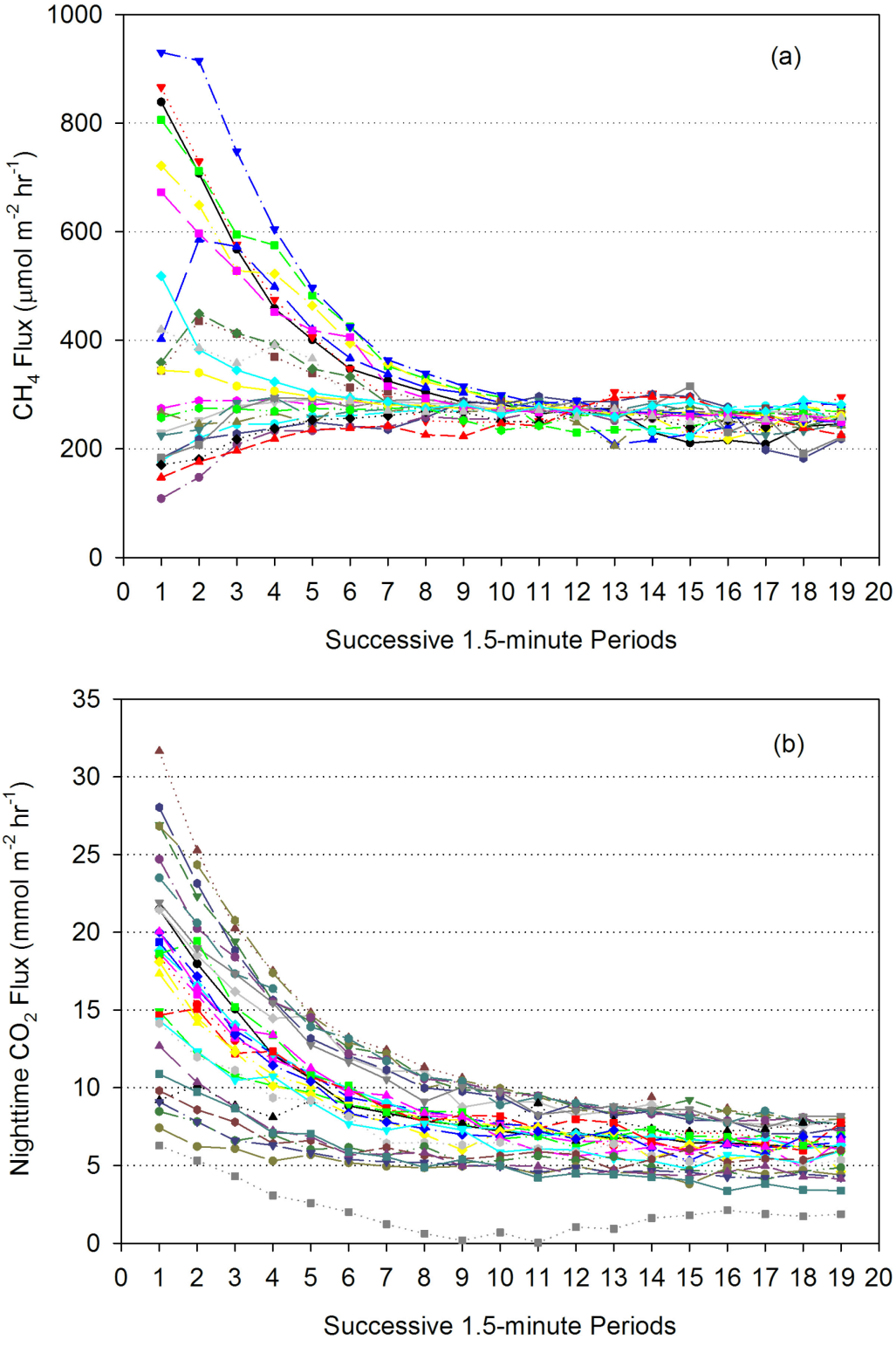
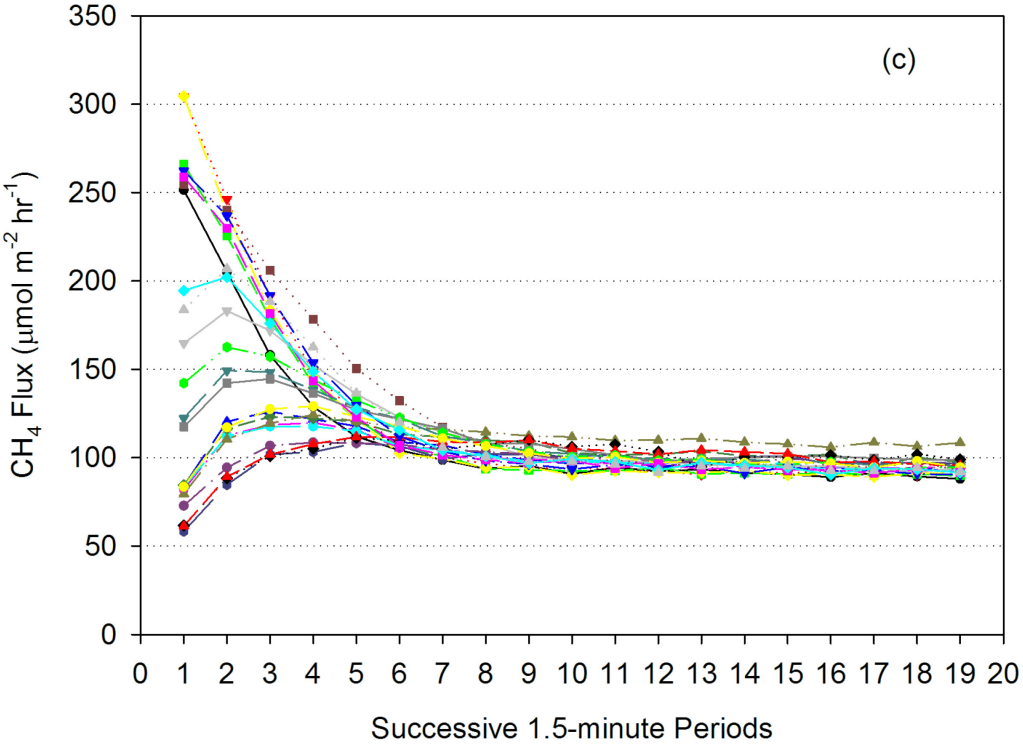


Figure 3.6. CH_4 flux (DOY 180) and nighttime CO_2 efflux (DOY 177-181) in 19 successive 1.5-minute periods over 30 minutes of chamber deployment, from: (a, b) a sedge-dominated chamber, and (c, d) a shrub-dominated chamber.




(c)
CH_4 Flux (µmol m^{-2} hr^{-1})
0
50
100
150
200
250
300
350
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Successive 1.5-minute Periods

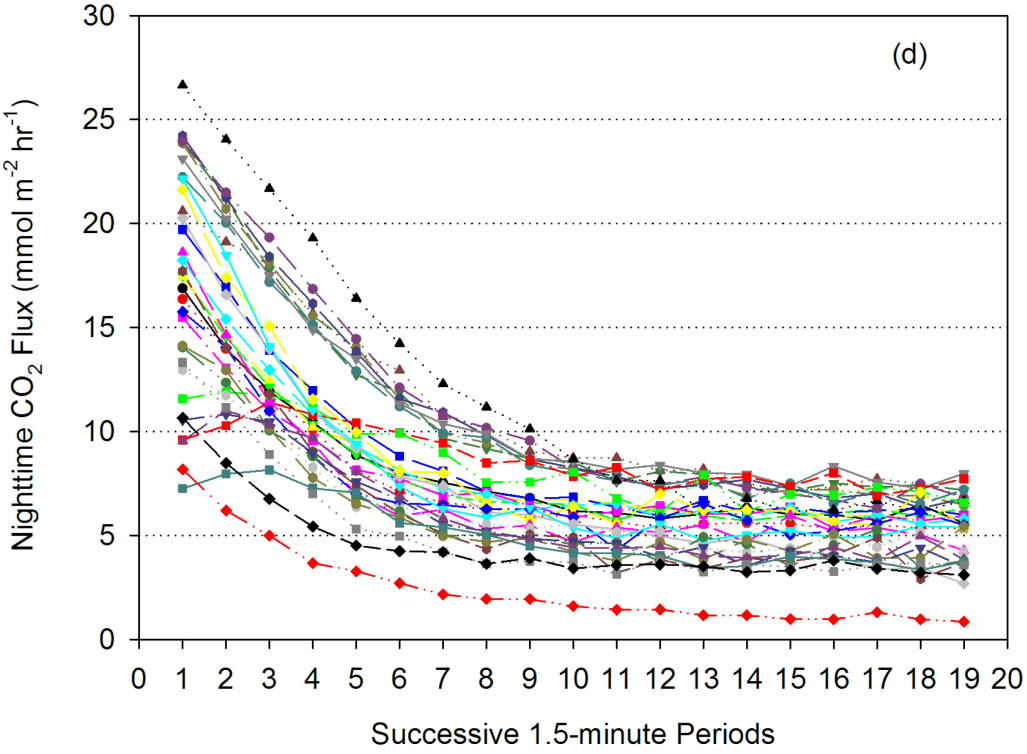

(d)
Nighttime CO_2 Flux (mmol m^{-2} hr^{-1})
0
5
10
15
20
25
30
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Successive 1.5-minute Periods

Figure 3.7. Time series of friction velocity and CH_4 flux from a sedge-dominated chamber determined from the 1st, 5th, 9th, 13th and 17th 1.5-minute periods over 30 minutes of chamber deployment. Note the logarithmic scale used on the y-axis.

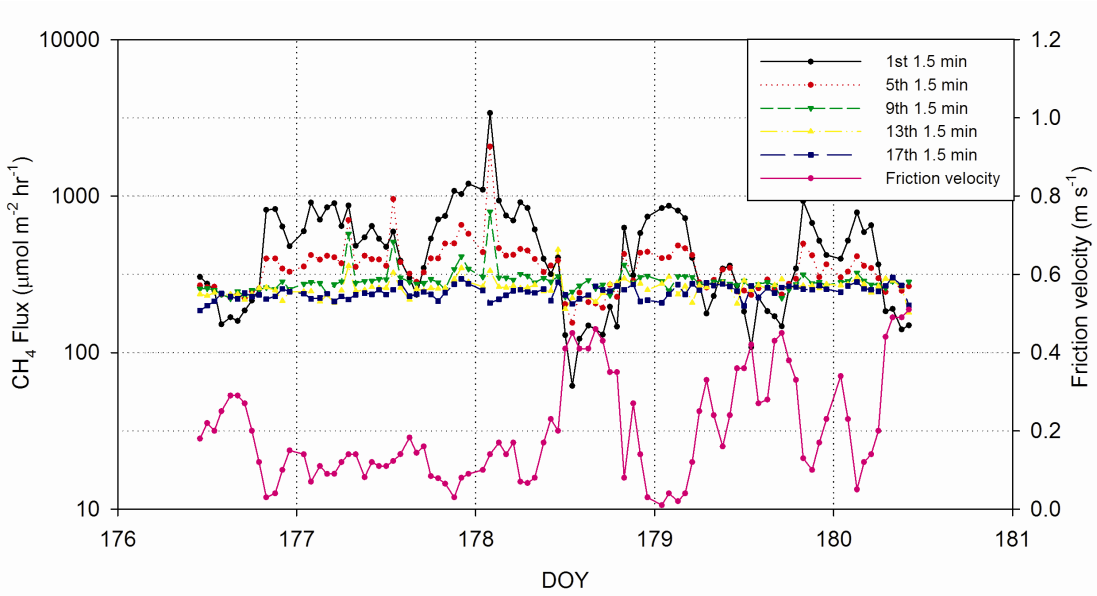


Figure 3.8. Percent overestimation of autochamber CH_4 and nighttime CO_2 flux associated with the use of a short deployment period of 2.5 minutes as a function of friction velocity, from (a, b) sedge-dominated hollow, (c, d) shrub-dominated hollow, and (e, f) shrub-dominated hummock, assuming that fluxes calculated based on headspace concentration change in the 9th 1.5-minute period were more realistic.

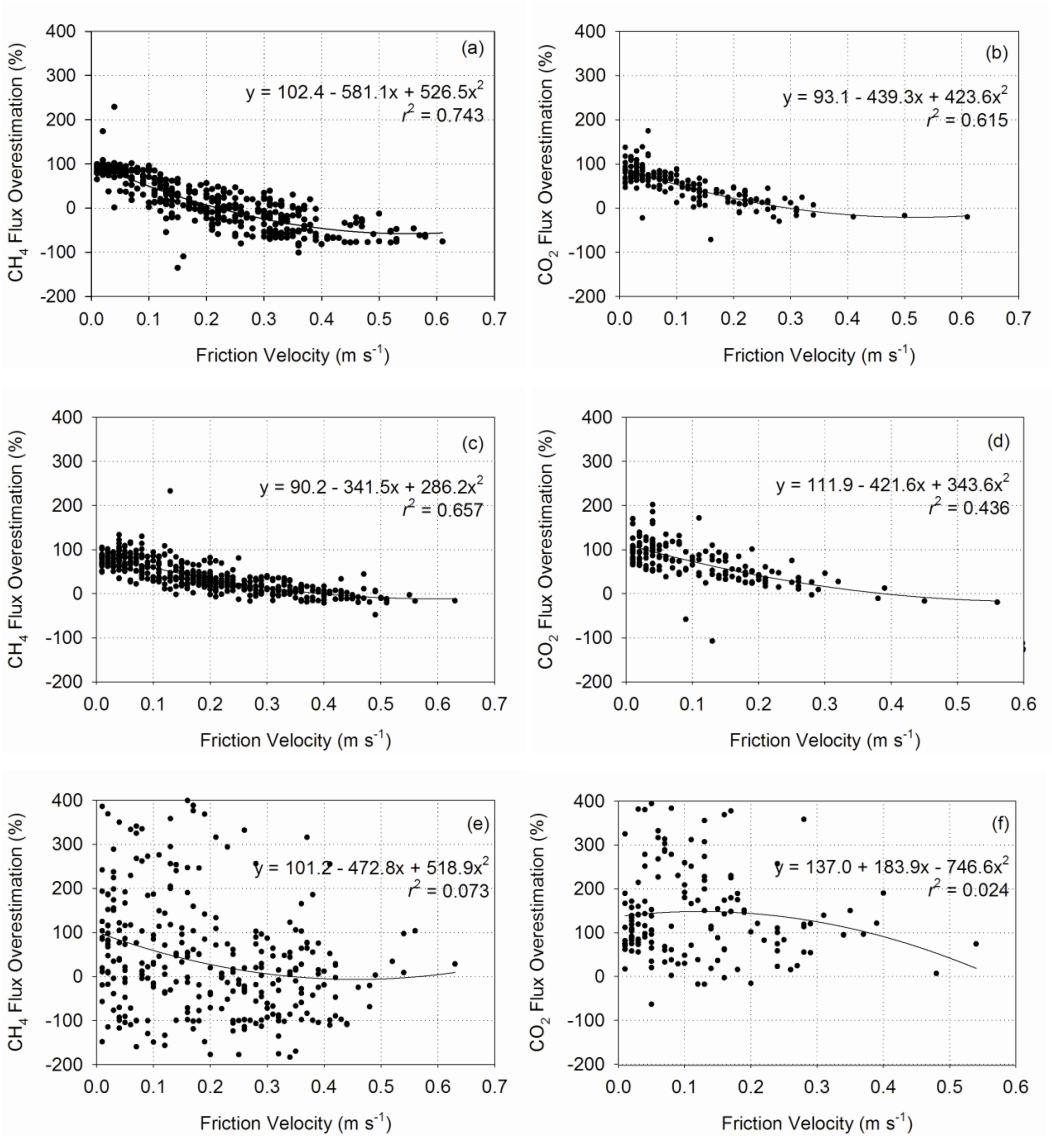


Figure 3.9. Diel variability of monthly mean autochamber CH_4 flux from (a) sedge-dominated hollow, (b) shrub-dominated hollow, and (c) shrub-dominated hummock in 2009 after filtering with thresholds in friction velocity. Error bar indicates ± 1 standard error.

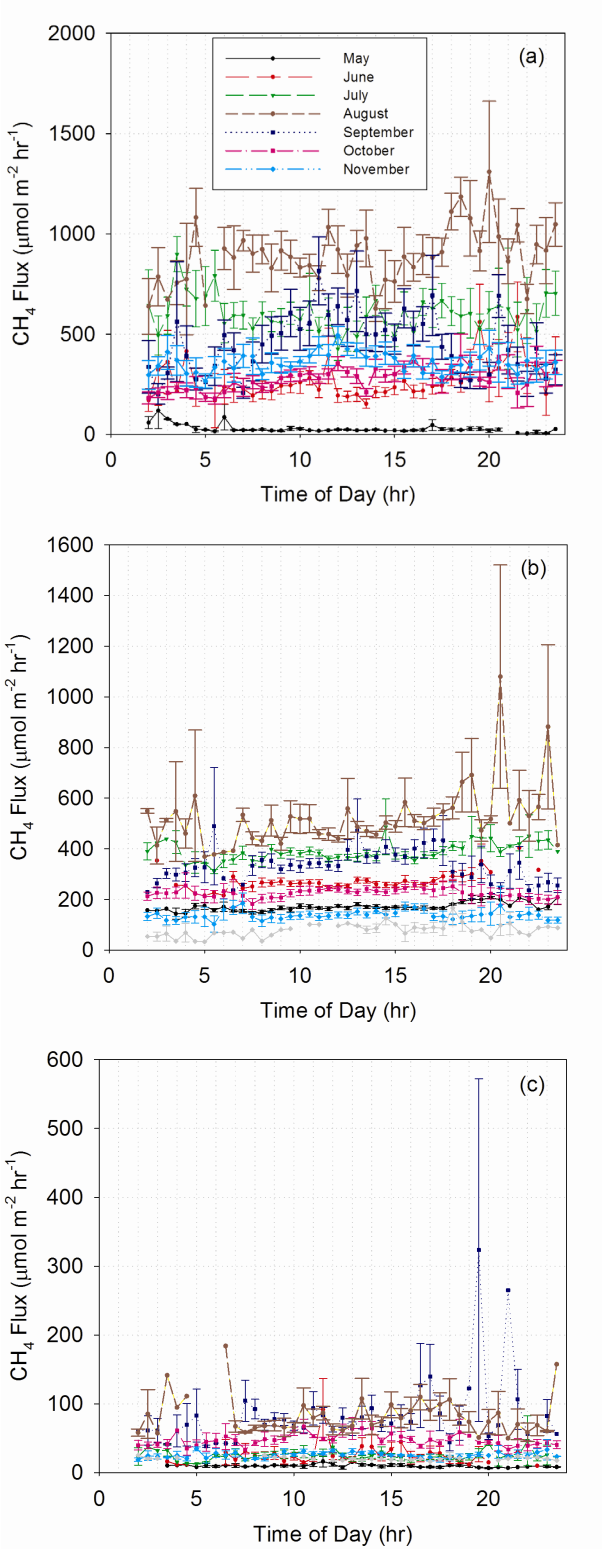


Table 3.1. Vascular plant species, mean water table depth (maximum and minimum depths in parentheses) and peak vascular green area index (VGA) for the 10 autochambers.

Chamber number	Vascular plant species[a]	Water table depth (cm)		VGA (m^2 m^{-2})
		2009[b]	2010[c]	
Sedge-dominated				
1	Ev, Vm, Lg, Ka	-24.8 (-36.3, -16.3)	-25.5 (-48.9, -13.7)	0.82
2	Ev, Cc, Lg, Vm, Ka	-29.5 (-45.3, -18.4)	-31.4 (-57.3, -18.7)	1.08
4	Ev, Lg, Cc, Ka	-18.7 (-29.2, -7.5)	-21.0 (-48.9, -7.3)	1.35
7	Ev, Cc, Mt, Lg	-19.1 (-32.8, -9.4)	-21.9 (-45.2, -8.2)	1.13
Shrub-dominated hollow				
8	Mt, Lg	-19.4 (-34.6, -8.8)	-18.9 (-44.1, -3.9)	2.09
10	Mt, Lg	-19.9 (-33.6, -9.6)	-22.2 (-45.9, -7.9)	2.00
Shrub-dominated lawn				
3	Cc, Vm, Mt, Lg	-29.2 (-41.9, -19.0)	-30.1 (-54.3, -14.5)	1.52
9	Lg, Mt, Ka	-24.0 (-36.4, -15.4)	-26.6 (-48.3, -12.7)	0.47
Shrub-dominated hummock				
5	Cc, Lg, Vm	-35.3 (-47.1, -24.8)	-37.0 (-63.1, -24.1)	1.12
6	Cc, Vm	-37.2 (-49.1, -26.0)	-38.0 (-61.8, -26.3)	1.56

Cc: *Chamaedaphne calyculata*, Ev: *Eriophorum vaginatum*, Ka: *Kalmia angustifolia*,

Lg: *Ledum groenlandicum*, Mt: *Maianthemum trifolium*, Vm: *Vaccinium myrtilloides*.

[a]In descending order of peak VGA. Only species with peak VGA > 0.1 m^2 m^{-2} are included.

[b]From DOY 142 to 341.

[c]From DOY 85 to 339.

Table 3.2. Correlation coefficients (*r*) between friction velocity and autochamber CH_4 flux stratified by air temperature in 5 ºC classes from June to September 2009[a].

	0-5 °C		5-10 °C		10-15 °C		15-20 °C		20-25 °C		25-30 °C	
Chamber	***r***	***N***	***r***	***N***	***r***	***N***	***r***	***N***	***r***	***N***	***r***	***N***
Sedge-dominated												
1	-0.20*	135	-0.41**	373	-0.45**	836	-0.46**	1326	-0.48**	1033	-0.22**	275
2	NS	129	-0.23**	341	-0.23**	756	-0.25**	1112	-0.37**	878	-0.18**	242
4	NS	133	-0.28**	352	-0.18**	768	-0.24**	1142	-0.28**	898	NS	241
7	-0.36**	119	-0.51**	313	-0.50**	769	-0.55**	1261	-0.49**	994	-0.34**	268
Shrub-dominated hollow												
8	-0.32**	137	-0.52**	381	-0.28**	837	-0.29**	1329	-0.24**	1037	NS	276
10	-0.34**	139	-0.47**	379	-0.38**	833	-0.30**	1330	-0.35**	1031	-0.20**	275
Shrub-dominated lawn												
3	-0.22**	137	-0.39**	378	-0.16**	828	-0.20**	1314	-0.35**	1027	NS	271
9	-0.26**	101	-0.41**	325	-0.11**	741	-0.16**	1193	-0.21**	940	-0.23**	270
Shrub-dominated hummock												
5	NS	130	-0.23**	278	-0.14**	625	-0.21**	1027	-0.36**	905	NS	260
6	-0.22**	137	-0.30**	376	-0.21**	828	-0.25**	1321	-0.29**	1023	-0.26**	276

[a]*r*, correlation coefficient; *N*, sample size; NS, not significant.

* significant at the 0.05 level; ** significant at the 0.01 level.

Table 3.3. Correlation coefficients (*r*) between friction velocity and autochamber nighttime CO_2 efflux stratified by air temperature in 5 ºC classes from June to September 2009[a].

	0-5 °C		5-10 °C		10-15 °C		15-20 °C		20-25 °C	
Chamber	***r***	***N***	***r***	***N***	***r***	***N***	***r***	***N***	***r***	***N***
Sedge-dominated										
1	-0.70**	134	-0.74**	278	-0.71**	453	-0.73**	440	-0.80**	86
2	-0.40**	127	-0.48**	255	-0.40**	403	-0.44**	369	-0.77**	77
4	-0.41**	126	-0.51**	242	-0.44**	393	-0.49**	371	-0.52**	69
7	-0.57**	102	-0.63**	216	-0.60**	390	-0.58**	423	-0.67**	84
Shrub-dominated hollow										
8	-0.29**	132	-0.50**	277	-0.48**	453	-0.41**	440	-0.54**	86
10	-0.40**	127	-0.49**	263	-0.34**	443	-0.49**	439	-0.66**	86
Shrub-dominated lawn										
3	-0.53**	134	-0.67**	278	-0.58**	453	-0.66**	440	-0.70**	86
9	-0.65**	103	-0.71**	243	-0.62**	406	-0.51**	399	-0.70**	82
Shrub-dominated hummock										
5	-0.33**	129	-0.56**	248	-0.42**	381	-0.36**	393	-0.60**	80
6	-0.48**	132	-0.55**	276	-0.55**	449	-0.64**	439	-0.78**	86

[a] *r*, correlation coefficient; *N*, sample size.

** significant at the 0.01 level.

Chapter 4

Spatial and Temporal Variations of Methane Flux Measured by Autochambers in a Temperate Ombrotrophic Peatland

Context within Thesis

I use the filtering protocol developed in Chapter 3 to produce a reliable data set of CH_4 flux unaffected by turbulence conditions prior to chamber deployment for analysis presented in this chapter. This chapter compares the seasonal mean CH_4 flux, determines the temporal variability of CH_4 emissions, and investigates the environmental and biotic controls over the season, among three vascular plant communities in a bog. In this study, I employ Pearson correlation analysis to examine the temporal relationships between simultaneously measured individual CH_4 fluxes and environmental and biotic parameters, while lagged relationships between CH_4 flux and plant production will be explored in greater detail in Chapter 6.

4.1 Abstract

We measured CH_4 flux at high temporal resolution with triplicate autochambers from three different plant communities at the ombrotrophic Mer Bleue bog in Canada to investigate the spatial and temporal variations, and factors that related to the CH_4 flux. Our results show that seasonal mean CH_4 fluxes from *Eriophorum*-dominated community were 1.4-2.2 and 3.7-5.5 times higher than those from *Maianthemum/Ledum* and *Chamaedaphne* communities, respectively. Despite covering only 30% of the peatland area, *Eriophorum* and *Maianthemum/Ledum* communities together contributed over half of the total CH_4 emission from this bog. Significant interannual variations in CH_4 flux were observed in *Maianthemum/Ledum* and *Chamaedaphne* communities, attributable to a 55-60% reduction of mean summer (July-September) CH_4 flux in 2010 as a consequence of a 5.5-9.0 cm lower mean summer water table compared to 2009. Temporal variability of log-transformed CH_4 flux was correlated ($r \geq 0.4$) with peat temperature only when water table was less than 20, 30 and 40 cm below the peat surface for *Maianthemum/Ledum*, *Chamaedaphne*, and *Eriophorum* communities, respectively. This difference in water table threshold among communities might partly be related to differences in rooting depth and hence the ability of plants to sustain CH_4 flux in dry conditions. Moreover, we found moderate relationships between CH_4 flux and maximum net ecosystem CO_2 exchange in both years from the *Eriophorum* community but only in the wet 2009 from the *Maianthemum/Ledum* community. These results suggest that modelling of CH_4 flux from ombrotrophic peatlands over time should take into account the role of different vegetation types, since the relationships between CH_4 emissions and environmental factors vary among vascular plant communities.

4.2 Introduction

Boreal and subarctic peatlands of the world contain between 270 and 370 Pg carbon (C) in peat (Turunen *et al.*, 2002), which comprises 12 to 16% of global C stored in the top 3 m of soils (Jobbágy and Jackson, 2000). These estimates become even higher when peatlands containing permafrost and at higher latitudes in the circumpolar region are included (McGuire *et al.*, 2009; Tarnocai *et al.*, 2009). Owing to the predominantly anaerobic conditions, northern peatlands release a large amount of C into the atmosphere in the form of methane (CH_4) gas, amounting to 12 to 37 Tg CH_4 annually (Chen and Prinn, 2006; Fung *et al.*, 1991; Mikaloff Fletcher *et al.*, 2004). There is a need to accurately quantify CH_4 emission as it is one of the key components of the net ecosystem carbon balance of peatlands (Roulet *et al.*, 2007). Moreover, CH_4 emission from northern ecosystems can cause strong feedbacks in atmospheric chemistry that substantially enhance climate warming (Isaksen *et al.*, 2011), and hence should be taken into account when assessing the overall radiative forcing impact of peatlands that continuously exchange greenhouse gases with the atmosphere (Frolking *et al.*, 2006).

The magnitude of CH_4 flux from peatlands is governed by the rates of CH_4 production by methanogens, CH_4 consumption by methanotrophs, and CH_4 transport via various pathways, which are in turn influenced by a number of environmental and biotic factors (Bubier and Moore, 1994). Because of the complex and co-dependence of the relationships among these controls, high spatial and temporal variability in CH_4 flux is often observed in northern peatlands (e.g. Dinsmore *et al.*, 2009; Hendriks *et al.*, 2010; Moore *et al.*, 1990). Most of the previous studies of CH_4 flux used manual chambers to investigate the spatial variations at plant community scale, but measurement was typically done only at weekly to monthly intervals because of labour and time constraints (e.g. Dinsmore *et al.*, 2009; Moore *et al.*, 2011; Treat *et al.*, 2007). This can potentially miss out some transient high CH_4 emissions induced by weather fluctuations within hours to days, which are more likely to be captured by autochambers that

carry out high temporal frequency flux measurements (Frolking and Crill, 1994). Autochambers have recently been used in an Arctic tundra to demonstrate a surprisingly large increase in CH_4 emission during the freeze-in period (Mastepanov *et al.*, 2008), though eddy covariance measurements at the same site show that such CH_4 burst does not always occur (Tagesson *et al.*, 2012). Autochambers have also been deployed in temperate and boreal fens to establish the relationships between CH_4 flux and its controls (Kettunen *et al.*, 2000), as well as quantify CH_4 ebullition events (Goodrich *et al.*, 2011). However, there is still a paucity of studies deploying autochambers in ombrotrophic bogs to measure community-scale CH_4 flux with a high temporal resolution.

Numerous studies have identified water table, peat temperature, and vegetation as the major controls of CH_4 emission from northern peatlands (Bellisario *et al.*, 1999; Laine *et al.*, 2007b; Moore *et al.*, 2011; Pelletier *et al.*, 2007). Seasonal mean water table in particular is often reported as the primary control of the spatial variability of CH_4 flux over long periods (Bubier *et al.*, 1993b; Moore *et al.*, 2011). Plant community can also serve as good predictors of seasonal mean CH_4 flux across some peatland sites because plants integrate numerous environmental drivers of CH_4 emission (Bubier, 1995; Dias *et al.*, 2010). However, no studies thus far have used high frequency flux data from ombrotrophic peatlands to quantify mean and total seasonal CH_4 emissions from individual plant communities and investigate how differences in CH_4 flux among communities vary over time with changing environmental conditions.

Seasonal variability of CH_4 flux is mostly influenced by temporal changes in peat temperature (Laine *et al.*, 2007b; Pelletier *et al.*, 2007), and is poorly correlated with water table depth (Frolking and Crill, 1994; Jackowicz-Korczyski *et al.*, 2010). However, Frolking *et al.* (2011) found that peatland CH_4 emissions cease completely once water table drops by a depth of 20-25 cm, based on a review of studies using lab and field manipulations, or in the events of extreme weather. Christensen *et al.* (2003a) observed that peat temperature was the

dominant factor influencing large-scale spatial variations in mean annual CH_4 flux across wet sites, but emissions could decrease considerably once water table dropped to over 10 cm below the peat surface. It is unclear whether water table can similarly override peat temperature in governing the temporal change of CH_4 flux especially over dry periods, and if so, whether the water table thresholds vary among plant communities in a bog.

Plant productivity is closely linked to peatland CH_4 emission through supplying labile carbon compounds to methanogens via root turnover and exudation (Joabsson and Christensen, 2001). Strong correlations between seasonal mean net ecosystem CO_2 exchange (NEE) and CH_4 emissions have been found at peatland sites with water tables close to or above the soil surface (Bellisario *et al.*, 1999). Yet, no significant relationship was observed among ridge sites of a boreal peatland with low water tables, as the majority of root exudates from plants were released into the aerobic zone and subsequently oxidized, instead of being utilized by methanogens in the anaerobic zone (Waddington *et al.*, 1996). There is a need to better understand whether CH_4 flux is correlated to plant production over the season, and whether the relationship changes between wet and dry periods as well as among plant communities with different rooting depths.

The objectives of this study are to use high temporal resolution flux data collected by autochambers at the Mer Bleue ombrotrophic bog to: (1) compare the seasonal mean CH_4 flux among three different plant communities, (2) characterize the seasonal and interannual variations of CH_4 flux from each plant community, (3) determine the environmental and biotic controls of CH_4 flux over the season for each plant community. We hypothesize that seasonal mean CH_4 flux is highest from a community dominated by the deep-rooted sedge *Eriophorum vaginatum*, followed by a community dominated by the forb *Maianthemum trifolium* and shrub *Ledum groenlandicum*, and lowest from a community dominated by the shrub *Chamaedaphne calyculata*. We also hypothesize that peak seasonal CH_4 flux occurs in late summer when peat temperature reaches a maximum, and

seasonal mean CH_4 flux is significantly lower in drier years than wetter years for *Maianthemum/Ledum* and *Chamaedaphne* communities with roots too shallow to reach the anaerobic zone at times of a low water table. We further hypothesize that peat temperature is the dominant temporal control of CH_4 flux, while water table becomes an overriding control when it drops to sufficiently low levels. *Eriophorum* community is hypothesized to have the deepest water table threshold above which strong flux-temperature relationships are maintained over time.

4.3 Methods

4.3.1 Site Description

Mer Bleue peatland is a 28 km^2 ombrotrophic bog located near Ottawa, Canada (45.41ºN, 75.52ºW). This region has a cool continental climate, with a mean annual temperature of 6.0 ± 0.8 ºC and mean annual precipitation of 944 mm (1971-2000 climate normals) (Environment Canada, 2011). Field measurements were made at a dome-shaped bog in the northwest part of this peatland. Peat depth reaches about 5 to 6 m near the centre of the bog, and is shallower (< 0.3 m) near the beaver pond margin (Roulet *et al.*, 2007). The surface of this peatland is completely covered by *Sphagnum* moss (*Sphagnum capillifolium*, *Sphagnum magellanicum*, *Sphagnum fallax*, *Sphagnum angustifolium*) and the vascular plant cover is dominated by low growing ericaceous evergreen shrubs (*Chamaedaphne calyculata*, *Ledum groenlandicum*, *Kalmia angustifolia*), with an occasional mix of deciduous shrub (*Vaccinium myrtilloides*), sedge (*Eriophorum vaginatum*) and forb (*Maianthemum trifolium*).

This bog has a hummock-lawn microtopography, with a mean difference of 17 cm in elevation between the hummock and lawn surfaces (Wilson, 2012). It is relatively dry, with a mean growing season (May to October) water table depth of 42.7 cm from the top of hummock over 1998-2008 (Teklemariam *et al.*, 2010). Depending on the microtopographic location, the top 10-30 cm peat at Mer Bleue is fibric and has a total porosity of greater than 0.9 (Dimitrov *et al.*, 2010).

4.3.2 Autochamber System

We installed nine autochambers at the Mer Bleue bog within a 15-m radius about 50 m south of the eddy covariance tower. These included three replicates each representing plant communities dominated by *Eriophorum*, *Chamaedaphne*, and *Maianthemum/Ledum*, respectively while covering a range of water table and leaf area (Table 4.1). Wooden boardwalks were constructed to minimize disturbance during access to the chambers. The dynamic, closed autochamber system established at this bog was identical to the one deployed in a moderately rich fen (Cai *et al.*, 2010) and several forests with mineral soils (Drewitt *et al.*, 2002; Griffis *et al.*, 2004). The autochamber consisted of a transparent Plexiglas dome fitted to a PVC cylinder with a hinged aluminum frame. The near semi-spherical dome had a height of 20.5 cm and the PVC cylinder had an internal diameter of 52 cm, a thickness of 1 cm and a height of 38.5 cm. Hence each autochamber covered a surface area of 0.21 m^2. The PVC cylinders were inserted 16 to 31 cm deep into the peat, leaving about 7 to 22 cm above the peat surface, but below the height of the top of the shrubs. A partially inflated bicycle tube sealed to the top of the cylinder and a foam gasket on the aluminum flange at the dome base ensured a good seal when the chamber was closed. A small brushless fan within the dome mixed the air in the chamber headspace and a coiled 50-cm long open-ended vent tube on the dome top ensured equilibration of pressure between the inside and outside of chamber during flux measurements.

Chamber selection, measurement timing and data acquisition of the autochamber system were controlled by a datalogger (CR23X, Campbell Scientific, UT, USA). A pneumatic cylinder assembly (Model BFT-173-DB, Bimba Manufacturing, IL, USA) connected to an oil-free air compressor (Model CPFAC2600P, Porter Cable, TN, USA) opened and closed the chamber domes. Sampling tubes (Synflex 1300, 4.3 mm i.d., Saint-Gobain Performance Plastics, NJ, USA) connected to the gas inlet and outlet located at the top of chamber dome led to a sampling manifold controlled by solenoid valves. Concentrations of CO_2

and CH_4 were measured by a closed-path infrared gas analyzer (LI-6262, LI-COR, NE, USA) and a fast methane analyzer based on off-axis integrated cavity output spectroscopy (DLT-100, Los Gatos Research, CA, USA), respectively. The LI-6262 was manually calibrated weekly using ultra-high purity nitrogen gas containing no CO_2 (for zero) and 356 μmol mol^{-1} of CO_2 (for span), and the fast methane analyzer was calibrated with CH_4 standard gas (1.8 and 5.01 μmol mol^{-1}) once at the beginning of measurement season. Air was circulated to the LI-6262 and back to the chambers at a flow rate of 3.5 L min^{-1} by an AC linear pump (Model DDL, Gast Manufacturing, MI, USA). The internal pump on the fast methane analyzer sub-sampled the air stream at approximately 0.5 L min^{-1}. The datalogger, pump, and gas analyzers were all placed inside temperature-controlled housings.

The autochamber system was in operation between 22 May (day of year [DOY] 142) and 7 December (DOY 341) in 2009 and between 26 March (DOY 85) and 5 December (DOY 339) in 2010. The chambers did not operate during the middle of the winter because of concern of damaging the pneumatics with heavy snow loads on the chamber domes. Chambers were left open over the winter when not in use. Prior to 6 July 2010, the autochambers were programmed to close sequentially to measure gas fluxes for 2.5 minutes to provide one measured flux for each chamber every 30 minutes. Fluxes were continuously measured between 0200 and 2400 h daily. From 6 July 2010 onwards, the chamber deployment period was increased from 2.5 to 15 minutes, and one flux measurement was made for each chamber every three hours. Analog outputs from the gas analyzers were sampled at 1 Hz by the datalogger, averaged every 5 seconds, and downloaded automatically to a PC located in a hut on site. All high frequency data were retained for flux processing.

4.3.3 Vegetation Monitoring

We monitored the seasonal change in vascular green area index (VGA) inside each autochamber following the method of Wilson *et al.* (2007). For each

vascular plant species, the total number of green leaves within the chamber and the width and length of 10 leaves from each of 3 selected plants were measured at 2- to 5-week intervals between May and October 2009. Species-specific formulae based on leaf geometry were then applied to determine the average leaf size that was further multiplied by the number of leaves and divided by chamber surface area to give the green area index of a vascular plant species (m^2 m^{-2}) on the day of measurement. This was followed by fitting green area index and day of year into a Gaussian model to estimate the daily green area index at the species level over the season. Finally, daily VGA of each autochamber was calculated by summing the green area index of all vascular plant species present.

4.3.4 Ancillary Field Measurements

We installed thermocouples into the peat at 10 cm depth inside each of the chamber cylinders to monitor peat temperature at 1 Hz for the calculation of half-hourly averages. Continuous 30-minute records of water table position were obtained with a capacitance water level probe (Model Odyssey, Dataflow Systems, New Zealand) placed inside a perforated ABS tube (3.8 cm i.d.) inserted in the peat besides each chamber. Friction velocity was computed every 30 minutes from 20 Hz measurements of wind velocity in three dimensions with a sonic anemometer (Model R3-50, Gill Instruments, UK) mounted on an instrument tower at a height of 3 m. In addition, we measured air temperature (Model HMP35CF, Campbell Scientific Inc., UT, USA) 2 m above the surface, incoming photosynthetically active radiation (PAR, Model LI-190SA, LI-COR, NE, USA), barometric pressure (Model CS105, Campbell Scientific Inc., UT, USA), and peat temperature at 20 and 40 cm depth beneath the hollow surface at the site every 5 seconds and averaged them half-hourly.

4.3.5 Data Analysis

Concentrations of CO_2 and CH_4 measured in the autochamber headspace were first corrected for water vapour dilution effects using water vapour concentration data from LI-6262. We calculated CH_4 effluxes from the

autochambers based on regression of the concentration trace over a period of 1.5 minutes, after discarding the data in the initial 45 seconds and 12.75 minutes for a chamber deployment period of 2.5 and 15 minutes, respectively. For the calculation of CO_2 uptake rate, the initial 45 seconds of concentration data were removed regardless of the chamber deployment period. Fluxes were accepted only if $r^2 > 0.9$ ($p < 0.01$, N=19), except when CH_4 flux measured with a 15-minute deployment period was ≤ 15 mg m^{-2} d^{-1} then a r^2 threshold of 0.7 was used due to both lower flux magnitude and sensitivity of analyzer signal output. Poor quality flux data obtained during periods of equipment failure and system maintenance were also discarded from analysis. These quality control procedures led to the removal of 3 to 17% and all CO_2 fluxes and 2 to 28% of all CH_4 fluxes collected for a given chamber. To minimize the turbulence-related measurement bias associated with a chamber deployment period of 2.5 minutes, correction of CO_2 efflux and filtering of CH_4 flux by friction velocity were done following the protocol of Lai *et al.* (2012), with only 10-55% of the cleaned CH_4 flux data set obtained prior to 6 July 2010 being retained for analysis. We logarithmically transformed CH_4 fluxes ($\log_{10}$ mg m^{-2} d^{-1} + 20) before statistical analysis to reduce variance heteroscedasticity and enable all data to be used. Data processing and statistical analyses were conducted in MATLAB R2009a (MathWorks, MA, USA) and PASW Statistics 18 (SPSS Inc., IL, USA).

4.4 Results

4.4.1 Seasonal Variations in Environmental Conditions

The 1971-2000 climate data showed an annual mean minimum monthly temperature of -2.5 ºC in March to a maximum of 20.9 ºC in July (Figure 4.1). Average monthly rainfall was fairly constant in the middle of growing season, with 85-91 mm recorded in each month between June and September. In 2009, the summer was cooler and wetter than the 30-year average, particularly in July when mean temperature was 2.6 ºC lower than normal and monthly rainfall reached a record high of over 220 mm (Figure 4.1). In 2010, average monthly temperature was not significantly different from normal except in March and April that were

3.1-5.5 ºC warmer. Monthly rainfall in May and July was 49-62% lower than the long-term average, but in August and September was 65-92% greater than normal.

Figures 4.2a and 4.2b show the seasonal variations in daily average water table depth and peat temperature at 5 cm depth in three different plant communities in 2009 and 2010 respectively. At the beginning of measurement period in late May 2009, peat temperature at 5 cm depth was around 10 ºC. It gradually rose to a peak of 19-22 ºC in mid-August on DOY 230 and then decreased steadily to below 4 ºC in early December. In 2010, measurement was started earlier in late March when peat temperature at 5 cm depth was still close to 0 ºC. It increased to a maximum of 19-24 ºC in early July (DOY 188), remained near there for about two months and then decreased from early September (DOY 246) onwards. For peat temperature measured at 40 cm depth in a hollow, a seasonal peak of 14 ºC was reached in late August (DOY 238) in 2009 and in early September (DOY 251) in 2010. On the other hand, water table depth had very different seasonal pattern between the two years of measurement. In 2009, water table was higher throughout the whole period, averaging -23 cm (negative number represents water table below the peat surface) at both *Eriophorum*- and *Maianthemum/Ledum*-dominated sites and -35 cm at *Chamaedaphne*-dominated sites. The highest water tables were uncharacteristically observed in late July at all sites, owing to exceptionally large amount of rainfall received in this month. In contrast, water tables were closest to the peat surface near the beginning and end of the growing season in 2010, while dropping considerably to maximum depths of -45 cm at *Eriophorum*- and *Maianthemum/Ledum*-dominated sites and -59 cm at *Chamaedaphne*-dominated sites in early August (DOY 214).

4.4.2 Temporal Variations in Methane Fluxes

The overall seasonal CH_4 flux patterns at the Mer Bleue bog were generally consistent across plant communities dominated by *Eriophorum*, *Chamaedaphne*, and *Maianthemum/Ledum*. In 2009, daily average CH_4 flux from triplicate chambers rose gradually from late May to mid July (DOY 198), and

then increased sharply by more than 100 mg CH_4 m^{-2} d^{-1} within a month to a seasonal peak in mid August around DOY 229 (Figure 4.3a). This was followed by a steady decrease in CH_4 emission until late October after which fluxes remained relatively small. In 2010, there were three seasonal peaks in CH_4 emission (Figure 4.3b). After a period of low flux in the early growing season in April, CH_4 flux rapidly increased to a peak in late May (DOY 146) and then decreased abruptly to a minimum in about a week. Methane flux rose again from early June to the second peak in early July (DOY 185) and subsequently dropped to low levels in early August (DOY 215). Then it increased for the third time to the last seasonal peak in mid September (DOY 259) for *Eriophorum* chambers, and in early October (DOY 277) for *Maianthemum/Ledum* and *Chamaedaphne* chambers before slowly decreasing towards the end of measurement period.

We investigated the interannual variability of CH_4 flux by comparing the daily average flux values obtained by autochambers on the same day of year between 2009 and 2010 with Kruskal-Wallis test. No significant difference in CH_4 flux was found from *Eriophorum* sites between the two study years, while significantly higher mean CH_4 flux was observed in 2009 compared to 2010 from both *Chamaedaphne* (32 *vs.* 22 mg m^{-2} d^{-1}, $p < 0.01$) and *Maianthemum/Ledum* chambers (83 *vs.* 53 mg m^{-2} d^{-1}, $p < 0.01$) (Table 4.2). By analyzing the data in two separate time periods, we further detected a significantly higher CH_4 flux during the mid-growing season (DOY 180-270) in 2009 than in 2010 from both *Chamaedaphne* and *Maianthemum/Ledum* chambers, but no flux difference in the early and late growing season combined between the two years ($p > 0.01$) (Table 4.2).

4.4.3 Controls on Temporal Variations in Methane Fluxes

We conducted Pearson correlation analyses to investigate the relationships between CH_4 flux and environmental variables over time. While $\log_{10}$ CH_4 flux had an overall positive relationship with peat temperature across all chambers ($p < 0.01$) (Table 4.3), scatter plots of the two variables showed more complicated

patterns. When the peat was still cool at the beginning of growing season, CH_4 flux from *Eriophorum* chambers increased sharply with peat temperature at a rate much greater than that in the later period (Figures 4.4a and 4.4b). In contrast, CH_4 flux from *Maianthemum/Ledum* chambers did not exhibit such a drastic initial increase with peat temperature. Log-transformed CH_4 flux had a linear relationship with peat temperature throughout the measurement period in 2009 (Figure 4.4c), while in 2010, CH_4 flux remained at about 100 mg m^{-2} d^{-1} once peat temperature reached over 10 ºC in the mid growing season (Figure 4.4d).

Correlation analyses between CH_4 flux and peat temperature at 40 cm depth were conducted by month to investigate temporal changes in the relationship, with emphasis on data collected in 2010 owing to a longer study period and larger variation in environmental conditions. Significant, positive correlations (r = 0.12 to 0.69, $p < 0.01$) between peat temperature and $\log_{10}$ CH_4 flux were found for all three plant communities in May and June, consistent with the overall seasonal trend (Table 4.3). However, we observed strong, negative correlations (r = -0.36 to -0.86) between $\log_{10}$ CH_4 flux and peat temperature from most of the chambers in July, and weak or even insignificant relationships between the two in September. In October and November, strong positive relationships (r = 0.19 to 0.91) between $\log_{10}$ CH_4 flux and peat temperature were again obtained from all autochambers.

Table 4.4 shows the correlation coefficients between water table depth and $\log_{10}$ CH_4 flux from individual autochambers grouped by month in 2010. Negative or insignificant relationships between the two variables were often observed in months with a high water table, for example April, May and November. However, during the dry period in July and August, we found strong, positive correlations between $\log_{10}$ CH_4 flux and water table depth (r = 0.34-0.85, $p < 0.01$), i.e. lower CH_4 flux was associated with a deeper water table, except for the two driest *Chamaedaphne* chambers.

Correlation analyses between CH_4 flux and peat temperature were further conducted after dividing the data set into groups by water table range to determine if water table position had an influence on the flux-temperature relationship. For *Eriophorum* chambers, moderate to strong relationships between $\log_{10}$ CH_4 flux and peat temperature ($r \geq 0.4$) were observed as long as water table was less than 40 cm below the peat surface (Figures 4.5a and 4.5b). For *Chamaedaphne* chambers, the two variables were strongly correlated ($r > 0.6$) until water table dropped to a depth of more than 30 cm (Table 4.5). For *Maianthemum/Ledum* chambers, the relationship between $\log_{10}$ CH_4 flux and peat temperature became weaker with increasing water table depth (Figures 4.5c and 4.5d). The correlation coefficient decreased from 0.86 when water table was within the top 10 cm peat to ≤ 0.38 when water table was more than 20 cm below peat surface (Table 4.5).

Daily maximum net ecosystem CO_2 exchange (NEE_{max}) of each chamber was calculated by averaging all CO_2 flux data measured at PAR $\geq$ 1000 mol m^{-2} s^{-1} within a day (we adopted the convention that negative value represents a net uptake). We observed a strong, negative correlation between NEE_{max} and $\log_{10}$ CH_4 flux (i.e. higher methane emissions associated with greater CO_2 uptake) from *Eriophorum* chambers in 2010 (r = -0.64, $p < 0.01$) (Figure 4.6a), but weaker relationship in 2009 (r = -0.48, $p < 0.01$). For the *Maianthemum/Ledum* chambers, moderate negative relationship between the two variables was obtained in the wetter year of 2009 (r = -0.40, $p < 0.01$) (Figure 4.6b), but no significant relationship in 2010 ($p = 0.65$). NEE_{max} and CH_4 flux were only weakly correlated in *Chamaedaphne* chambers (r = -0.11 to -0.20, $p < 0.05$).

4.4.4 Variations in Methane Fluxes Among Plant Communities

We conducted ANOVA with Tukey's post hoc test to determine if there is any significant difference in daily average environmental variables and log-transformed CH_4 flux between three different plant communities at the Mer Bleue bog. Figure 4.7a shows that mean CH_4 flux differed significantly across all plant communities over the measurement period in both years. *Chamaedaphne*-

dominated community had the lowest CH_4 flux at this bog, averaging 33.8 and 18.8 mg m^{-2} d^{-1} in 2009 and 2010 respectively. Average CH_4 fluxes from *Maianthemum/Ledum* community were 86.0 mg m^{-2} d^{-1} in 2009 and 48.3 mg m^{-2} d^{-1} in 2010, which were about 2.5 times greater than those from *Chamaedaphne* sites. Significantly higher CH_4 fluxes were obtained from the *Eriophorum*-dominated community, with average values of 124.4 and 104.3 mg m^{-2} d^{-1} in 2009 and 2010 respectively. On the other hand, no significant difference was found in both peat temperature at 5 cm depth between all three communities (Figure 4.7b), and in water table depth between *Eriophorum* and *Maianthemum/Ledum* communities ($p > 0.05$). Sites dominated by *Chamaedaphne* had significantly lower average water table position than the other two communities (34-35 *vs.* 21-23 cm below peat surface) (Figure 4.7c).

In addition to the highest average CH_4 flux, *Eriophorum*-dominated community also had the highest seasonal peak CH_4 emission among the three plant communities. In 2009, peak daily average CH_4 fluxes from *Eriophorum*, *Maianthemum/Ledum* and *Chamaedaphne* chambers were 326, 203 and 153 mg m^{-2} d^{-1} respectively (Figure 4.3a). In 2010, maximum daily average CH_4 fluxes from *Eriophorum* and *Maianthemum/Ledum* chambers were 213 and 99 mg m^{-2} d^{-1} respectively (Figure 4.3b). Peak CH_4 flux from *Chamaedaphne* community was high with 264 mg m^{-2} d^{-1}, owing to an ebullition event from one of the chambers. If this daily average flux value was removed, peak CH_4 flux would be reduced to 64 mg m^{-2} d^{-1}. In spite of a high mean seasonal CH_4 emission, it is worth noting that daily average CH_4 flux from *Eriophorum* community was consistently lower than that from *Maianthemum/Ledum* community in the early growing season of both 2009 and 2010 (Figures 4.3a and 4.3b).

In order to gap-fill missing half-hourly flux values, we conducted stepwise multiple linear regression of $\log_{10}$ CH_4 flux on water table depth, peat temperature at 40 cm depth, air temperature, atmospheric pressure (a factor affecting CH_4 ebullition (Tokida *et al.*, 2007)) and vascular green area for individual chambers

by month. The relationship obtained was then used to estimate fluxes in the corresponding month. On a seasonal scale, coefficients of determination (r^2) between observed and modelled CH_4 fluxes after back-transformation of log values were 0.57 to 0.91 for *Eriophorum*, 0.25 to 0.76 for *Maianthemum/Ledum*, and 0.11 to 0.36 for *Chamaedaphne* chambers (Table 4.6). We summed the gap-filled values at all half-hour periods to determine the seasonal integrated CH_4 flux from each autochamber. From June to November, seasonal CH_4 emissions ranged between 9.8 and 35.3 g CH_4 m^{-2} from *Eriophorum*, 5.0 and 22.8 g CH_4 m^{-2} from *Maianthemum/Ledum*, and 1.7 and 9.0 g CH_4 m^{-2} from *Chamaedaphne* chambers in 2009 and 2010 (Table 4.6).

4.5 Discussion

4.5.1 Methane Fluxes Among Plant Communities

The *Eriophorum*-dominated community was a CH_4 emission hotspot at the Mer Bleue ombrotrophic bog, with 1.4 to 2.2 and 3.7 to 5.5 times higher seasonal mean CH_4 fluxes compared to *Maianthemum/Ledum* and *Chamaedaphne* communities, respectively, in the two years of measurement (Figure 4.7a). The observed difference in CH_4 flux between *Eriophorum* and *Maianthemum/Ledum* communities was likely caused by plant-related factors, given that there was no significant difference in average peat temperature and water table depth between them. While both *Eriophorum* and *Maianthemum* possess aerenchymatous tissues that provide a conduit for CH_4 to transport from the anaerobic zone directly to the atmosphere while bypassing the aerobic surface peat (Greenup *et al.*, 2000; King *et al.*, 1998), *Eriophorum* has much larger aboveground biomass and proportion of deep roots 20-50 cm below the peat surface (Moore *et al.*, 2011), and thus is likely more efficient in plant-mediated CH_4 transport by tapping into the CH_4 pool under the water table even in dry conditions. Moreover, roots of *Eriophorum* are much more effective than other wetland vascular plants (*Carex* and *Juncus*) in producing acetate, a major substrate used for CH_4 production (Ström *et al.*, 2005). With a longer greening period and higher maximum NEE (Figure 4.6), *Eriophorum* community could produce more root exudates than the

Maianthemum/Ledum counterpart to support a higher methanogenesis. Although the surface litter of forbs decomposes much faster than sedges in peatlands (exponential decay *k*: 0.63 *vs.* 0.25 yr^{-1}) (Moore *et al.*, 2007), the total aboveground biomass of *M. trifolium* at Mer Bleue is probably too small to exert considerable effects on peat chemistry. We had no data on the decomposition rate of *Maianthemum* roots, unfortunately, to compare with the *k* value of 0.09 yr^{-1} for sedge roots (Moore *et al.*, 2007).

Meanwhile, we observed consistently lower CH_4 fluxes from *Eriophorum* than *Maianthemum/Ledum* communities in the early growing season of both years (Figures 4.3a and 4.3b). Peat beneath *E. vaginatum* demonstrated a high aerobic CH_4 consumption potential in laboratory incubation (Moore *et al.*, 2011) and significant CH_4 oxidation in the field (Moosavi and Crill, 1998). Results of ^{14}C-acetate labelling also showed that over 90% of $^{14}CH_4$ produced was oxidized in the *Eriophorum* rhizosphere, probably due to a high efficiency of oxygen transport via aerenchyma to belowground tissues (Ström *et al.*, 2005). On the other hand, CH_4 production during this period was likely limited by the low temperature and small release of root exudates as a result of the low photosynthetic activity. As a result, the high methanotrophic activity at *Eriophorum* site might help keeping a lower net CH_4 emission rate than at *Maianthemum/Ledum* site until methanogenesis increased rapidly later in the growing season. *Chamaedaphne* community had the lowest seasonal mean CH_4 flux at the bog, because shrub root production mostly occurred above the water table which limited substrate supply to methanogens (Murphy and Moore, 2010), and the significantly lower mean water table (Figure 4.7c) favoured CH_4 oxidation with the absence of aerenchyma for plant-mediated transport. Although Treat *et al.* (2007) found no significant difference in CH_4 flux between sedge- and shrub-dominated sites in Sallie's fen, it is worth noting that shrubs were distributed throughout the fen without a clear microtopographic association.

4.5.2 Controls of Temporal Variations in Methane Fluxes

The overall positive relationships between peat temperature and CH_4 flux observed across time in this study were in agreement with other field studies in northern peatlands (e.g. Kettunen *et al.*, 1996; Laine *et al.*, 2007b; Pelletier *et al.*, 2007). With a rise in peat temperature, the relative methanogen abundance in peat soils is increased (Turetsky *et al.*, 2008), the organic matter breakdown and hence substrate availability for methanogens is enhanced (Valentine *et al.*, 1994), and the rate of microbial CH_4 production has a much greater increase than that of CH_4 consumption (Dunfield *et al.*, 1993), leading to an overall enhanced CH_4 emission. Also, we observed from *Eriophorum*-dominated chambers a much larger rate of increase in CH_4 flux with peat temperature in the early growing season between March and May than in mid-summer (Figures 4.4a and 4.4b). This rapid flux increase was likely caused by not only a rise in temperature, but also a concomitant increase in plant production and root exudation of labile carbon for methanogenesis. The lack of supply of a suitable substrate from vascular plants in the early growing season leads to a stronger control of CH_4 production by substrate availability than temperature, but not later in the season when plants photosynthesize actively (Kettunen *et al.*, 2000).

Water table is another important environmental control of peatland CH_4 flux, with a lowered water table resulting in a thicker oxic peat layer for CH_4 oxidation and a thinner anaerobic layer for CH_4 production (Waddington *et al.*, 1996). Numerous studies have reported a lower seasonal mean CH_4 flux in association with a lower seasonal mean water table in northern peatlands (Bubier, 1995; Laine *et al.*, 2007b; Moore *et al.*, 2011; Moore and Roulet, 1993). Temporally within a site, we found a similar positive relationship between individual CH_4 flux and water table depth in July and August when water table was low and fluctuated greatly (Table 4.5). In contrast, during the early and late growing seasons at Mer Bleue when water table was relatively high (< 25 cm below peat surface), CH_4 flux was negatively or insignificantly correlated with water table depth (Table 4.5). It should be noted that correlation does not necessarily imply causation and CH_4 emission over this wetter period was

probably more strongly governed by changes in peat temperature and/or plant productivity than water table, as there was already a thick layer of saturated anaerobic peat. Previous studies have also reported no significant relationships between daily mean CH_4 flux and water table depth at very wet peatland and tundra ecosystems where water table was close to the soil surface (Jackowicz-Korczyski *et al.*, 2010; Sachs *et al.*, 2010; Wille *et al.*, 2008). This hypothesis was further supported by the seasonal CH_4 flux pattern identified at Mer Bleue in 2009. With a shallow water table maintained throughout the measurement period of 2009, CH_4 emission had a single seasonal peak in mid-August corresponding to a seasonal maximum in peat temperature, while in 2010, large drops in water table in early June and early August led to two distinct seasonal troughs in CH_4 emission (Figures 4.2b and 4.3b).

Besides water table depth, peat temperature also demonstrated varying relationships with CH_4 flux over time. In spite of an overall positive relationship between $\log_{10}$ CH_4 flux and peat temperature in 2010, we found significant, negative correlations between the two variables in July (Table 4.3). This was also the period in which water table dropped considerably and hence water table could possibly be an overriding control of CH_4 emission. When correlation analyses between CH_4 flux and peat temperature were further conducted on data divided into groups by water table depth, we observed a general decrease in the strength of flux-temperature relationship across chambers as water table dropped to greater depths (Table 4.4). Christensen *et al.* (2003a) regarded water table as an "on-off switch" controlling the large scale spatial variations in wetland CH_4 emissions. As long as water table is shallower than a certain threshold, differences in CH_4 flux between wetlands would be controlled by factors other than water table, while there would be a substantial flux reduction once water table drops below the threshold. Our findings suggest that water table could also act as an on-off switch governing the temporal variability of CH_4 flux within a wetland. Low summer water table led to deviations from the positive flux-temperature relationship at the high end of peat temperature in 2010 but not in the constantly wet 2009 (Figures

4.4c and 4.4d). Moreover, we found a clear difference among plant communities in the threshold of water table depth that supported a moderate to strong flux-temperature relationship over the season. Correlation coefficients between $\log_{10}$ CH_4 flux and peat temperature were ≥ 0.4 when water table was above a depth of 20, 30 and 40 cm for *Maianthemum/Ledum*, *Chamaedaphne*, and *Eriophorum* chambers, respectively (Table 4.4). As the majority of root biomass of *M. trifolium* are found in the top 20 cm peat (Moore *et al.*, 2011), a drop in water table below 20 cm depth would lead to considerable decrease in both supply of root exudates to and plant-mediated transport of CH_4 from the anaerobic zone, resulting in a poor flux-temperature relationship. On the other hand, the deeply-rooted *Eriophorum*-dominated community had the largest threshold of water table depth and could maintain a strong correlation between temperature and CH_4 flux throughout the year except under very dry conditions.

A number of studies have found correlations between net ecosystem CO_2 exchange and CH_4 emission in wetlands (Bellisario *et al.*, 1999; Joabsson and Christensen, 2001; Waddington *et al.*, 1996; Whiting and Chanton, 1993). The increase in peatland CH_4 emission with vascular plant production has often been attributed to the translocation of photosynthate belowground and subsequent root exudation of labile carbon compounds (e.g. acetate) for methanogenesis (Ström *et al.*, 2003). At Mer Bleue, we also observed strong, negative correlations between NEE_{max} and CH_4 flux on a daily timescale from *Eriophorum* chambers in both years, i.e. a higher CH_4 emission associated with a higher photosynthetic CO_2 uptake (Figure 4.6a). Although methanogenesis at *Sphagnum*-dominated ombrotrophic bogs is usually dominated by the hydrogenotrophic pathway (Galand *et al.*, 2010), acetoclastic methanogens may be present locally in peat under the *Eriophorum* stand to metabolize acetate in root exudates into CH_4. *Öquist and Svensson* (2002) have shown with shading experiments the importance of plant-mediated carbon input to CH_4 emission in the sedge-dominated ombrotrophic area of a Swedish peatland, where a 25% reduction in gross photosynthesis resulted in a corresponding 20% decrease in CH_4 flux. Moreover,

in a moist tussock tundra dominated by *Eriophorum vaginatum*, King *et al.* (2002) found that 2% of assimilated ^{14}C was emitted as CH_4 in mid-season, and recent photosynthate contributed to over 75% of the mean growing season CH_4 flux. For *Maianthemum/Ledum* chambers, we found a significant, negative NEE_{max}-CH_4 relationship in 2009 but not in 2010 (Figure 4.6b). The absence of significant correlations in 2010 was likely due to the difficulty for root exudates from these shallow-rooted species to reach the methanogens in anaerobic zones below the deep water table in summer. Weak correlation between NEE_{max} and CH_4 flux from *Chamaedaphne* chambers in our study could probably be explained by a low seasonal water table, absence of acetoclastic methanogens, lack of root exudation of labile substrates, or a combination of them. Waddington *et al.* (1996) also found strong correlations between seasonal NEE and CH_4 flux only at wetter, sedge-dominated lawn sites but not the drier, shrub-dominated ridge sites in a Swedish peatland. Pulse-labelling of ^{14}C and seasonal monitoring of organic acid concentrations in peat should be done across plant communities to further confirm the coupling between plant-mediated substrate supply and CH_4 emission at the Mer Bleue bog.

We observed a significant difference in CH_4 flux from two plant communities between 2009 and 2010, which could mostly be attributed to a difference in CH_4 emission during the mid-growing season between July and September. Over this period, average peat temperature at 40 cm depth was only 0.4ºC higher, but mean water table depth increased by 5.5 to 9.0 cm in 2010 than in 2009. This lowering of water table led to a substantial decrease in mean CH_4 flux by 60% and 55% from *Chamaedaphne* and *Maianthemum/Ledum* communities, respectively, in the summer of 2010 (Table 4.2). Bubier *et al.* (2005) reported an average increase of 60% in CH_4 flux from northern wetlands in Manitoba as mean water table rose by 2-5 cm in a wet summer, while Laine *et al.* (2007b) did not observe any interannual variation in CH_4 flux from an Irish lowland blanket bog as differences in precipitation and temperature among the three measurement years were small. Summer water table depth largely governs

the between-year variability of peatland CH_4 flux, serving as an on-off switch that controls whether emissions can be significantly enhanced at times of seasonal peak temperature and plant productivity with the highest potential CH_4 production. Interannual variability of water table position in a peatland is not only a function of total annual precipitation, but also depends on the timing of precipitation (Treat *et al.*, 2007) and beaver dam activity (Moore *et al.*, 2011), which together exert a large influence on CH_4 emissions. Meanwhile, we detected no significant difference in CH_4 flux between 2009 and 2010 from *Eriophorum* communities at Mer Bleue, presumably due to the greater ability of *E. vaginatum* in sustaining CH_4 emission even in dry periods with its deep root system.

4.5.3 Implications to Peatland Carbon Cycling

The seasonal integrated CH_4 fluxes from June to November in 2009 and 2010 at the Mer Bleue bog were found to be 9.8 to 35.3 g CH_4 m^{-2} from *Eriophorum*, 5.0 to 22.8 g CH_4 m^{-2} from *Maianthemum/Ledum*, and 1.7 to 9.0 g CH_4 m^{-2} from *Chamaedaphne* chambers, after gap-filling missing half-hourly fluxes based on regression equations established by month (Table 4.6). Based on an areal coverage of 70%, 27%, and 3% by *Chamaedaphne*, *Maianthemum/ Ledum* and *Eriophorum* communities, respectively (Kalacska, pers. comm.), we calculated that ecosystem level CH_4 flux at Mer Bleue over our whole measurement period was 9.1 g CH_4 m^{-2} in 2009 and 6.9 g CH_4 m^{-2} in 2010. Although *Chamaedaphne* community dominated the bog area, *Maianthemum/Ledum* and *Eriophorum* communities had a disproportionately large impact on peatland CH_4 emissions, contributing to 47% and 8-11% of spatially averaged fluxes, respectively, in the two years. This has significant implications to the upscaling of CH_4 fluxes. Baird *et al.* (2009) pointed out the importance of considering the spatial variability of water table to reduce the bias in extrapolating small-scale CH_4 fluxes to the whole peatland, given a nonlinear spatial relationship between water table and CH_4 emission. Our results suggest that vegetation types can further increase the complexity of estimating peatland CH_4 flux, since emissions can vary between communities by over 2 times even

with the same seasonal mean water table, and the coverage of plant communities can change dynamically over time. If future climate change leads to drier conditions, peatland CH_4 flux may decrease drastically because of the expected vegetation shift from high CH_4-emitting sedges to low CH_4-emitting ericaceous shrubs (Breeuwer *et al.*, 2009) as well as the limited ability of *Maianthemum/ Ledum* community to support a high CH_4 flux in response to a lower water table.

We were able to use our autochamber data to identify seasonal changes in the dominant control of CH_4 flux, and quantify the water table threshold above which a moderate relationship between peat temperature and CH_4 flux could be maintained. These findings, unlikely to be deducible from low temporal resolution data from manual chambers, show the importance of considering the interactions of environmental controls in modelling the temporal variability of CH_4 flux. A single temperature function developed for the whole year probably would not be able to simulate peatland CH_4 emissions accurately over some drier periods. Also, predicting the seasonal change of CH_4 flux using only an empirical relationship with water table established across space like the one in Bubier *et al.* (1993a) will be error-prone particularly when the peatland is wet. Moreover, the observed differences in the effects of changing environmental conditions on CH_4 flux among the three peatland plant communities suggest that the variations in ecosystem level CH_4 flux measured by the eddy covariance technique are difficult to interpret in relation to only a specific vegetation type, and more importantly, to a common set of environmental controls.

Previous studies reported winter CH_4 fluxes from northern peatlands ranging between 0.7 and 5.0 g CH_4 m^{-2} (Jackowicz-Korczyski *et al.*, 2010; Melloh and Crill, 1996; Rinne *et al.*, 2007). Assuming a total CH_4 flux of 2.5 g m^{-2} over the snow-covered period without flux measurements, we estimated the annual CH_4 flux from the Mer Bleue bog to be 9.4 to 11.6 g CH_4 m^{-2} yr^{-1}. These were higher than annual CH_4 fluxes obtained in Atlantic blanket bogs (5.5 to 6.2 g m^{-2} yr^{-1}) (Koehler *et al.*, 2011; Laine *et al.*, 2007b) and Finnish bogs (5.2 to 6.8 g m^{-2}

yr^{-1}) (Alm *et al.*, 1999), but lower than the range reported for poor fens in Finland, Sweden and Minnesota (12.0 to 19.5 g m^{-2} yr^{-1}) (Nilsson *et al.*, 2008; Rinne *et al.*, 2007; Shurpali *et al.*, 1993). Year-long measurements of NEE by eddy covariance tower at Mer Bleue indicated a net annual CO_2-C uptake of 109 g C m^{-2} yr^{-1} in 2009 and 55 g C m^{-2} yr^{-1} in 2010 (Humphreys, pers. comm.). This implies that annual CH_4-C emission could offset 8.0 to 12.8% of the carbon sequestered yearly by plants in this ombrotrophic bog, providing further evidence that CH_4 emission plays a key role in the net ecosystem carbon balance of peatlands.

4.6 Conclusions

We reported high temporal resolution CH_4 flux data collected by autochambers in an ombrotrophic peatland in 2009 and 2010. Mean seasonal CH_4 flux was significantly higher from *Eriophorum* than *Maianthemum/Ledum* and *Chamaedaphne* communities. Both *Eriophorum* and *Maianthemum/Ledum* communities had a disproportionately large influence on ecosystem level CH_4 flux, in spite of their comparatively small areal coverage. CH_4 emission was shown to be an important component of the net carbon balance of this peatland, with its magnitude equivalent to 8.0 to 12.8% of annual NEE. We observed strong interannual variations in CH_4 flux from *Maianthemum/Ledum* and *Chamaedaphne* communities only, mainly driven by a difference in summer water table depth between July and September.

Peat temperature was an important control of seasonal variation in CH_4 flux across all chambers, especially during the early and late growing season when the bog was generally wet. However, when there was a large drop in water table, CH_4 flux could decrease substantially overriding any effects of temperature. We found that the relationship between peat temperature and CH_4 flux was moderate to strong ($r \geq 0.4$) only when water table was above 20, 30, and 40 cm depth for *Maianthemum/Ledum*, *Chamaedaphne*, and *Eriophorum* chambers, respectively, suggesting that water table could act as an on-off switch in governing the temporal flux variability. The difference in water table threshold

between plant communities was probably in part due to a difference in rooting depth and thus the ability to sustain CH_4 flux under dry conditions. We also observed higher CH_4 flux with higher CO_2 uptake (NEE_{max}) from *Eriophorum* community in both years and *Maianthemum/Ledum* community in 2009, indicating a possible link between substrate supply and CH_4 emission when water table was around the plant rooting zone. Our findings suggest that modelling of peatland CH_4 flux should take into account the interaction of environmental and biotic controls as well as its variations among plant communities, rather than using a 'bucket-and-slab" model with no considerations given to spatial and temporal heterogeneities (Baird *et al.*, 2009).

Figure 4.1. Average monthly air temperature and rainfall from March to November measured at the Ottawa International Airport during 1971-2000 and at the Mer Bleue bog in 2009 and 2010. Error bar indicates ± 1 standard deviation.

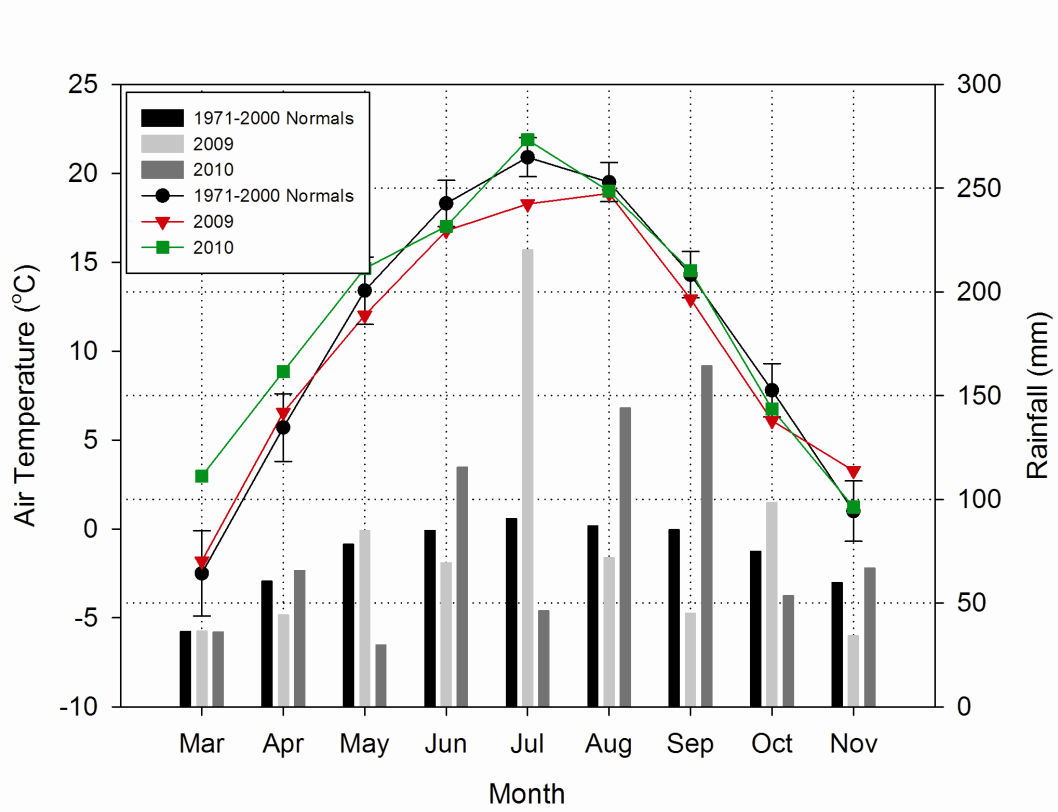


Figure 4.2. Seasonal variations in daily average water table depth and peat temperature at 5 cm depth in three different plant communities, and peat temperature at 40 cm depth in a hollow at the Mer Bleue bog in (a) 2009 and (b) 2010. Error bar indicates ± 1 standard error of triplicate chambers.

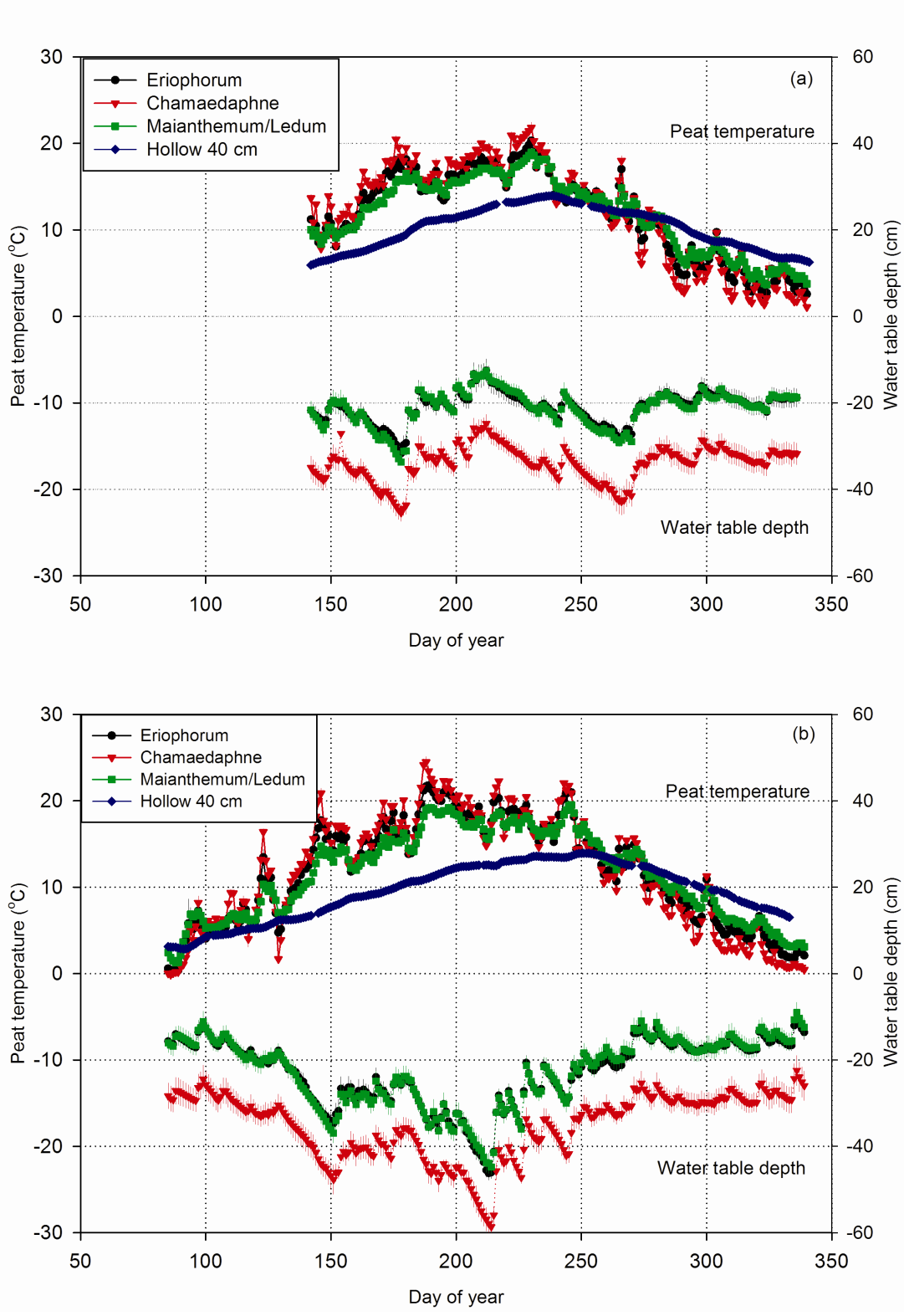


Figure 4.3. Seasonal variations in daily average CH_4 flux from three different plant communities at the Mer Bleue bog in (a) 2009 and (b) 2010. Error bar indicates ± 1 standard error of triplicate chambers.

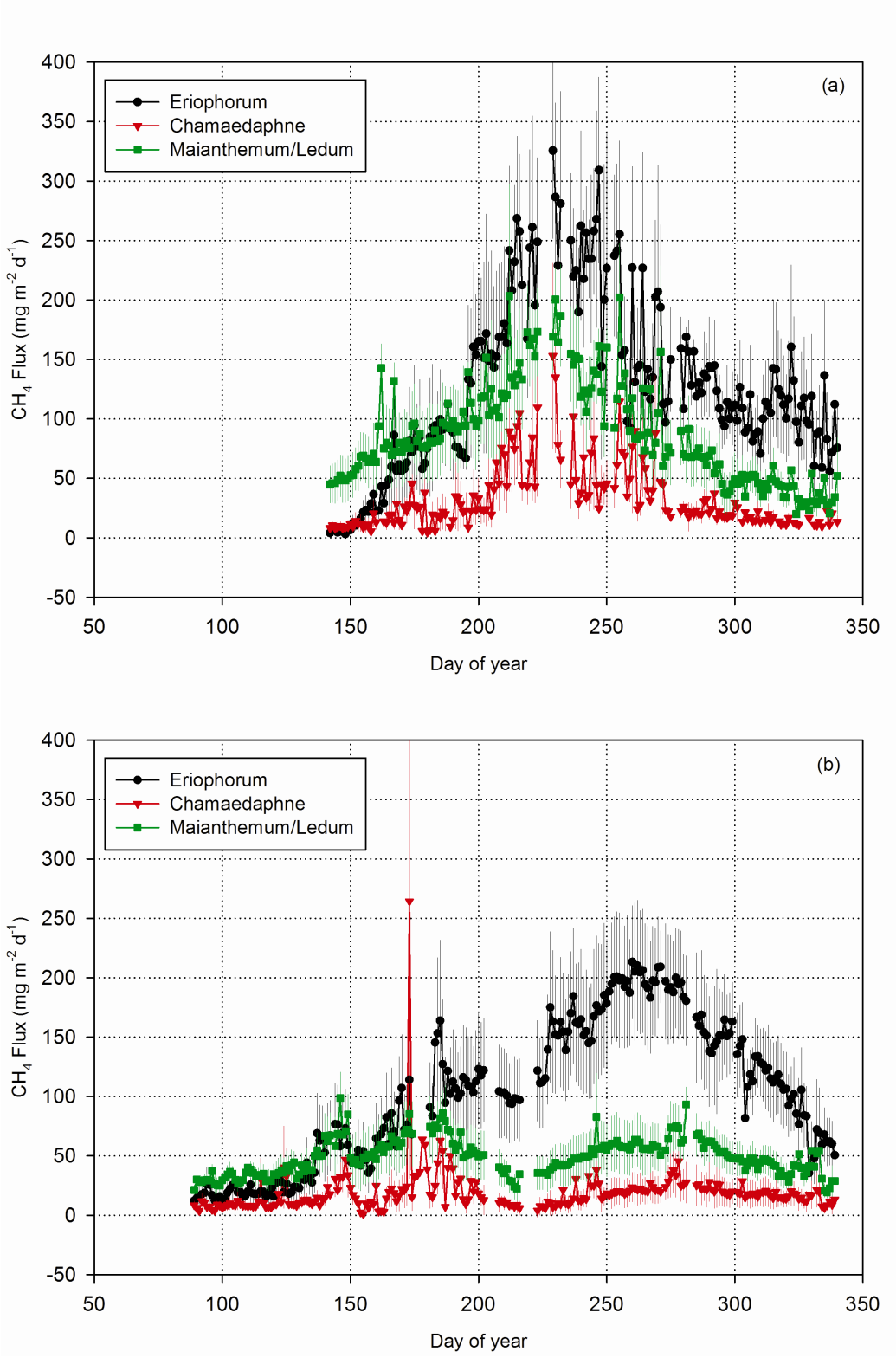


Figure 4.4. Individual CH_4 flux from an *Eriophorum* chamber (Chamber 4) in (a) 2009 and (b) 2010, and from a *Maianthemum/Ledum* chamber (Chamber 10) in (c) 2009 and (d) 2010, against peat temperature at 40 cm depth.

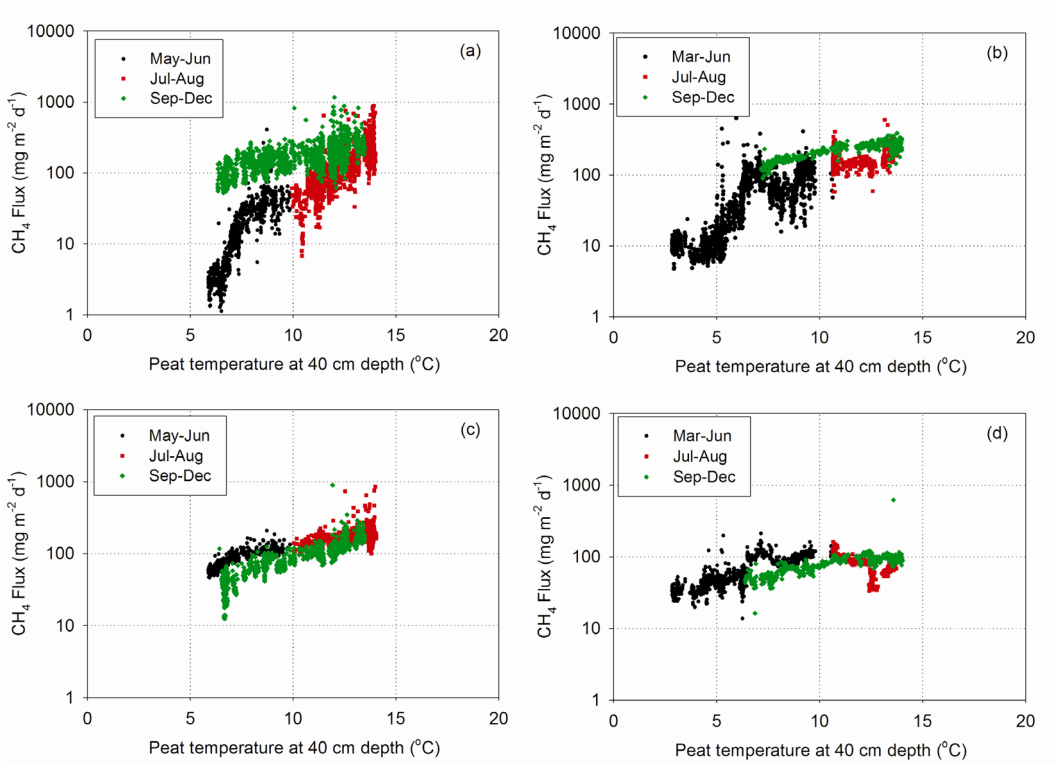


Figure 4.5. Individual CH_4 flux from triplicate *Eriophorum* chambers with water table (a) between 10-15 cm, and (b) between 25-30 cm, and from triplicate *Maianthemum/Ledum* chambers with water table (c) between 10-15 cm, and (d) between 25-30 cm, against peat temperature at 40 cm depth in 2010.

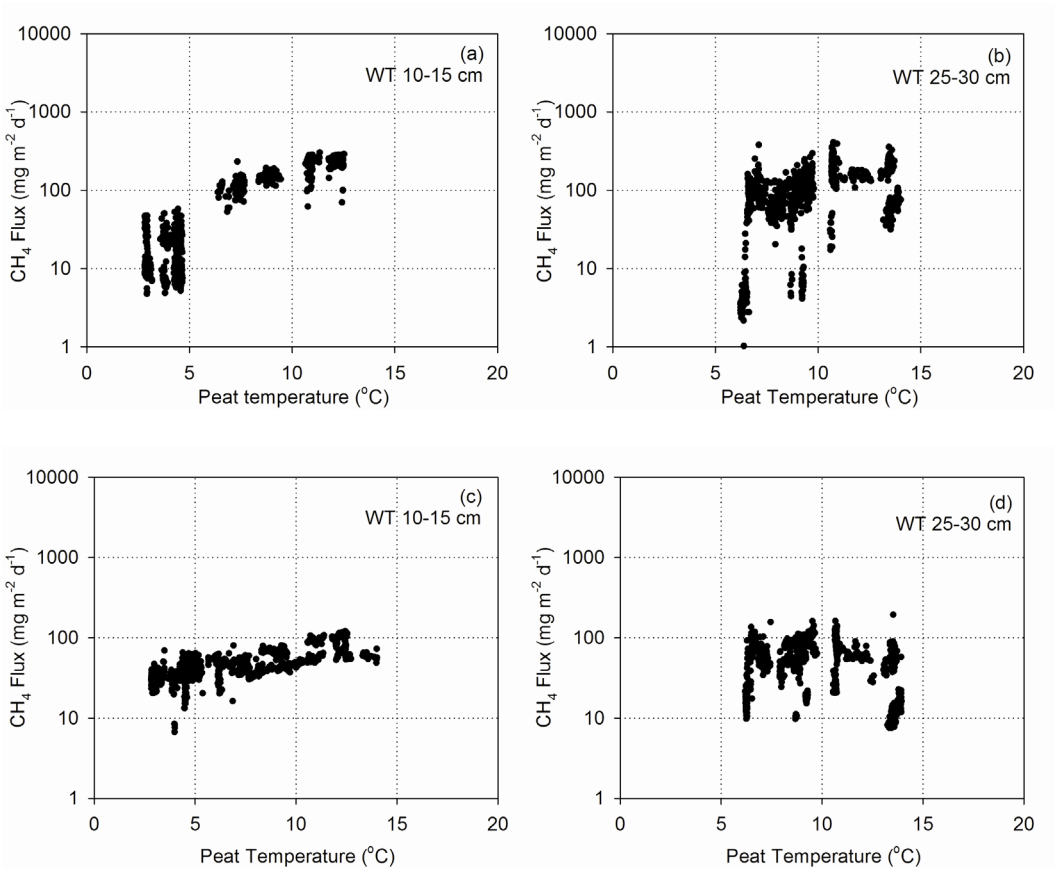


Figure 4.6. Relationships between daily average maximum net ecosystem CO_2 exchange and CH_4 flux from (a) triplicate *Eriophorum* chambers in 2010, and (b) triplicate *Maianthemum/Ledum* chambers in 2009.

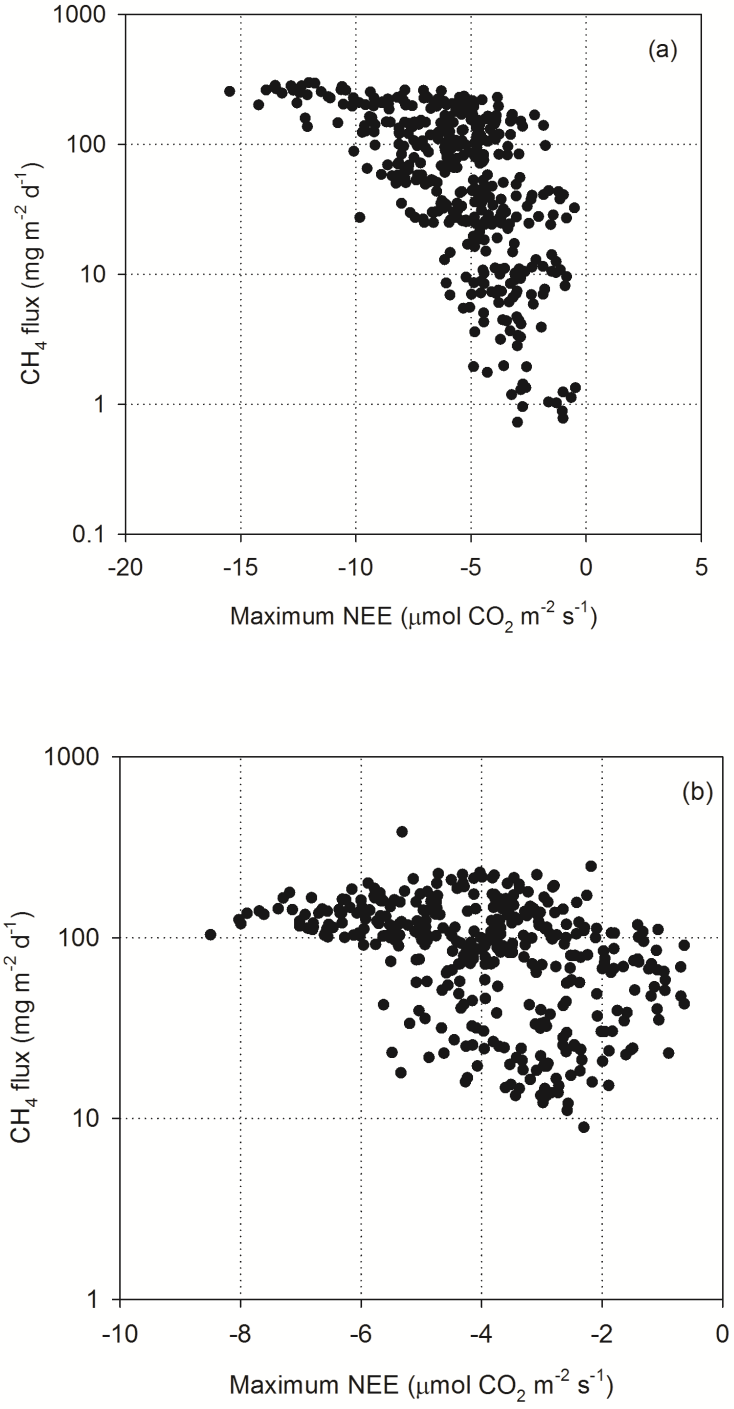


Figure 4.7. Mean daily average (a) CH_4 flux, (b) peat temperature at 5 cm depth, and (c) water table depth from three different plant communities over the measurement periods in 2009 and 2010. Error bar indicates ± 1 standard error. Means with the same letter indicate no significant difference ($p > 0.05$) between communities in a given year.

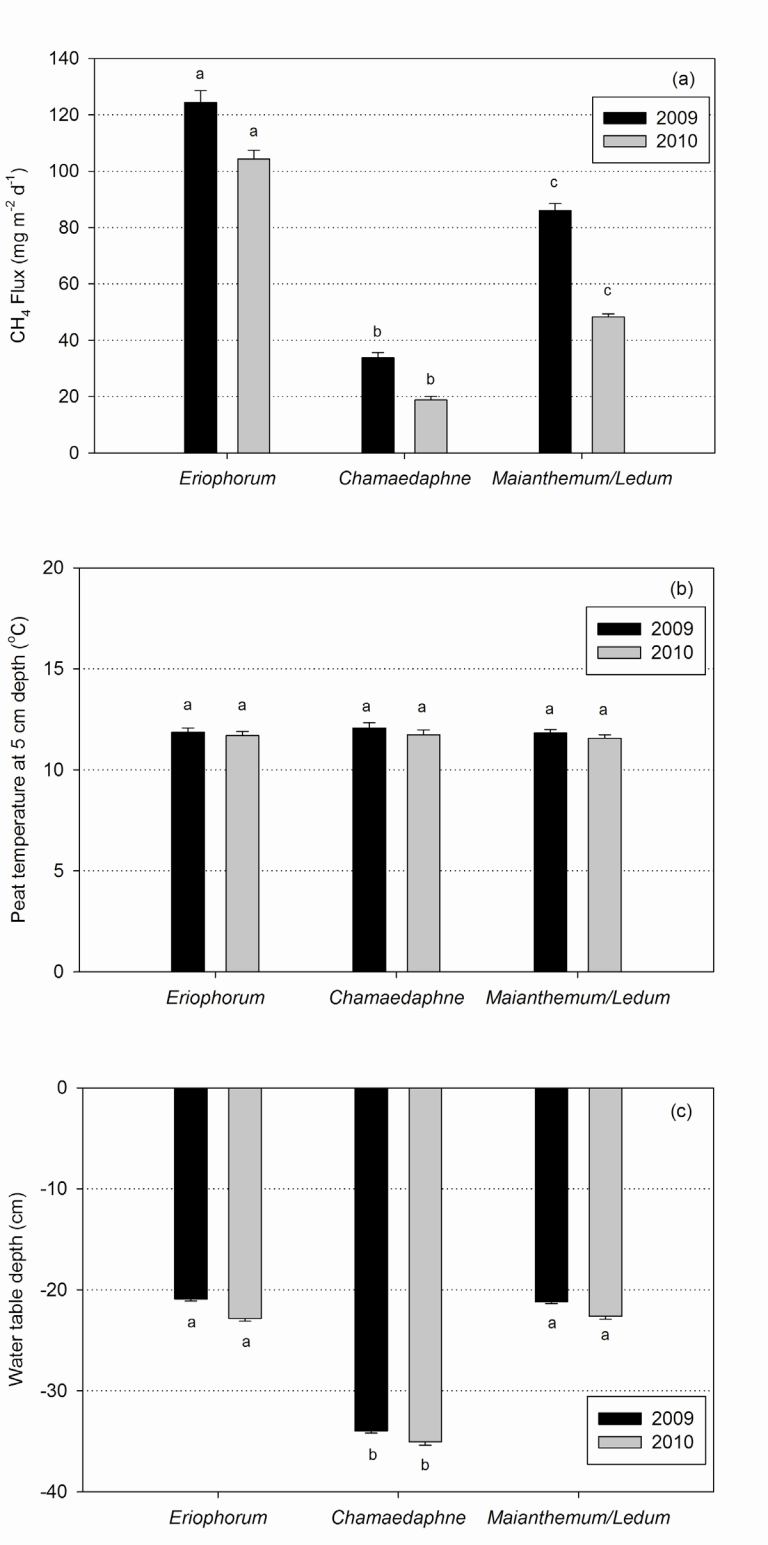


Table 4.1. Vascular plant species, mean water table depth, and peak vascular green area index (VGA) for the 9 autochambers.

Chamber number	Vascular plant species[a]	Water table depth (cm)		Peat temperature (°C)		VGA (m^2 m^{-2})
		2009[b]	2010[c]	2009[b]	2010[c]	
Eriophorum-dominated						
1	Ev, Vm, Lg, Ka	-24.8	-25.5	11.6	11.6	0.82
4	Ev, Lg, Cc, Ka	-18.7	-21.0	11.8	11.6	1.35
7	Ev, Cc, Mt, Lg	-19.2	-21.9	12.1	11.8	1.13
Chamaedaphne-dominated						
3	Cc, Vm, Mt, Lg	-29.3	-30.1	12.1	11.8	1.52
5	Cc, Lg, Vm	-35.4	-37.1	11.5	11.5	1.12
6	Cc, Vm	-37.2	-38.1	12.4	11.9	1.56
Maianthemum/Ledum-dominated						
8	Mt, Lg	-19.5	-19.0	11.6	11.2	2.09
9	Lg, Mt, Ka	-24.0	-26.7	11.9	11.9	0.47
10	Mt, Lg	-20.0	-22.2	11.8	11.5	2.00

Cc: *Chamaedaphne calyculata*, Ev: *Eriophorum vaginatum*, Ka: *Kalmia angustifolia*,

Lg: *Ledum groenlandicum*, Mt: *Maianthemum trifolium*, Vm: *Vaccinium myrtilloides*.

[a]In descending order of peak VGA. Only species with peak VGA > 0.1 m^2 m^{-2} are included.

[b]Over the whole measurement period (DOY 142-341).

[c]Over the whole measurement period (DOY 85-339).

Table 4.2. Pairwise comparison of daily average CH_4 flux (mg CH_4 m^{-2} d^{-1}) from three plant communities at the Mer Bleue bog between 2009 and 2010.

Eriophorum			*Chamaedaphne*			*Maianthemum/Ledum*		
2009	2010	*N*	2009	2010	*N*	2009	2010	*N*
Whole period (DOY 142-339)								
124	122	162	32**	22**	153	83**	53**	162
(5.7)	(3.8)		(2.2)	(1.8)		(3.2)	(1.1)	
DOY < 180 or DOY > 270								
93	84	93	18	24	85	57	52	93
(4.8)	(4.7)		(0.9)	(3.0)		(2.4)	(1.5)	
DOY ≥ 180 and DOY ≤ 270								
176	149	69	50**	20**	68	119**	54**	69
(8.3)	(4.8)		(3.9)	(1.4)		(3.9)	(1.6)	

Number in parentheses indicates 1 standard error of means.

N: Total number of paired fluxes, ** Significant difference at 0.01 level between two years.

Table 4.3. Correlation coefficients between peat temperature at 40 cm depth and individual log_{10} CH_4 flux from 9 autochambers grouped by month in 2010.

Month	*Eriophorum*			*Chamaedaphne*			*Maianthemum/Ledum*		
	1	4	7	3	5	6	8	9	10
Apr	NS	0.12**	-0.33**	NS	NS	0.32**	0.33**	-0.10*	0.31**
May	0.55**	0.55**	0.57**	0.25**	0.21**	0.60**	0.12**	0.45**	0.69**
Jun	0.61**	0.49**	0.42**	0.36**	NS	0.21**	0.77**	0.70**	0.65**
Jul	0.29**	-0.45**	-0.36**	-0.76**	-0.34**	NS	-0.76**	-0.60**	-0.86**
Aug	0.78**	0.64**	0.81**	0.56**	NS	NS	0.76**	0.51**	0.91**
Sep	-0.45**	NS	NS	-0.17*	NS	NS	NS	-0.19**	0.15*
Oct	0.48**	0.74**	0.55**	0.56**	0.47**	0.41**	0.87**	0.51**	0.82**
Nov	0.91**	0.71**	0.68**	0.46**	NS	NS	0.66**	0.19*	0.63**
Apr-Nov	0.70**	0.89**	0.87**	0.36**	0.25**	0.13**	0.49**	0.10**	0.66**
Avg *N*	184	349	258	215	151	177	374	283	296

Avg *N*: Average number of valid paired measurements per month.

NS: Not significant, ** Significant at 0.01 level, * Significant at 0.05 level.

Table 4.4. Correlation coefficients between water table depth and individual log_{10} CH_4 flux from 9 autochambers grouped by month in 2010.

	Eriophorum			*Chamaedaphne*			*Maianthemum/Ledum*		
Month	1	4	7	3	5	6	8	9	10
Apr	NS	-0.50**	-0.11*	NS	-0.16**	NS	-0.33**	NS	-0.33**
May	-0.56**	-0.59**	-0.62**	-0.37**	-0.29**	-0.58**	-0.19**	-0.47**	-0.80**
Jun	NS	-0.24**	NS	0.12*	-0.21**	-0.30**	0.47**	NS	0.32**
Jul	NS	0.43**	0.44**	0.70**	NS	NS	0.65**	0.34**	0.80**
Aug	0.77**	0.69**	0.85**	0.50**	NS	NS	0.69**	0.38**	0.79**
Sep	0.73**	0.26**	0.24**	NS	NS	-0.33**	0.15*	NS	NS
Oct	0.26**	0.56**	0.43**	0.29**	0.23**	0.45**	0.64**	0.31**	0.61**
Nov	NS	-0.34**	-0.38**	NS	NS	NS	-0.17*	0.25**	-0.24**
Avg *N*	184	349	258	215	152	177	375	283	296

Avg *N*: Average number of valid paired measurements per month.

NS: Not significant, ** Significant at 0.01 level, * Significant at 0.05 level.

Table 4.5. Correlation coefficients between peat temperature at 40 cm depth and individual $\log_{10}$ CH_4 flux from three plant communities grouped by water table depth in 2010.

Water table below	*Eriophorum*		*Chamaedaphne*		*Maianthemum/Ledum*	
peat surface (cm)	*r*	*N*	*r*	*N*	*r*	*N*
0-10	0.97**	64	NA	NA	0.86**	196
10-15	0.91**	934	NA	NA	0.77**	1421
15-20	0.87**	1755	0.78**	59	0.59**	1633
20-25	0.70**	1323	0.85**	375	0.38**	1839
25-30	0.40**	1187	0.61**	752	-0.15**	1222
30-35	0.43**	691	0.38**	1558	NS	928
35-40	0.50**	301	0.17**	528	NS	316
40-50	NS	141	0.07*	993	0.26**	162

N: Number of paired measurements.

NS: Not significant, ** Significant at 0.01 level, * Significant at 0.05 level.

Table 4.6. Seasonal integrated CH_4 flux (g CH_4 m^{-2}) from three plant communities at the Mer Bleue bog in 2009 and 2010.

	Eriophorum			*Chamaedaphne*			*Maianthemum/Ledum*		
	1	4	7	3	5	6	8	9	10
2009									
Whole period[a]	13.4	25.4	33.8	9.0	5.0	3.4	18.4	6.5	22.8
Jun-Nov	13.3	24.8	32.9	8.7	4.9	3.3	17.5	6.3	21.9
r^2	0.70	0.57	0.67	0.36	0.27	0.31	0.56	0.25	0.63
N	1739	3513	2394	776	1270	1485	3887	2185	2334
2010									
Whole period[b]	9.9	35.9	32.0	8.1	2.2	1.8	12.4	5.2	18.5
Jun-Nov	9.6	33.1	28.6	6.6	1.8	1.2	9.5	3.9	15.0
r^2	0.91	0.88	0.85	0.15	0.11	0.35	0.67	0.34	0.76
N	1476	2828	2092	1728	1226	1432	3035	2288	2394

[a]From DOY 142 to 341.

[b]From DOY 85 to 339.

r^2: Coefficient of determination between measured and modelled fluxes.

N: Total number of flux measurements.

Chapter 5

Variations of CO_2 Exchange Among Vascular Plant Communities in a Temperate Ombrotrophic Peatland

Context within Thesis

I use the protocol developed in Chapter 3 to correct for the turbulence-related effects on CO_2 efflux before conducting the analysis of CO_2 exchange presented in this chapter. This chapter examines the magnitudes and controls of seasonal mean CO_2 exchange, and compares the photosynthetic and respiratory responses to changing environmental and biotic conditions among three peatland vascular plant communities dominated by different growth forms. This study addresses the important question of whether the three communities represent some distinct plant functional types with respect to CO_2 exchange.

5.1 Abstract

We measured CO_2 fluxes at half-hourly intervals with automatic chambers in three vascular plant communities (*Chamaedaphne*, *Maianthemum/Ledum*, and *Eriophorum*) at the Mer Bleue bog in 2009 to compare the magnitude of net ecosystem CO_2 exchange (NEE), gross ecosystem production (GEP), and ecosystem respiration (ER), as well as responses of GEP and ER to changing environmental and biotic conditions among communities. While seasonal mean NEE were similar among the three plant communities, seasonal mean GEP and ER were significantly lower in the *Maianthemum/Ledum* community owing to the lower green biomass and higher water table. Based on the parameterized GEP models, we detected a significant decrease in effective quantum yield in the order of *Eriophorum* > *Chamaedaphne* > *Maianthemum/Ledum* community, indicating the most efficient photosynthetic activity in sedges at lower light levels. The rate of linear increase in GEP with vascular green area index was considerably lower in the *Maianthemum/Ledum* community, in relation to the high specific leaf area of forb foliage. We found that maximum gross photosynthesis (P_{max}) per unit ground area had a clear seasonal pattern with a single peak in mid-summer, but P_{max} per unit green area varied much less over time. This suggests that temporal changes in community-level P_{max} are predominantly controlled by variations in green area rather than variations in photosynthetic capacity per unit green area. The ER model parameters were significantly different among communities, with the highest temperature sensitivity of ER in the *Eriophorum* community. We observed significant difference in the overall parameterized GEP and ER models among all three communities, which implies that modelling and the integrated measurement of CO_2 fluxes by micrometeorological approaches such as eddy covariance in this bog should take into account the functionally different plant communities separately in simulations or interpreting observations.

5.2 Introduction

Northern peatlands play a potentially key role in global carbon (C) cycling because of their large C stocks. Peatlands in the boreal and subarctic regions store 270 to 370 Pg C in peat (Turunen *et al.*, 2002), which comprises 12 to 16% of total C held in the top 3 m of soils globally (Jobbágy and Jackson, 2000). Recent studies suggest an even higher soil C storage when peatlands containing permafrost and at higher latitudes are included (McGuire *et al.*, 2009; Tarnocai *et al.*, 2009). Although northern peatlands have been sequestering C consistently for millennia (Frolking and Roulet, 2007), they can switch between a net sink and source of C in different years as shown by contemporary measurements (Roulet *et al.*, 2007). Quantifying the peatland-atmosphere exchange of carbon dioxide (CO_2) is important as it largely governs the net ecosystem C balance of peatlands (Nilsson *et al.*, 2008; Roulet *et al.*, 2007). The combination of magnitude and direction of CO_2 and CH_4 exchanges influence the radiative forcing attributable to peatlands (Frolking *et al.*, 2006). Micrometeorological methods collect high frequency, ecosystem level data of net ecosystem CO_2 exchange (NEE), but do not provide insight to the specific mechanistic details on the two main components of C exchange, namely gross ecosystem production (GEP) and ecosystem respiration (ER) at the plant community scale (Griffis *et al.*, 2000). Theoretically this might be possible if homogeneity of the ecosystem structure and function within the footprint of the micrometeorological measurements could be ensured but in reality few ecosystems are that spatially homogeneous. Hence, there remains a need to better understand the magnitude and controls of CO_2 exchange at smaller spatial scales to improve interpretations of observations at the micrometeorological scale and the parameterization of peatland C models for assessing how the C fluxes might change under natural variability and anthropogenic perturbations.

As complex adaptive systems, peatlands are known to demonstrate a high degree of spatial heterogeneity and strong nonlinearity in ecosystem functions (Belyea and Baird, 2006). Different microtopographic locations in northern

peatlands are typically occupied by different vascular and moss species according to their optimal moisture conditions for growth (Bubier *et al.*, 1995b; Bubier *et al.*, 2006). Distinct plant growth forms (e.g. evergreen and deciduous shrubs, graminoids, forbs) have morphologically different plant traits that could lead to differences in ecosystem functions such as biomass production and litter decomposition within peatland and tundra ecosystems (Chapin *et al.*, 1996; Dorrepaal, 2007). Ward *et al.* (2009) found in a blanket bog that graminoids had the greatest rate of CO_2 uptake and turnover because of their high growth rate, while the presence of ericaceous shrubs would reduce C fixation due possibly to enhanced shading, competition for resources and allelopathic effects. Leppälä *et al.* (2008) observed large differences in photosynthetic efficiency among plant growth forms of sedge, evergreen shrub, deciduous shrub, herb and moss in boreal peatlands owing to variations in phenology. Moreover, decomposition rates in peatlands are largely governed by the type of surface litter, with the decay constant *k* values following the decreasing order of shrub and sedge leaves > shrub stems > *Sphagnum* moss (Moore *et al.*, 2007). Root production is more sensitive to water table position for shrubs than herbs and trees in peatlands (Murphy and Moore, 2010), which can influence NEE as root respiration accounts for 19 to 32% of ER (Crow and Wieder, 2005). Hence, plant communities dominated by different species or growth forms could vary widely in their CO_2 exchange behaviour even within a single peatland (e.g. Laine *et al.*, 2007a; Riutta *et al.*, 2007a).

The exchange of CO_2 between peatland and the atmosphere is influenced by various environmental factors. GEP is strongly governed by light conditions and is often modelled based on a hyperbolic relationship with photosynthetically active radiation (PAR) (Frolking *et al.*, 1998). Water table has been found to affect the spatial variability of both GEP (Laine *et al.*, 2007a) and ER in peatlands (Bubier *et al.*, 1998; Pelletier *et al.*, 2011), although its influence on the temporal changes in C flux is more limited particularly in the drier bogs (Bubier *et al.*, 1998; Lafleur *et al.*, 2005). GEP is shown to be highly sensitive to changes in air

temperature (Laine *et al.*, 2007a), while ER changes over time are predominantly governed by peat temperature (Bubier *et al.*, 2003a; Lafleur *et al.*, 2005). However, Lund *et al.* (2010) identified different controls of peatland CO_2 exchange measured at the ecosystem scale by eddy covariance towers. They found significant relationships of summertime NEE, GEP and ER with a combination of climatological and phenological parameters, including leaf area index, length of growing season, and sum of precipitation, based on stepwise regressions across 12 northern peatland and tundra sites. This suggests that environmental controls of CO_2 exchange operate on the plant scale but become less important at the larger peatland scale. Plant communities in peatlands have demonstrated varying responses to changes in environmental conditions (Bubier *et al.*, 2003a; Bubier *et al.*, 2003b). Most studies of the controls of peatland C exchange at the plant community level are based on manual chambers, which are limited by the frequency of flux measurements that can be made and potential bias in the estimation of GEP model parameters owing to fluxes not being measured at naturally varying light levels (Burrows *et al.*, 2005). Yet, we are unaware of any studies that employ automatic chambers to compare the CO_2 fluxes among different vascular plant communities in an ombrotrophic peatland measured at natural light conditions with a high temporal resolution.

Determining the different plant functional types (PFTs) is crucial for modelling and reconstructing peatland CO_2 exchange since a scale too small would require huge data inputs for model parameterization while a scale too large might fail to capture the spatial heterogeneity (Dorrepaal, 2007; Laine *et al.*, 2009). Shaver *et al.* (2007) observed a high functional convergence of NEE in arctic tundra communities, with the NEE in plant communities being predicted reasonably well based on leaf area without consideration of the vegetation composition. Moreover, Williams *et al.* (2006) measured C exchange at 23 chamber locations along a toposequence in an arctic catchment and found using the maximum likelihood technique that only seven generic parameter sets were needed to describe the NEE response to light and temperature variations across

space and time, regardless of the vegetation cover. On the other hand, Laine *et al.* (2012) suggest that the CO_2 exchange function is more diverse among plant communities in northern peatlands compared to the tundra, because of a much larger variability in the composition of different growth forms among plant communities within a peatland ecosystem. As a result, variations in CO_2 response to changing environmental conditions at the plant community level should be taken into account in simulating and upscaling NEE in peatlands (Laine *et al.*, 2009). It has recently been shown in a northern patterned fen that four different plant communities could be classified into two distinct functional groups based on similarities in their photosynthetic and respiratory responses (Maanavilja *et al.*, 2011), but explicit comparison of the CO_2 exchange response among plant communities in an ombrotrophic bog is lacking. Peatland C models have generally assumed that peatlands are made up of a number of different PFTs, for example, the Holocene Peat Model aggregates peatland vegetation into 12 PFTs according to their productivity, rooting and litter characteristics (Frolking *et al.*, 2010), while the Lund-Potsdam-Jena-Wetland Hydrology model uses the 10 PFTs in the original LPJ model with the addition of flood-tolerant graminoids and *Sphagnum* as two peatland-specific PFTs (Wania *et al.*, 2009). Yet, there is so far little empirical evidence to justify the PFTs chosen in these models that represent groups with different CO_2 exchange behaviour.

The objectives of our study are to: (1) determine the magnitude and controls of mean NEE, GEP and ER across three vascular plant communities dominated by different growth forms at the Mer Bleue bog, and (2) investigate the temporal controls of community level CO_2 fluxes and compare the GEP and ER responses to changing environmental and biotic conditions among plant communities. We hypothesize that seasonal mean GEP and ER is higher in a community dominated by the sedge *Eriophorum vaginatum*, owing to a high rate of CO_2 uptake and turnover, than the two communities dominated by the shrub *Chamaedaphne calyculata*, and by a mix of forb *Maianthemum trifolium* and shrub *Ledum groenlandicum*, but the overall seasonal mean NEE is not

significantly different among all communities. We also hypothesize that the three vascular plant communities dominated by different growth forms demonstrate significantly different GEP and ER responses to changing environmental conditions, and hence represent three distinct PFTs for CO_2 exchange.

5.3 Methods

5.3.1 Site Description

Mer Bleue peatland is a 28 km^2 ombrotrophic bog located near Ottawa, Canada (45.41ºN, 75.52ºW). This region has a cool continental climate, with a mean annual temperature of 6.0 ± 0.8 ºC and mean annual precipitation of 944 mm (1971-2000 climate normals) (Environment Canada, 2011). Field measurements were made at a dome-shaped bog in the northwest part of this peatland. Peat depth reaches about 5 to 6 m near the centre of the bog, and is shallower (<0.3 m) near the beaver pond margin (Roulet *et al.*, 2007). The surface of this peatland is completely covered by *Sphagnum* moss (*Sphagnum angustifolium*, *Sphagnum capillifolium*, *Sphagnum fallax*, *Sphagnum magellanicum*) and the vascular plant cover is dominated by low growing ericaceous evergreen shrubs (*Chamaedaphne calyculata*, *Ledum groenlandicum*, *Kalmia angustifolia*), with an occasional mix of deciduous shrub (*Vaccinium myrtilloides*), sedge (*Eriophorum vaginatum*) and forb (*Maianthemum trifolium*).

This bog is relatively dry, with a mean growing season (May to October) water table depth of 42.7 cm from the top of hummock over 1998-2008 (Teklemariam *et al.*, 2010). It has a hummock-lawn microtopography, with a mean difference of 17 cm in elevation between the hummock and lawn surfaces (Wilson, 2012). Depending on the microtopographic location, the top 10-30 cm peat at Mer Bleue is fibric and has a total porosity of greater than 0.9 (Dimitrov *et al.*, 2010).

5.3.2 Autochamber System

We installed nine autochambers at the Mer Bleue bog within a 15-m

radius about 50 m south of the eddy covariance tower. These included three replicates each representing plant communities dominated by *Eriophorum*, *Chamaedaphne*, and *Maianthemum/Ledum* respectively while covering a range of water table and leaf area (Table 5.1). The dynamic, closed autochamber system established at this bog had been previously deployed in a moderately rich treed fen (Cai *et al.*, 2010) and several temperate and boreal forest ecosystems (Bergeron *et al.*, 2009; Drewitt *et al.*, 2002; Gaumont-Guay *et al.*, 2008; Griffis *et al.*, 2004). The autochamber consisted of a transparent Plexiglas dome fitted to a PVC cylinder with a hinged aluminum frame. The near semi-spherical dome had a height of 20.5 cm and the PVC cylinder had an internal diameter of 52 cm, a thickness of 1 cm and a height of 38.5 cm. Each autochamber thus covered a surface area of 0.21 m^2. The PVC cylinders were inserted 16 to 31 cm deep into the peat, leaving about 7 to 22 cm above the peat surface, but below the height of the top of the shrubs. A partially inflated bicycle tube sealed to the top of the cylinder and a foam gasket on the aluminum flange at the dome base ensured a good seal when the chamber was closed. A small brushless fan within the dome mixed the air in the chamber headspace and a coiled 50-cm long open-ended vent tube on the dome top ensured equilibration of pressure between the inside and outside of chamber during flux measurements.

Chamber selection, measurement timing and data acquisition of the autochamber system were controlled by a datalogger (CR23X, Campbell Scientific, UT, USA). A pneumatic cylinder assembly (Model BFT-173-DB, Bimba Manufacturing, IL, USA) connected to an oil-free air compressor (Model CPFAC2600P, Porter Cable, TN, USA) opened and closed the chamber domes. Sampling tubes (Synflex 1300, 4.3 mm i.d., Saint-Gobain Performance Plastics, NJ, USA) connected to the gas inlet and outlet located at the top of chamber dome led to a sampling manifold controlled by solenoid valves. CO_2 concentrations were measured by a closed-path infrared gas analyzer (LI-6262, LI-COR, NE, USA). The LI-6262 was manually calibrated weekly using ultra-high purity nitrogen gas containing no CO_2 (for zero) and 356 μmol mol^{-1} of CO_2 (for span).

Air was circulated to the LI-6262 and back to the chambers at a flow rate of 3.5 L min^{-1} by an AC linear pump (Model DDL, Gast Manufacturing, MI, USA). The datalogger, pump, and gas analyzers were all placed inside temperature-controlled housings.

The autochamber system was operated between 22 May (day of year [DOY] 142) and 30 November (DOY 334) in 2009. Every half hour, the nine autochambers were programmed to close sequentially for 2.5 minutes to measure the net ecosystem exchange of CO_2 once for each chamber. Flux measurements were continuously made between 0200 and 2400 h daily. Between midnight and 0200 h, the system was used to estimate the effective volume of the chamber (Drewitt *et al.*, 2002). Analog outputs from the infrared gas analyzer were sampled at 1 Hz by the datalogger, averaged every 5 seconds, and downloaded automatically to a PC located in a hut on site. All high frequency data were retained for flux processing.

5.3.3 Vegetation Monitoring

We monitored the seasonal change in vascular green area index (VGA) inside each autochamber following the method of Wilson *et al.* (2007). For each vascular plant species, the total number of green leaves within the chamber and the width and length of 10 leaves from each of 3 selected plants were measured at 2- to 5-week intervals between May and October 2009. Species-specific formulae based on leaf geometry were then applied to determine the average leaf size that was further multiplied by the number of leaves and divided by chamber surface area to give the green area index of a vascular plant species (m^2 m^{-2}) on the day of measurement. This was followed by fitting green area index and day of year into a Gaussian model to estimate the daily green area index at the species level over the season. Finally, daily VGA of each autochamber was calculated by summing the green area index of all vascular plant species present.

5.3.4 Ancillary Field Measurements

We installed thermocouples into the peat at 10 cm depth inside each of the chamber cylinders to monitor peat temperature at 1 Hz for the calculation of half-hourly averages. Continuous 30-minute records of water table position were obtained with a capacitance water level probe (Model Odyssey, Dataflow Systems, New Zealand) placed inside a perforated ABS tube (3.8 cm i.d.) inserted in the peat besides each chamber. Friction velocity was computed every 30 minutes from 20 Hz measurements of wind velocity in three dimensions with a sonic anemometer (Model R3-50, Gill Instruments, UK) mounted on an instrument tower at a height of 3 m. In addition, we measured air temperature (Model HMP35CF, Campbell Scientific Inc., UT, USA) 2 m above the surface, incoming photosynthetically active radiation (PAR, Model LI-190SA, LI-COR, NE, USA), and barometric pressure (Model CS105, Campbell Scientific Inc., UT, USA) at the site every 5 seconds and averaged them half-hourly (Lafleur *et al.*, 2003).

5.3.5 Data Analysis

Concentrations of CO_2 measured in the autochamber headspace were first corrected for water vapour dilution effects using the water vapour concentration data from LI-6262. We calculated the net ecosystem exchange of CO_2 (μmol CO_2 m^{-2} s^{-1}) based on regression of the concentration trace in the chamber headspace over a period of 1.5 minutes, after discarding the data in the initial 45 seconds following chamber closure. We used the atmospheric sign convention for NEE, with a positive value indicating a net release by peatland or a net gain by the atmosphere.

Fluxes were accepted only if $r^2 > 0.9$ ($p < 0.01$, N=19). We also discarded any CO_2 fluxes showing a net plant uptake when PAR was zero. In addition, poor quality flux data obtained during periods of equipment failure and system maintenance were removed from analysis. These quality control procedures led to the removal of 3 to 17% of all fluxes collected for a given chamber. The use of r^2 as a filtering criterion likely introduced some bias into our analysis by removing some near-zero fluxes that might be of good quality. However, the near-zero (±

0.1 μmol m^{-2} s^{-1}) fluxes rejected due to low r^2 comprised only 1.5-2.5% of the total flux measurements. Moreover, this filtering protocol had little effect on the estimation of seasonal integrated fluxes. Even when all the near-zero fluxes with low r^2 were retained in the data set, the seasonal integrated NEE determined was on average 2% different from that calculated with gap-filled fluxes replacing the rejected near-zero values. Furthermore, we found that 13% of measurements made in the field with a calibration chamber with a sealed bottom (i.e. a zero flux chamber) had a CO_2 flux greater than the minimal detectable flux of 0.04 μmol m^{-2} s^{-1} based on the chamber volume and analytical uncertainty of gas analyzer. We thus did not manually add any rejected near-zero fluxes back into the data set, as this might introduce additional uncertainty by incorrectly including zero fluxes as non-zero fluxes. Overall, the r^2 filtering protocol we used was effective in eliminating poor quality fluxes and was conservative in focusing our analysis on data with high degrees of statistical and analytical confidence (Burrows *et al.*, 2005).

To minimize the turbulence-related measurement bias associated with a short chamber deployment period, all CO_2 effluxes were corrected based on the relationships established with friction velocity following Lai *et al.* (2012). We denoted both GEP and ER as positive values. GEP during the daytime (i.e. PAR > 0) was determined as ER - NEE, while at night (i.e. PAR = 0), GEP was set to zero and ER was equivalent to the measured CO_2 flux.

5.3.6 Modelling of CO_2 Exchange

We used a process-based modelling approach to investigate the CO_2 exchange response of plant communities to changing environmental conditions as well as reconstruct half-hourly CO_2 exchange over the whole measurement period. We adapted and modified the non-linear multivariate regression models for GEP and ER from Riutta *et al.* (2007b) and Tuittila *et al.* (2004), which were based on ecophysiological principles and hence were ecologically meaningful. Using our NEE data at Mer Bleue, we parameterized these models separately for each

chamber as well as for each of the three vascular plant communities with a Levenberg-Marquardt algorithm for nonlinear least squares in MATLAB R2009a (MathWorks, MA, USA).

We described the saturating response of GEP to PAR with a Michaelis-Menten rectangular hyperbola following Ruimy *et al.* (1995). In addition, GEP had a unimodal, Gaussian relationship with air temperature such that maximum GEP only occurred at the optimum temperature. Furthermore, GEP had a linear relationship with VGA, with a parameter s added to describe the contribution of moss to the total green area (Laine *et al.*, 2007a). The GEP model had a multiplicative form shown:

$$GEP = \left(\frac{\alpha * PAR * P_{\max}}{\alpha * PAR + P_{\max}} \right) * \exp\left(-0.5 * \left(\frac{T - T_{opt}}{T_{tol}} \right)^2 \right) * \left(s + VGA\right) \quad (5.1)$$

where α is the apparent quantum yield, P_{max} is the VGA-dependent maximum gross photosynthesis when PAR and temperature are not limiting, T is air temperature, T_{opt} is the optimum temperature for GEP, T_{tol} is the temperature tolerance (deviation from the optimum at which GEP was 60% of its maximum), and s is an estimate of the *Sphagnum* moss green area.

We modelled the response of ER to peat temperature as an exponential function based on Lloyd and Taylor (1994). As the increase in microbial respiration with water table depth is limited by moisture in very dry conditions, it is ecologically reasonable to describe the relationship between ER and water table with a sigmoidal curve (Tuittila *et al.*, 2004). However, we used an exponential function instead since water table remained high throughout 2009. A linear response of ER to VGA was also included. The overall ER model form was as follows:

$$ER = R_{10} * \exp\left(E_0 * \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{soil} - T_0} \right) \right) * \exp\left(-b * WT\right) + v * VGA \quad (5.2)$$

where R_{10} is the respiration rate at 10°C when water table is not limiting and VGA is zero, E_0 is a parameter related to the activation energy, T_{ref} is a reference

temperature (283.15 K), T_0 is the temperature at which ER becomes zero (227.13 K), T_{soil} is the peat temperature at 10 cm depth, b is the initial slope of the water table response function, WT is the water table depth, and v is the change in respiration rate per VGA unit.

We assessed the influence of a single environmental factor on GEP and ER while keeping other factors constant following the approach of Tuittila *et al.* (2004). First, the residuals were calculated as the difference between the measured values and corresponding modelled values based on the prevailing environmental conditions and parameterized models in Equations (5.1) and (5.2). Then, the measured GEP and ER values were adjusted to chosen conditions of PAR = 2000 μmol m^{-2} s^{-1}, air temperature = 20 ºC, peat temperature = 15 ºC, water table = -25 cm, and VGA = 1 m^2 m^{-2}, while allowing only one factor to vary at a time. Lastly, the residuals were added to the adjusted measured values, enabling variations in GEP and ER unexplained by the models to be shown.

5.3.7 Reconstruction of CO_2 Exchange

For each chamber, we fit the measured CO_2 efflux and environmental data at night into the ER model in Equation (5.2) to estimate the parameters. Then, missing nighttime ER data were gap-filled and daytime ER estimated at half-hourly intervals using the chamber-specific parameterized model as well as peat temperature, water table and VGA data. Following the procedures of Barr *et al.* (2004), we adjusted for seasonal variations of modelled RE with a time-varying factor that was determined by linear regression of modelled values against measured values with a moving window of 200 data points in increments of 40 points. We then calculated daytime GEP as the difference between modelled ER and measured NEE, and parameterized the GEP model in Equation (5.1) with daytime GEP, PAR, air temperature and VGA data for GEP estimation when NEE data were not available. Lastly, missing NEE data during the day were gap-filled as the difference between modelled ER and GEP.

5.3.8 Statistical Analysis

We employed ANOVA with Tukey's post hoc test to compare the mean daily NEE, GEP, ER, and environmental parameters among three vascular plant communities at the Mer Bleue bog. To compare the mean difference in GEP and ER among plant communities while accounting for the influence of environmental factors, we added dummy variables to the ecophysiological models in Equations (5.1) and (5.2) to indicate the presence (coded as 1) or absence (coded as 0) of specific community, and tested for significant difference of the dummy variable coefficients from zero with a t-test after parameterizing the model with our full data set. To examine whether plant communities responded to changes in environmental conditions differently, we conducted t-test to compare the parameters of the GEP and ER models among the three different communities. We also tested for significant difference in the overall GEP and ER models among plant communities with an F-test. All the data filtering and statistical analyses were conducted in MATLAB R2009a (MathWorks, MA, USA) and PASW Statistics 18 (SPSS Inc., IL, USA).

5.4 Results

5.4.1 Variations in Environmental and Biotic Conditions

We did not observe any significant difference in seasonal mean peat temperature at 10 cm depth among the three vascular plant communities ($p > 0.05$, Figure 5.1a). Overall, all communities had a similar seasonal pattern of peat temperature, increasing gradually from about 10ºC in May to a peak of 19 to 22ºC in mid-August and then decreasing to a minimum of less than 4ºC in November (Figure 5.2a). *Maianthemum/Ledum*-dominated community had the smallest annual range of peat temperature, with significantly lower mean from May to August, but significantly higher average in November (Table 5.2). *Chamaedaphne*-dominated community had a significantly lower water table than both *Eriophorum* and *Maianthemum/Ledum* communities throughout the measurement period ($p < 0.01$, Figures 5.1b and 5.2a). Owing to a record-high rainfall amount of over 220 mm in July, the water table remained high during the

summer period of 2009 in spite of the high temperature that enhanced evapotranspiration (Figure 5.2a).

We observed a significantly higher seasonal mean VGA in the *Chamaedaphne* community (0.80 m^2 m^{-2}) than in the other two communities (0.64-0.65 m^2 m^{-2}) ($p < 0.01$, Figure 5.1c). Yet, the *Maianthemum/Ledum* community had the highest seasonal peak VGA of 1.52 m^2 m^{-2} that was attained earliest in the beginning of July (DOY 186), with *Maianthemum* leaves alone contributing to a maximum of 1.15 m^2 m^{-2} (Figure 5.2b). In contrast, mean VGA in the *Chamaedaphne* and *Eriophorum* communities reached a maximum of 1.38 and 1.08 m^2 m^{-2}, respectively, around mid-August (DOY 219-224). This difference in phenological patterns resulted in the *Maianthemum/Ledum* community having a significantly higher VGA between May and June, but a significantly lower VGA between September and November among the three communities ($p < 0.01$, Table 5.2).

5.4.2 Variations in CO_2 Exchange Among Plant Communities

Figure 5.1d shows the seasonal mean NEE, GEP and ER in the three vascular plant communities at the Mer Bleue bog. No significant difference ($p > 0.05$) in seasonal mean NEE was found among the three communities, which ranged between -0.62 and -0.71 g CO_2-C m^{-2} d^{-1}. We found a significantly lower seasonal mean GEP in the *Maianthemum/Ledum* community with 1.72 g CO_2-C m^{-2} d^{-1} ($p < 0.01$), but no significant difference between the *Chamaedaphne* and *Eriophorum* communities (2.17 and 2.24 g C m^{-2} d^{-1} respectively, $p = 0.57$). Seasonal mean ER was significantly different among the three communities ($p < 0.01$), with the highest rate observed in the *Eriophorum* community (1.61 g C m^{-2} d^{-1}), followed by the *Chamaedaphne* community (1.46 g C m^{-2} d^{-1}), and lowest in the *Maianthemum/Ledum* community (1.09 g C m^{-2} d^{-1}).

The seasonal pattern of daily NEE measured by autochambers from the three plant communities generally resembled that obtained by the eddy covariance

method at the same site (Figure 5.3). The magnitude of C uptake by plants decreased (i.e. towards a less negative NEE) from late May to end of June, then increased to a seasonal maximum in mid-July, and dropped again to eventually become a persistent source of C from mid-November onwards. When comparing the mean NEE among communities by time period, the *Maianthemum/Ledum* community had a significantly larger C uptake (-1.01 g C m^{-2} d^{-1}) between May and June, but was a significantly smaller C sink (-0.32 g C m^{-2} d^{-1}) between September and October ($p < 0.01$, Figure 5.5a).

Although daily GEP in all three plant communities exhibited a unimodal pattern over the measurement period, the timing at which GEP reached the highest value was different (Figure 5.4a). We observed maximum GEP in the *Chamaedaphne* and *Eriophorum* communities in mid-August, while GEP in the *Maianthemum/Ledum* community decreased quickly after peaking in mid-July. Between May and June, mean GEP was not significantly different among communities ($p > 0.05$), while between July and October, average GEP in the *Maianthemum/Ledum* community was significantly lower ($p < 0.01$, Figure 5.5b). Moreover, the *Eriophorum* community had a significantly higher GEP than the other two communities starting from September ($p < 0.05$).

The seasonal pattern of daily ER was highly similar across the three communities, increasing from the beginning of the study period to two distinct peaks in late June (DOY 180) and mid-August (DOY 230) before decreasing consistently to very low values at the end of season (Figure 5.4b). Regardless of the time of year, mean ER was significantly higher in the *Eriophorum* than in the *Chamaedaphne* community, which was in turn significantly higher than ER in the *Maianthemum/Ledum* community ($p < 0.05$, Figure 5.5c).

5.4.3 Variations in the Functional Response of CO_2 Exchange

The GEP model parameterized by fitting the daytime GEP data and dummy variables for plant communities had an R^2 of 0.72 (Table 5.3). The

dummy variable coefficients for the *Eriophorum* and *Maianthemum/Ledum* communities were significantly different from zero ($p < 0.01$), indicating that the mean GEP in these two communities were statistically different from that in the *Chamaedaphne* community. GEP in the *Eriophorum* and *Maianthemum/Ledum* communities were on average 0.44 μmol CO_2 m^{-2} s^{-1} higher and 0.58 μmol CO_2 m^{-2} s^{-1} lower, respectively than in the *Chamaedaphne* community, when given the same PAR, air temperature and VGA. On the other hand, the ER model parameterized based on nighttime flux data had an R^2 of 0.69 (Table 5.3). Given the same peat temperature, water table and VGA, ER in the *Eriophorum* and *Maianthemum/Ledum* communities were 0.39 μmol CO_2 m^{-2} s^{-1} higher and 0.04 μmol CO_2 m^{-2} s^{-1} lower, respectively than in the *Chamaedaphne* community ($p < 0.01$).

All five estimated parameters of the GEP model were significantly different among the three plant communities ($p < 0.01$), except for T_{tol} between the *Eriophorum* and *Chamaedaphne* communities ($p = 0.93$, Table 5.4). We obtained the highest apparent quantum yield in the *Eriophorum* community and lowest in the *Maianthemum/Ledum* community with 0.015 and 0.006 μmol CO_2 μmol^{-1} PAR, respectively. This corresponded to the higher initial slope of GEP against PAR observed in the *Eriophorum* community, when other environmental variables were adjusted to selected values (Figure 5.6). PAR was the most dominant factor governing GEP, alone explaining 49 to 60% of the variations in the three communities. It is also worth noting that at PAR levels > 500 μmol m^{-2} s^{-1}, GEP in November typically deviated from the overall relationship with much lower values. Furthermore, we found P_{max} values (expressed in μmol CO_2 m^{-2} s^{-1} VGA $unit^{-1}$) decreasing significantly in the order of *Chamaedaphne* (8.4) > *Eriophorum* (7.8) > *Maianthemum/Ledum* community (3.3) (Table 5.4). Yet, when VGA was fixed at 1 m^2 m^{-2}, maximum GEP at the high end of PAR was greater in the *Eriophorum* than in the *Chamaedaphne* community (Figure 5.6).

Green area was another important factor controlling the photosynthetic

activity of plant community, alone accounting for 22 to 30% of the variations in GEP. Inclusion of VGA improved the R^2 of the GEP model by 0.15 to 0.21 compared to the model based solely on PAR. The rate of linear increase in GEP with VGA was considerably lower in the *Maianthemum/Ledum* community with a slope of 2.55, compared to 5.93 and 6.21 in the *Eriophorum* and *Chamaedaphne* communities, respectively, under the selected environmental conditions (Figure 5.7). Moreover, the estimated parameter s (in m^2 m^{-2}) increased in the order of *Chamaedaphne* (0.25) < *Eriophorum* (0.49) < *Maianthemum/Ledum* (1.54), implying a significantly greater contribution of moss to GEP in the latter community (Table 5.4). On the other hand, air temperature alone was able to explain 25 to 33% of the variations in GEP, but was less important in increasing the proportion of variance explained by the overall GEP model. *Maianthemum/Ledum* community had the highest optimum temperature of 18.2ºC for photosynthesis, but all communities generally had a high temperature tolerance ranging between 13.3 and 19.3ºC (Table 5.4).

The ER model parameterized using the available nighttime CO_2 flux and environmental data had an R^2 of 0.70 to 0.72 in the three plant communities (Table 5.5). Peat temperature was the single most dominant factor governing the rate of ecosystem respiration at the Mer Bleue bog, alone explaining 64 to 69% of the variations. ER increased exponentially with peat temperature, with the highest sensitivity seen in the *Eriophorum* community (Figure 5.8). Meanwhile, we did not observe hysteresis in ER between the periods of rising and decreasing temperature in any of the plant communities. As shown in Table 5.5, *Chamaedaphne* community had a significantly higher R_{10} and lower E_0 than the other two communities ($p < 0.05$). Moreover, when compared to the *Eriophorum* community, the *Maianthemum/Ledum* community had a significantly lower R_{10} but no significant difference in E_0 value.

Inclusion of both water table depth and VGA into the temperature-based ER model only improved the R^2 value by 0.03 to 0.07 in the three communities.

Yet, VGA alone was capable of explaining 37 to 48% of the variations in ER. The *Eriophorum* community had the greatest value of parameter v with 0.36 μmol CO_2 m^{-2} s^{-1} VGA $unit^{-1}$ ($p < 0.05$, Table 5.5), and hence the largest increase in ER with VGA. In contrast, water table alone just accounted for 9 to 11% of the variance in ER. The parameter b was significantly smaller in the *Chamaedaphne* community ($p < 0.01$, Table 5.5), indicating a less sensitive response of ER to water table. Table 5.6 shows the results of F-test comparing the parameterized GEP and ER models among plant communities. Both the GEP and ER models were significantly different among the three communities ($p < 0.01$), further confirming that the three sets of parameter values generated different overall curves.

To further investigate the temporal change in the parameters of the light response function of the GEP model, we fit the GEP and PAR data by month to Equation (5.1) without the air temperature and VGA terms. The R^2 value of these curves ranged between 0.45 and 0.76 across time and community. The apparent quantum yield generally increased from May to a peak in summer around July and August, and then decreased consistently to a minimum in November (Figure 5.9a). We found the largest between-community difference in α in August, when a seasonal maximum of 0.023 μmol CO_2 μmol^{-1} PAR was reached in *Chamaedaphne* but a 37% drop to 0.012 μmol CO_2 μmol^{-1} PAR seen in the *Maianthemum/Ledum* community. P_{max} also demonstrated a similar seasonal pattern in the three communities, with the highest values attained in mid-summer and lowest in November (Figure 5.9b). We obtained seasonal highest P_{max} of 8.82 μmol m^{-2} s^{-1} in July in *Maianthemum/Ledum*, 10.88 μmol m^{-2} s^{-1} in August in *Eriophorum*, and 12.22 μmol m^{-2} s^{-1} in August in the *Chamaedaphne* community. However, the temporal variability of P_{max} was much reduced when normalized by the community-specific monthly mean green area (VGA + s). Mean normalized P_{max} between May and October were 2.92, 7.30, and 8.02 μmol CO_2 m^{-2} s^{-1} VGA $unit^{-1}$ in the *Maianthemum/Ledum*, *Eriophorum* and *Chamaedaphne* communities, respectively, before decreasing sharply to much lower values in November

(Figure 5.9c). The coefficient of variation of normalized P_{max} (May-October) in the three communities ranged between 10.8 and 19.3%, compared to 23.3 to 34.4% for P_{max} over the same period without adjustment for green area.

5.5 Discussion

5.5.1 Variations in CO_2 Exchange Among Plant Communities

Peatland ecosystem typically has a high spatial heterogeneity at a scale length of as short as 1 to 10 m (Baird *et al.*, 2009). Water table in particular has a strong influence on the fine-scale distribution of peatland vascular plant species. Results of vegetation survey at the Mer Bleue bog showed that *Chamaedaphne calyculata* had an optimal water table position of about 10 cm deeper than *Eriophorum vaginatum*, *Ledum groenlandicum* and *Maianthemum trifolium* (Bubier *et al.*, 2006). Hence, community dominated by the evergreen shrub *C. calyculata* was largely seen at hummocks with a significantly lower seasonal mean water table (Figure 5.1b). In contrast, lawns with a higher water table were usually occupied by communities dominated by either the sedge *E. vaginatum*, or a mixture of evergreen shrub (*L. groenlandicum*) and forb (*M. trifolium*).

Based on over 19,000 flux measurements made by autochambers in each of the three vascular plant communities in 2009, we observed considerable difference in the two main components of NEE among communities (Figure 5.1d). Seasonal mean GEP was significantly lower in the *Maianthemum/Ledum* community, while there was no difference between *Eriophorum* and *Chamaedaphne* communities. Bubier *et al.* (2003b) reported a higher maximum NEE per unit biomass from the sedge/herb than the evergreen shrub chamber (0.046 *vs.* 0.016 μmol s^{-1} g^{-1}) in a temperate fen. Moreover, foliar N concentration that relates positively to the light-saturated photosynthetic rate, follows the order of *M. trifolium* > sedge > evergreen shrub at Mer Bleue (Bubier *et al.*, 2006; Small, 1972). The higher photosynthetic efficiency of *Eriophorum* probably offset the effect of a smaller VGA compared to the *Chamaedaphne* community, leading to similar GEP rates between the two. On the other hand, low GEP values in the

Maianthemum/Ledum community might be a result of a difference in leaf structure. The specific leaf area (SLA, leaf area per unit dry mass) of *Maianthemum spp.* is very high ranging between 300-600 cm^2 g^{-1} (Lezberg *et al.*, 2001), compared to ~50 cm^2 g^{-1} for *E. vaginatum* (Kool and Heijmans, 2009) and 60-80 cm^2 g^{-1} for *L. groenlandicum* and *C. calyculata* leaves (Bubier *et al.*, 2011). The higher SLA in the *Maianthemum/Ledum* community led to a smaller amount of photosynthetically active vascular biomass and subsequently a lower GEP rate, even though its seasonal mean VGA was the same as that in the *Eriophorum* community.

Seasonal mean ER was significantly different among the three communities, with the rate in *Eriophorum* > *Chamaedaphne* > *Maianthemum/Ledum* (Figure 5.1d). McNamara *et al.* (2008) have similarly observed a higher rate of ER in *Eriophorum* than in shrub community in a British blanket bog. Peat temperature at 10 cm depth was similar across communities (Figure 5.1a) and thus failed to account for the spatial variations in ER. A linear increase in CO_2 efflux with water table depth has been shown in both laboratory incubation of peat columns (Moore and Knowles, 1989) and field measurements in a boreal peatland (Bubier *et al.*, 1998), owing to an increase in the thickness of aerobic zone for peat decomposition. In addition, a positive relationship between mean summer vascular plant foliar biomass, maximum NEE, and ER has been found across 10 autochambers in a temperate fen, indicating the important role of plant processes in governing the total respiration in a peatland ecosystem (Bubier *et al.*, 2003b). In view of the above, a significantly lower ER in the *Maianthemum/Ledum* community was likely caused by a combination of high seasonal mean water table position, small foliar biomass, and lower rates of gross photosynthesis, although *M. trifolium* has a large belowground live biomass that could contribute to ER via root respiration (Moore *et al.*, 2011). For the *Eriophorum* community, the high ER observed was probably a result of rapid C turnover. Through $^{13}CO_2$ pulse labelling and flux measurements, Ward *et al.* (2009) found a faster translocation and turnover of recent photosynthate as total

respired CO_2 in sedges, especially in the absence of ericaceous shrubs. Litter decomposition fails to adequately explain the difference in ER between *Eriophorum* and *Chamaedaphne* communities, as the decay constant *k* value is highly similar between sedge and shrub leaves at the surface, as well as between sedge and shrub roots belowground (Moore *et al.*, 2007).

Seasonal (May-November) mean NEE was not statistically different among the three plant communities, in spite of a significant difference in GEP and ER spatially (Figure 5.1d). Despite the *Maianthemum/Ledum* community had the lowest rate of gross photosynthesis, at the same time it had the smallest amount of C lost through ER, leading to an overall similar C sink strength as that in the other two communities. However, we detected significant between-community difference in mean NEE when looking at specific periods over the season, which appeared to be more strongly governed by variations in GEP than ER (Figure 5.5). The *Maianthemum/Ledum* community was a significantly larger C sink in May-June but a smaller C sink in September-October than the other two communities, probably related to the phenological change of the dominant vascular species in plant community. The forb *M. trifolium* has a short leaf longevity, reaching maximum growth in early July and then senescing very quickly in mid-summer (Figure 5.2b). In the early season, the *Maianthemum/Ledum* community had a significantly higher VGA and thus could sustain a relatively high rate of GEP. This led to a higher net C uptake than the other two communities as ER remained low with a significantly lower peat temperature (Table 5.2). In the late growing season, most of the *Maianthemum* leaves had senesced with a 71% reduction in mean VGA compared to mid-summer, resulting in significantly lower GEP and net C uptake. Bubier *et al.* (2003a) did not find any significant difference in maximum NEE, gross photosynthesis and ER in June-August between hummocks and hollows at the Mer Bleue bog, because of the small range of foliar biomass across sites. Yet, we found a significantly higher NEE in the *Chamaedaphne* community between July and August than the other two communities, as the evergreen shrub reached the maximum foliar growth with a significantly higher

mean VGA for photosynthesis while the turnover of recently fixed C was probably slower compared to sedges.

5.5.2 Variations in the Functional Response of CO_2 Exchange

Temporal variation of GEP in northern peatlands is often predominantly controlled by PAR. Previous studies have reported that PAR accounted for 58% of the seasonal variations in photosynthesis in a boreal collapse bog (Bubier *et al.*, 1998), and the fitting of PAR and daytime NEE data to a light response curve produced high r^2 values of 0.7 to 0.9 in some north European mires in the mid growing season (Lindroth *et al.*, 2007). At Mer Bleue, PAR alone explained 49 to 60% of the variability of GEP through a rectangular hyperbolic relationship. We obtained significantly different apparent quantum yields between each of the three communities, with the highest and lowest values in the *Eriophorum* and *Maianthemum/Ledum* communities, respectively (Table 5.4). This suggests that the rate of increase in CO_2 uptake with PAR at low light levels is greatest in the *Eriophorum* community, which agrees with other findings that sedge is highly efficient in photosynthetic activity (Leppälä *et al.*, 2008; Ward *et al.*, 2009). We obtained α values of 0.006 to 0.015 μmol CO_2 μmol^{-1} PAR across communities, which were smaller than the range of 0.014 to 0.028 μmol CO_2 μmol^{-1} PAR determined by manual chambers in the growing season in northern bogs (Bubier *et al.*, 2003a; Frolking *et al.*, 1998; Strilesky and Humphreys, 2012), probably because we also included data in the late season till November when photosynthetic activity was less active.

We also observed significant difference in P_{max} per unit green area among plant communities, with 8.42, 7.80 and 3.28 μmol m^{-2} s^{-1} VGA $unit^{-1}$ in the *Chamaedaphne*, *Eriophorum*, and *Maianthemum/Ledum* communities, respectively (Table 5.4). Both vascular plant and moss contribute to gross photosynthesis in a peatland plant community. When all communities had the same VGA of 1 m^2 m^{-2}, maximum GEP was greater in *Eriophorum* than in the *Chamaedaphne* community, as shown by a higher asymptote of the light response

curve (Figure 5.6). This could be due to a greater contribution of *Sphagnum* moss to total GEP in the *Eriophorum* community, as shown by a significant decrease in the estimated parameter s of our parameterized GEP model in the order of *Maianthemum/Ledum* (1.54) > *Eriophorum* (0.49) > *Chamaedaphne* (0.25 m^2 m^{-2}) (Table 5.4). Sonnentag *et al.* (2007) observed a much higher percent cover of vascular plants of 90.6% in hummocks than 40.6% in hollows at Mer Bleue. The dense shrub cover in the *Chamaedaphne* community likely enhanced shading of the understory *Sphagnum* layer and reduced the importance of moss photosynthesis to GEP (Douma *et al.*, 2007; Street *et al.*, 2007). An increased shrub cover in the fertilized plots of the Mer Bleue bog has been observed to considerably reduce the amount of PAR reaching the moss surface, and subsequently lower photosynthetic CO_2 uptake by *Sphagnum* moss (Chong *et al.*, 2012). While the contribution of moss photosynthesis was assumed to be constant over time in our GEP model, it is worth noting that the growth of *Sphagnum* moss has shown seasonal variability with higher rates in the spring and fall (Moore *et al.*, 2002). On the other hand, low P_{max} values in the *Maianthemum/Ledum* community might be partly caused by the lower vascular cover and hence greater contribution of moss photosynthesis, which is less efficient than that of shrubs and sedges (Leppälä *et al.*, 2008), to the community-level GEP. Moreover, previous work at Mer Bleue has shown that maximum photosynthetic rate per unit leaf area is lower for *L. groenlandicum* than *C. calyculata* foliage (Small, 1972), although Strilesky and Humphreys (2012) obtained similar P_{max} values among various shrub species. Based on the seasonal mean VGA and estimated parameter s, we calculated that P_{max} per unit ground area would be 8.89, 8.84 and 7.15 μmol m^{-2} s^{-1} in *Eriophorum*, *Chamaedaphne* and *Maianthemum/Ledum* communities, respectively. These values were comparable to the range of 5.23 to 11.96 μmol m^{-2} s^{-1} reported at Mer Bleue (Bubier *et al.*, 2003a; Moore *et al.*, 2002) and 4.1 to 7.1 μmol m^{-2} s^{-1} in a number of northern bogs (Frolking *et al.*, 1998) based on periodic manual chamber measurements.

VGA was another important variable governing GEP, with its addition in

the PAR-based GEP model improving the R^2 values by 0.15 to 0.21 in the three communities. Wilson *et al.* (2007) have also found in three different peatland vascular plant communities an improvement in the explanatory power of the GEP model by 23 to 58% following the inclusion of VGA. While all communities at Mer Bleue demonstrated a positive relationship between VGA and GEP, we observed a much lower rate of increase in *Maianthemum/Ledum* than the other two communities under selected environmental conditions (Figure 5.7). This suggests that VGA plays an important role in controlling the seasonal variations of GEP within community, but is less capable of explaining the spatial variability of GEP across communities, in contrary to findings in the Arctic tundra that leaf area alone could account for 81% of the spatio-temporal variations in plot-level GEP (Street *et al.*, 2007). The lower sensitivity of GEP to VGA in the *Maianthemum/Ledum* community might be related to the much higher SLA of forb leaves. Even with a modest increase in leaf nitrogen concentration by mass over time, the substantial increase in the area of *M. trifolium* leaves could lead to a lower foliar nitrogen content on a leaf area basis, thus posing a constraint on the photosynthesis rate per unit leaf area (Street *et al.*, 2007). This can potentially explain the very low photosynthetic efficiency of herbs per unit leaf area (Leppälä *et al.*, 2008), but high efficiency per unit foliar biomass observed in northern peatlands (Bubier *et al.*, 2003b). Further work should be done to better understand the temporal relationships between foliar nitrogen, leaf area, leaf biomass and C exchange at plant community level in peatlands.

Peat temperature at 10 cm depth was the single most dominant control of ecosystem respiration, explaining 64 to 69% of the variability in the three plant communities. This agreed well with previous studies using manual chambers and eddy covariance technique that peat temperature at 5 or 10 cm depth could explain 62 to 85% of the variations in ER in northern bogs (Bubier *et al.*, 1998; Bubier *et al.*, 2003a; Lafleur *et al.*, 2005). We found from our parameterized ER models a significantly higher R_{10} and significantly lower E_0 in the *Chamaedaphne* community (Table 5.5). This resulted in the lowest temperature sensitivity of ER

in this shrub-dominated community, while the response of ER to peat temperature especially at the higher range was strongest in the *Eriophorum* community due to the combination of moderate R_{10} and E_0 values (Figure 8). Updegraff *et al.* (1995) also observed a higher temperature sensitivity of aerobic C mineralization in peats from sedge than *Sphagnum* through an 80-week laboratory incubation, though the exact mechanism was not clearly known. The higher rate of ER increase with temperature in the *Eriophorum* community might at least be partly related to the enhanced plant production and hence turnover of recent photosynthate, with CO_2 emission arising from root exudation and mineralization shown to be much greater in peatland cores with sedge than with shrub (Crow and Wieder, 2005). Water table depth only correlated weakly with ER in the three communities over time, as observed similarly by eddy covariance measurements at Mer Bleue, which could be explained by the inherent dryness of this bog and the low sensitivity of both moisture content and CO_2 production in the deeper peat to water table changes (Lafleur *et al.*, 2005). Pelletier *et al.* (2011) observed that ER in a boreal bog increased as water table dropped from the peat surface to a depth of 20 cm, but then became relatively constant as water table was further lowered.

To further investigate the temporal variations in parameters of the GEP model, we parameterized a modified model using only GEP and PAR data by month. The apparent quantum yield demonstrated a clear seasonal pattern in the three communities, increasing from May to a peak in mid-summer and then decreasing continually towards very low values in November (Figure 5.9a). Similar seasonal pattern of α has been seen at the ecosystem level in other northern peatlands (Adkinson *et al.*, 2011; Lindroth *et al.*, 2007). The seasonal variability of α was similar to that of VGA, and hence was probably driven by phenological changes of vascular plants, as an increase in leaf area would lead to a corresponding increase in the amount of C fixed for the same amount of light received. We also observed seasonal variations in P_{max} per unit ground area in the three communities, with a seasonal peak in mid-summer and lower values in the early and late growing seasons (Figure 5.9b). However, the temporal variability of

P_{max} reduced considerably when normalized by the monthly mean green area of plant communities (Figure 5.9c). This suggests that changes in P_{max} over time were predominantly driven by variations in leaf area, rather than changes in photosynthetic rate per unit green area, except in November when the normalized P_{max} decreased greatly. This is contrary to the findings of Street *et al.* (2007) that increases in GEP in the evergreen-dominated tundra communities were contributed equally by increases in leaf area index and GEP per unit leaf area, respectively. The small influence of photosynthetic rate per unit green area to seasonal variations of P_{max} suggests a constant nitrogen content per unit green area over time, but further study is needed to test this hypothesis. We have not presented results on the seasonal variations of ER model parameters because of the generally poor fits (R^2 = 0.02 to 0.53) arising from the narrow range of peat temperature in a month. Yet, the seasonal variability of ER model parameters was usually much smaller than GEP parameters as found by other studies conducted in northern peatlands (Adkinson *et al.*, 2011; Glenn *et al.*, 2006).

5.5.3 Implications to the Simulation of Peatland CO_2 Exchange

We found that the three vascular plant communities at Mer Bleue were functionally different with respect to their response of CO_2 exchange to changes in environmental and biotic conditions. Parameterization of the two C exchange models with dummy variables representing the plant communities showed that *Eriophorum* and *Maianthemum/Ledum* communities had significantly higher and lower mean GEP and ER, respectively, than the *Chamaedaphne* community, when given the same environmental conditions (Table 5.3). Moreover, we found significant difference in the parameters of the GEP and ER models among communities, and results of F-test confirmed that the three parameter sets resulted in overall significantly different GEP and ER models among the three plant communities (Table 5.6). Previous studies have parameterized peatland CO_2 exchange models for botanically distinct plant communities due to differences in their photosynthetic and respiratory responses (e.g. Laine *et al.*, 2009; Riutta *et al.*, 2007a). Maanavilja *et al.* (2011) have specifically compared parameters of the

GEP and ER models among four different plant communities in a northern patterned fen and identified two functional types, namely the ombrotrophic and minerotrophic components. They found that the three minerotrophic community types, including *Carex-Scorpidium* wet flark, *Trichophorum* tussock flarks and *Betula-Sphagnum* string margins, had similar responses of GEP and ER. Meanwhile, their minerotrophic communities had much lower moss coverage (5 to 54%) and higher mean water table (5 cm above to 16 cm below peat surface) than the bog communities at Mer Bleue. All three vascular plant communities in our study were different in their GEP and ER responses to environmental conditions, probably due to the dominance of different plant growth forms, namely shrub, sedge, and forb, in these communities. The distinct parameterized GEP and ER models with high R^2 obtained suggest that CO_2 fluxes in this northern bog ecosystem could be adequately reconstructed over time based on plant communities, further supporting the findings of Laine *et al.* (2009) that the spatial heterogeneity of CO_2 exchange within peatlands could be well captured at the plant community level.

Our findings demonstrate the need to take into account vegetation characteristics in modelling CO_2 exchange from peatland plant communities. Not only does the magnitude of GEP vary with plant phenological development, leaf morphology, and foliar N content, the estimated P_{max} value is also a function of the green area of community. There is a potential bias in overestimating the community-specific P_{max} when chamber flux measurements are made preferentially at locations where the plants look healthier (Fox *et al.*, 2008). Moreover, it has been shown that upscaling of chamber fluxes without accounting for differences in community level VGA between the chambers and average of the whole peatland could lead to large bias in the estimation of ecosystem level CO_2 fluxes (Maanavilja *et al.*, 2011; Riutta *et al.*, 2007a). Moss photosynthesis also deserves further attention in GEP modelling. In this study, we only estimated the contribution of moss to total green area and hence GEP of a community based on a parameter in the GEP model. Normalized difference vegetation index (NDVI)

measured in the field is shown to provide a good prediction of the photosynthetic characteristics of moss (Douma *et al.*, 2007), and can be used to compare against our estimation of moss contribution to GEP by model parameterization. Moreover, light response curves have recently been established for sub-arctic bryophytes based on field measurements of NEE (Street *et al.*, 2012), which should be explored in ombrotrophic bogs to improve our modelling of CO_2 exchange as vascular plants and moss are expected to behave differently within a community.

It is worth noting that our study was only based on CO_2 flux measurements made in a single year of 2009 with a wetter than normal summer, whereas numerous studies have reported interannual variability of peatland CO_2 exchange at the plant community level. At the Mer Bleue peatland, significantly lower GEP was observed at the sedge site in a dry year due to early senescence of leaves, while GEP at the shrub site had no change (Bubier *et al.*, 2003a). In a wetter temperate fen, both CO_2 uptake and release from the shrub-dominated locations were greater in the dry summer, while GEP at the sedge-dominated locations remained the same in the dry and wet summers (Bubier *et al.*, 2003b). Given the observed interannual difference in the magnitude of C exchange, it is also probable that the responses of GEP and ER to environmental conditions differ between years and among communities to varying extents. The consistency of functional divergence among the three plant communities at Mer Bleue across years with different meteorological conditions warrants further attention.

5.6 Conclusions

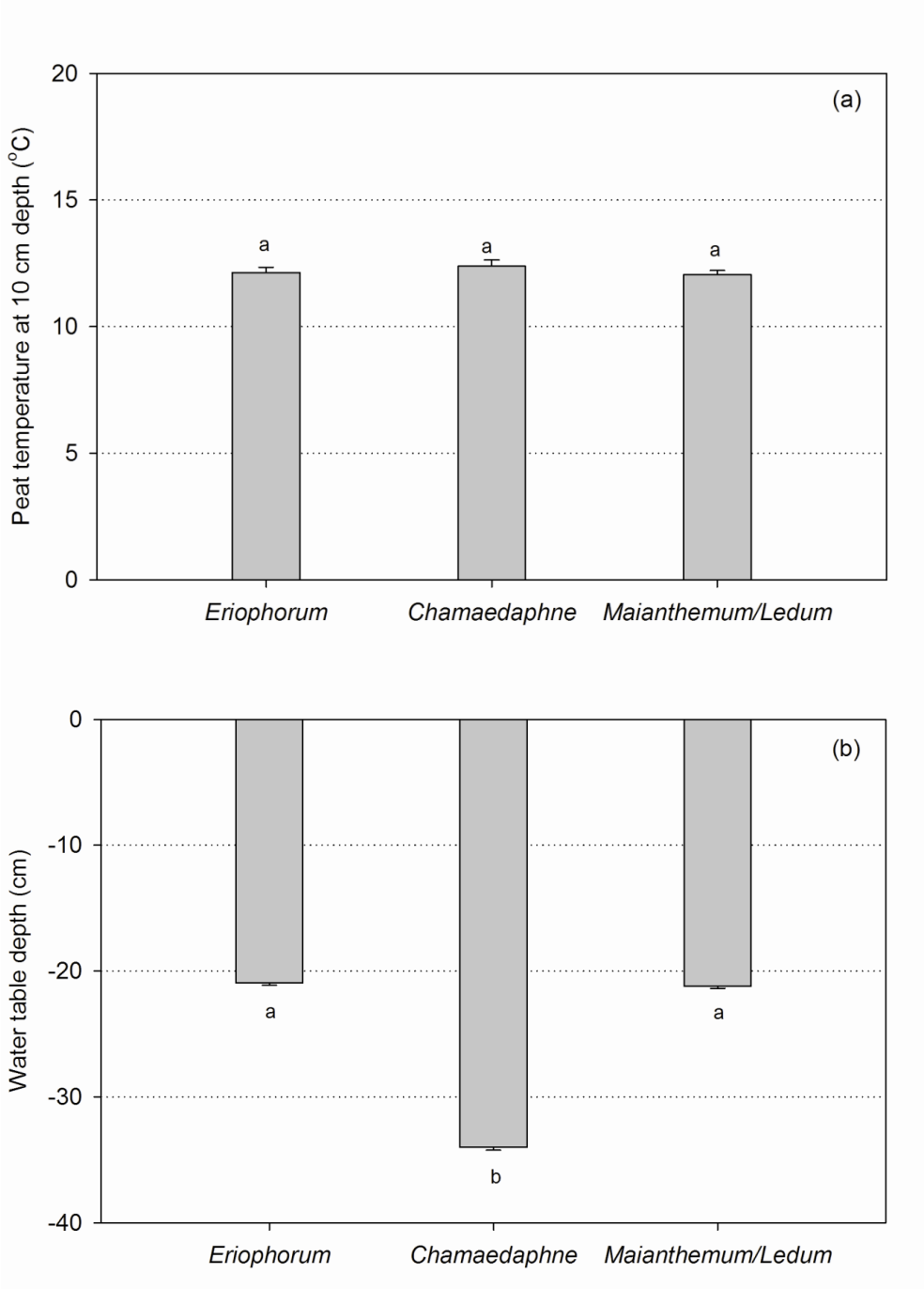
We measured CO_2 exchange from three vascular plant communities at the Mer Bleue bog quasi-continuously from May to November in 2009 with automatic chambers. We did not find significant difference in seasonal mean NEE between communities, but seasonal mean GEP and ER were significantly lower in the *Maianthemum/Ledum* community, probably due to a smaller photosynthetically active biomass and higher water table. Moreover, seasonal mean ER was significantly higher in *Eriophorum* than *Chamaedaphne* community, which might

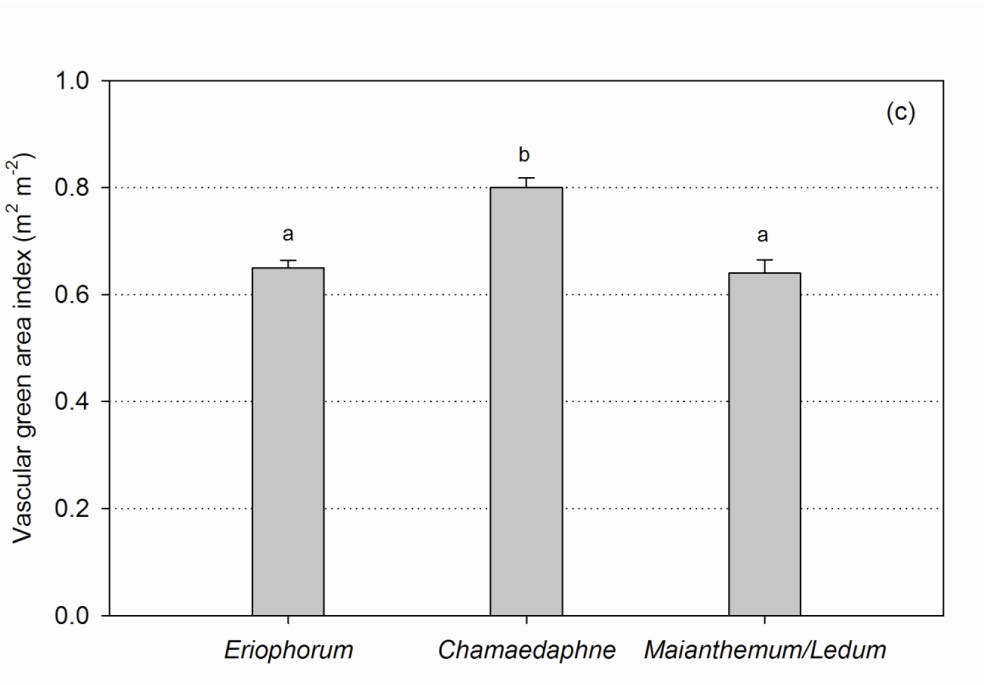
be explained by the faster turnover of recent photosynthate and decomposition of litter in sedges. Meanwhile, we observed significant differences in NEE among plant communities averaged at shorter time periods over the season, which were driven more by variations in GEP than ER.

Temporal variations of GEP in the three communities were strongly governed by PAR and VGA. Effective quantum yield was significantly higher in the *Eriophorum* community, indicating a more efficient photosynthesis by sedge at low light levels. However, P_{max} per unit green area was significantly lower in *Eriophorum* than *Chamaedaphne* community, likely because of a greater contribution of moss to total GEP. The seasonal variability of P_{max} per unit ground area was greatly reduced after adjusting for changes in the green area of community, which suggests that changes in P_{max} per unit ground area over time are predominantly caused by variations in leaf area than photosynthetic capacity per unit green area. The rate of increase in GEP with VGA was significantly lower in the *Maianthemum/Ledum* community, which could be explained by their considerably greater specific leaf area. On the other hand, seasonal variations of ER in the three communities were mostly controlled by peat temperature, with ER in the *Eriophorum* community being most sensitive to temperature changes.

Our results suggest that the three plant communities behave differently with respect to their CO_2 response to changing environmental and biotic conditions, and hence should be taken into account separately in modelling peatland CO_2 fluxes over time. This functional divergence among plant communities is likely due to the dominance of different plant growth forms, which vary in phenology and ecosystem functions. Incorporating variations of vascular and moss green area in C models would improve the simulation of CO_2 exchange, as changes in green area contribute greatly to temporal variations of photosynthetic activity.

Figure 5.1. Seasonal mean (a) peat temperature at 10 cm depth, (b) water table depth, (c) vascular green area index, (d) net ecosystem CO_2 exchange, gross ecosystem production, and ecosystem respiration in three vascular plant communities at the Mer Bleue bog. Error bar indicates ± 1 standard error of the mean. Different letters denote significant difference between plant communities ($p < 0.05$).




(c)
Vascular green area index (m^2 m^{-2})
1.0
0.8
0.6
0.4
0.2
0.0
a
b
a
Eriophorum
Chamaedaphne
Maianthemum/Ledum

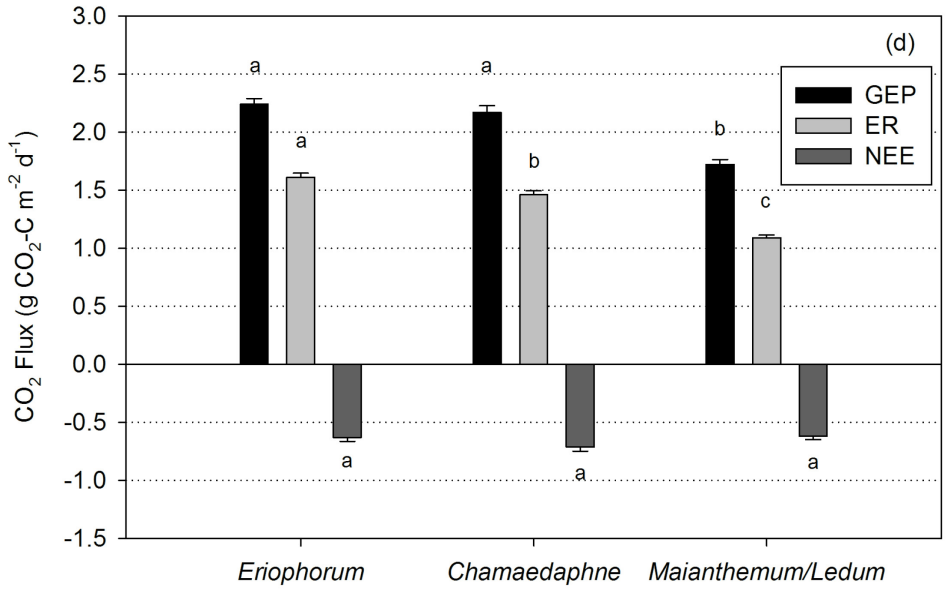
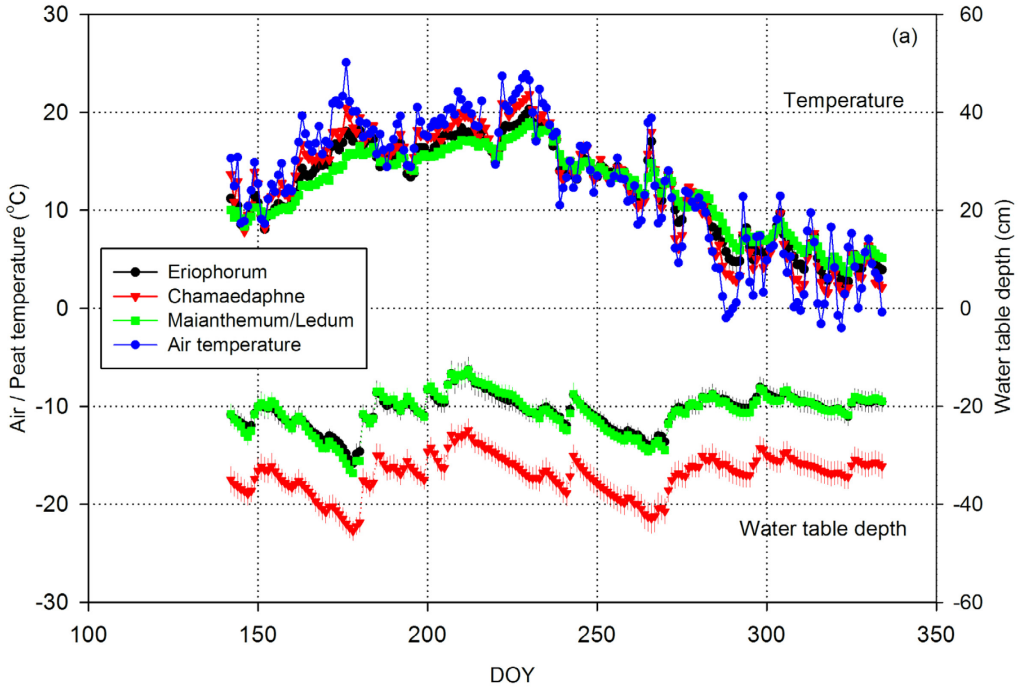

(d)
GEP
ER
NEE
CO_2 Flux (g CO_2-C m^{-2} d^{-1})
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
a
a
a
a
b
a
b
c
a
Eriophorum
Chamaedaphne
Maianthemum/Ledum

Figure 5.2. Seasonal variations in daily mean (a) water table depth, air temperature and peat temperature at 10 cm depth, and (b) vascular green area index at the Mer Bleue bog in 2009. Error bar indicates ± 1 standard error of triplicate chambers for each plant community.



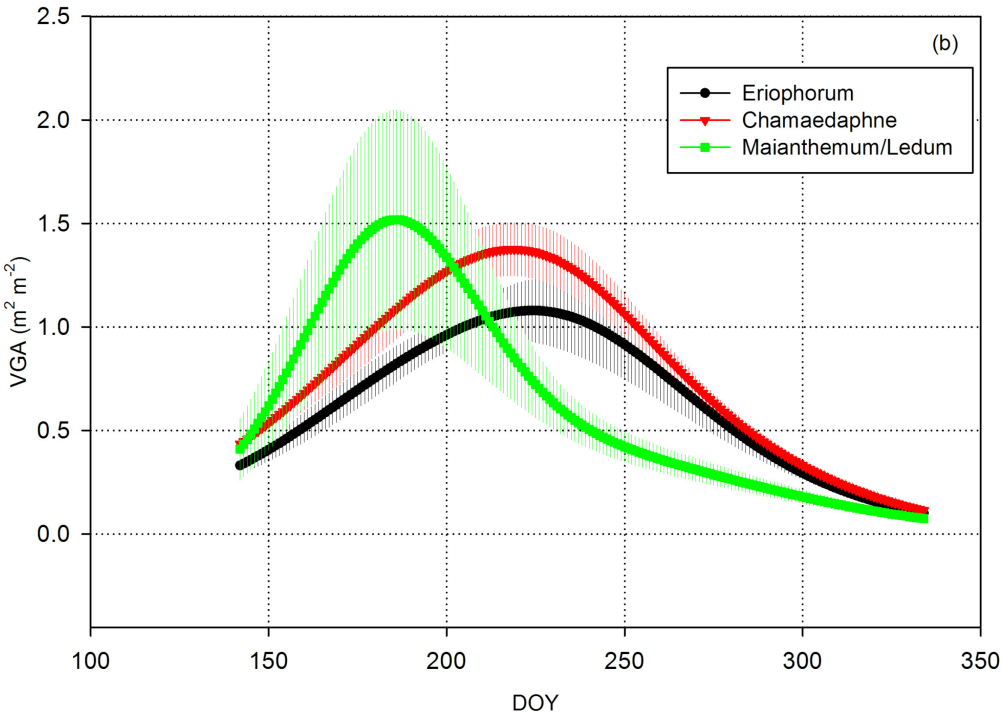


Figure 5.3. Seasonal variations in daily net ecosystem CO_2 exchange (g CO_2-C m^{-2} d^{-1} ± 1 standard error) measured by autochambers in three vascular plant communities and by eddy covariance at the Mer Bleue bog.

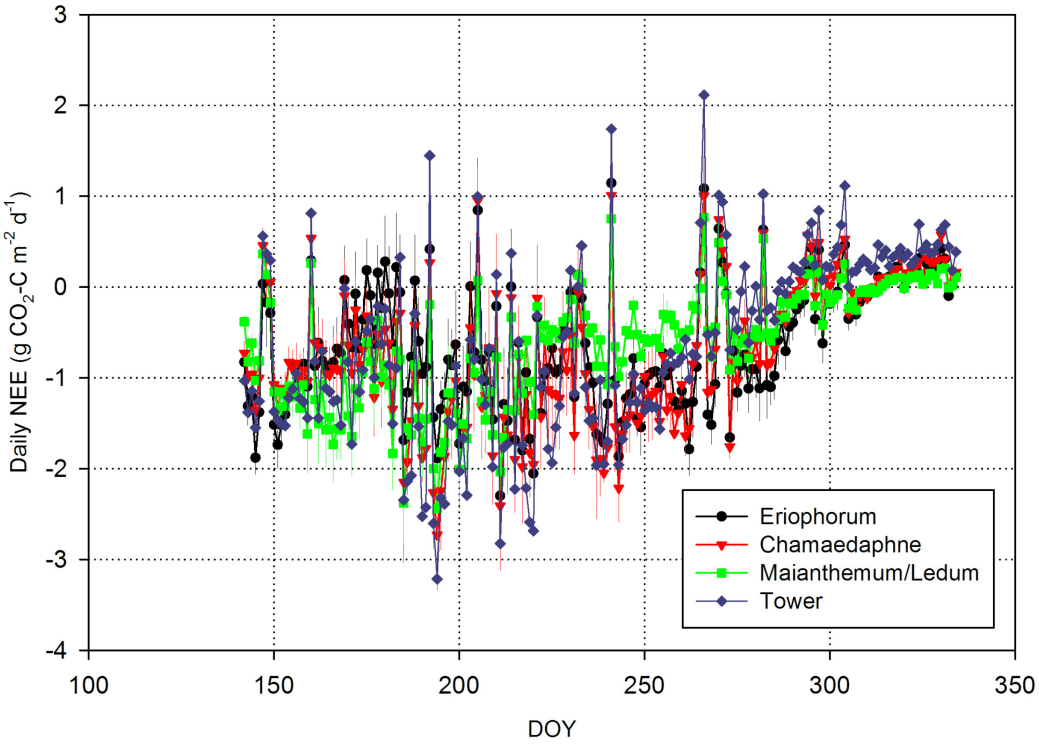


Figure 5.4. Seasonal variations in (a) daily gross ecosystem production and (b) daily ecosystem respiration (g CO_2-C m^{-2} d^{-1} ± 1 standard error) in three vascular plant communities at the Mer Bleue bog.

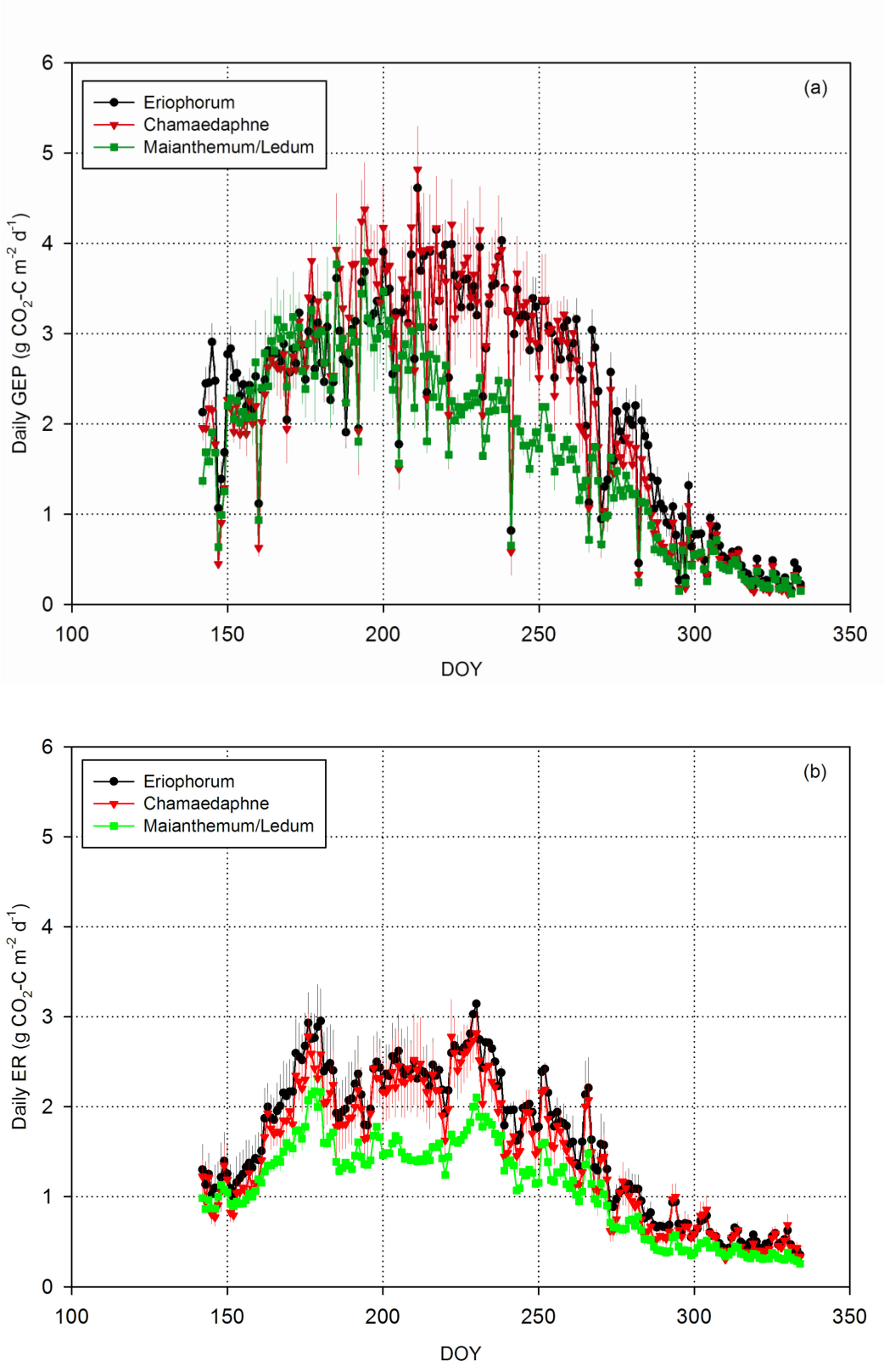


Figure 5.5. Mean daily (a) net ecosystem CO_2 exchange, (b) gross ecosystem production and (c) ecosystem respiration in three plant communities by time period. Error bar indicates ± 1 standard error of the mean. Different letters denote significant difference between plant communities (p<0.05).

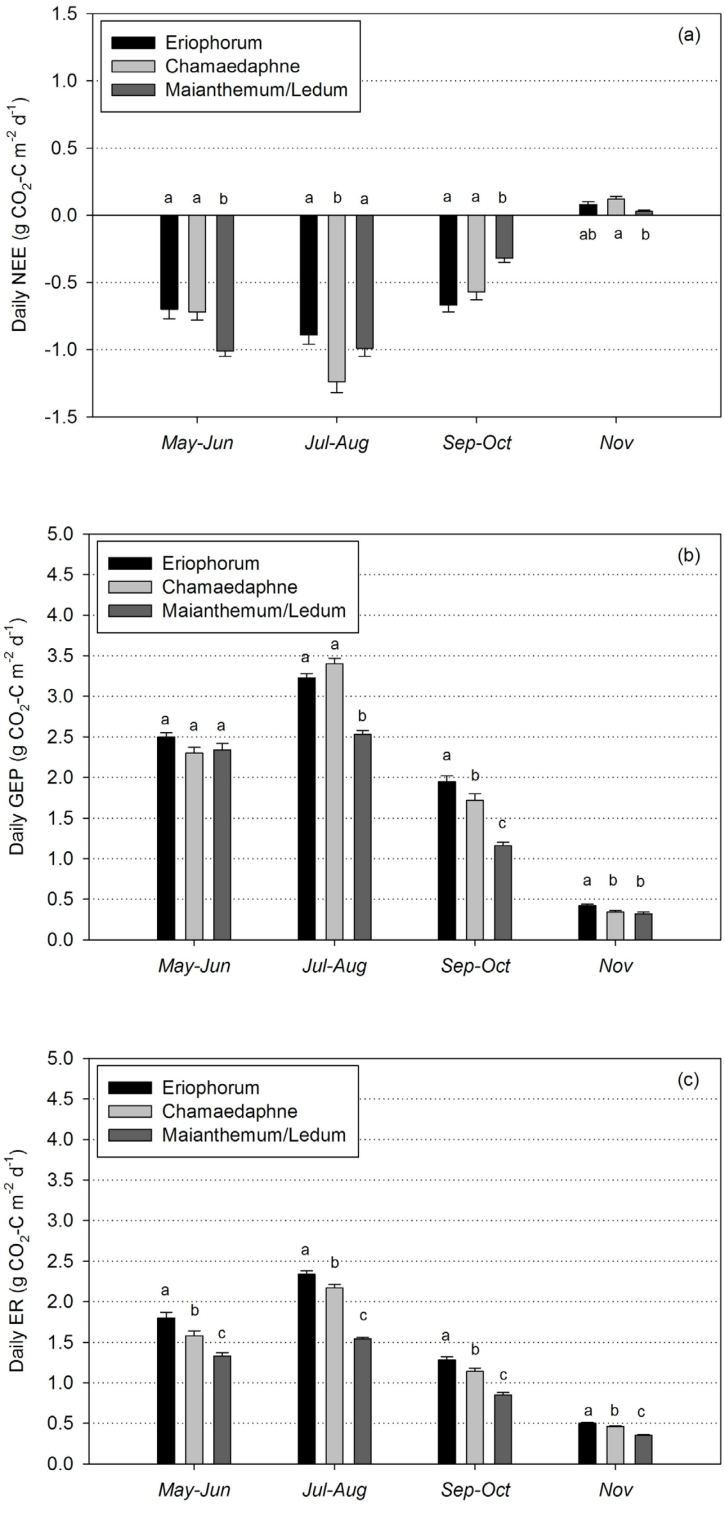


Figure 5.6. Relationship between half-hourly gross ecosystem production (GEP) and photosynthetically active radiation for (a) *Eriophorum*-, (b) *Chamaedaphne*-, and (c) *Maianthemum/Ledum*-dominated communities. All GEP values were adjusted to air temperature of 20 ºC and VGA of 1 m^2 m^{-2} and the solid line is the best fit using equation (2).

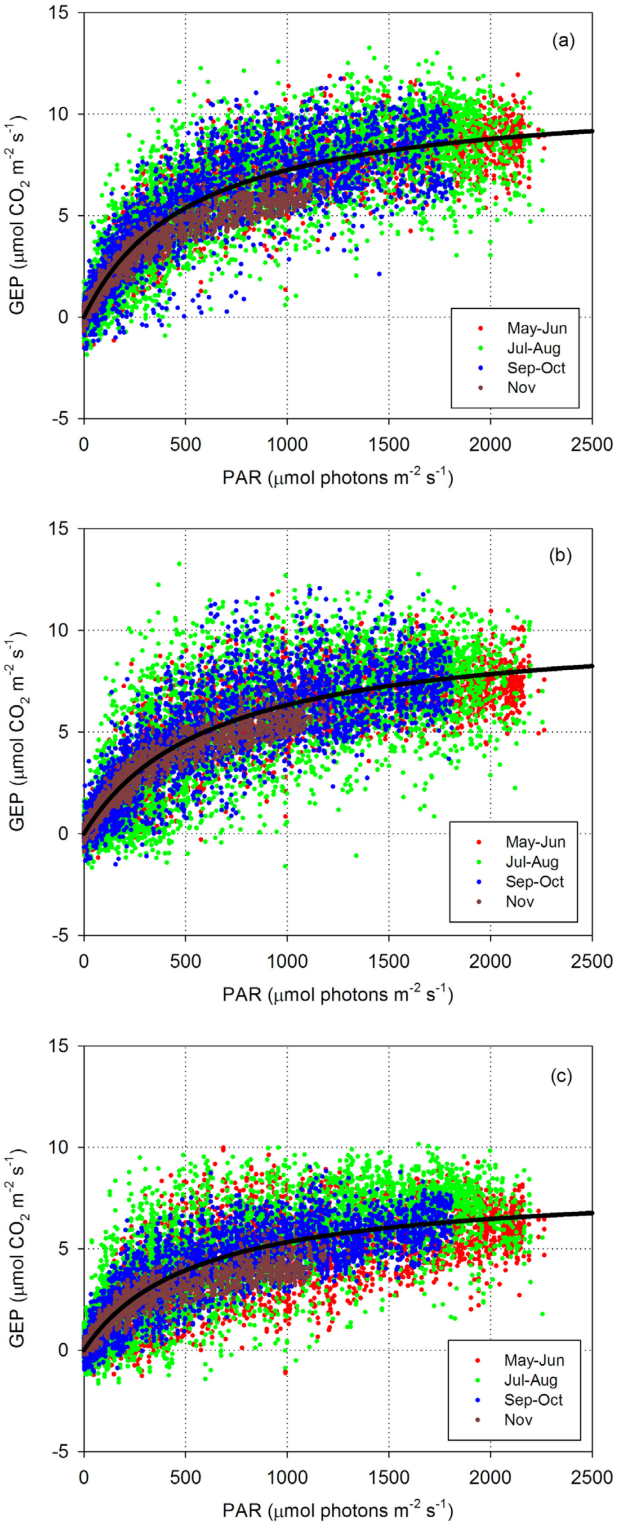


Figure 5.7. Relationship between half-hourly gross ecosystem production (GEP) and vascular green area index for (a) *Eriophorum*-, (b) *Chamaedaphne*-, and (c) *Maianthemum/Ledum*-dominated communities. All GEP values were adjusted to PAR of 2000 µmol m^{-2} s^{-1} and air temperature of 20 ºC and the solid line is the best fit using equation (2).

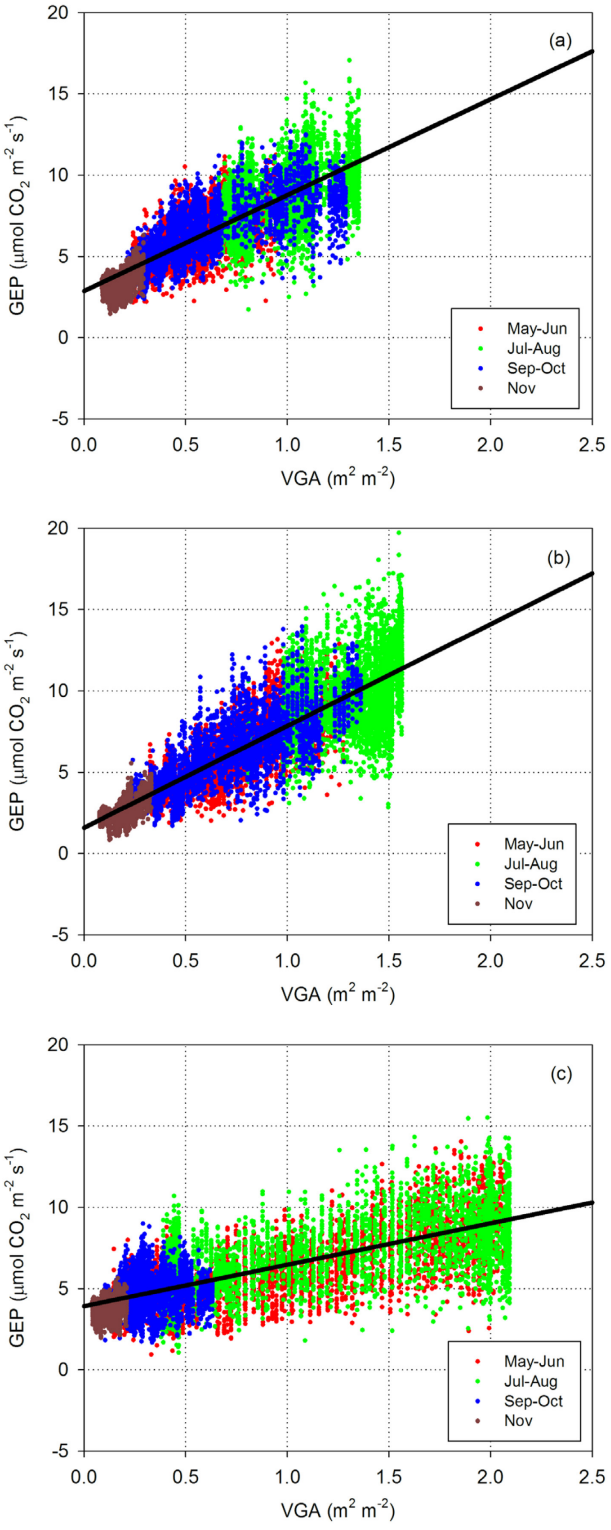


Figure 5.8. Relationship between half-hourly ecosystem respiration (ER) and peat temperature at 10 cm depth for (a) *Eriophorum*-, (b) *Chamaedaphne*-, and (c) *Maianthemum/Ledum*-dominated communities. All ER values were adjusted to water table depth of -25 cm and VGA of 1 m^2 m^{-2} and the solid line is the best fit using equation (3).

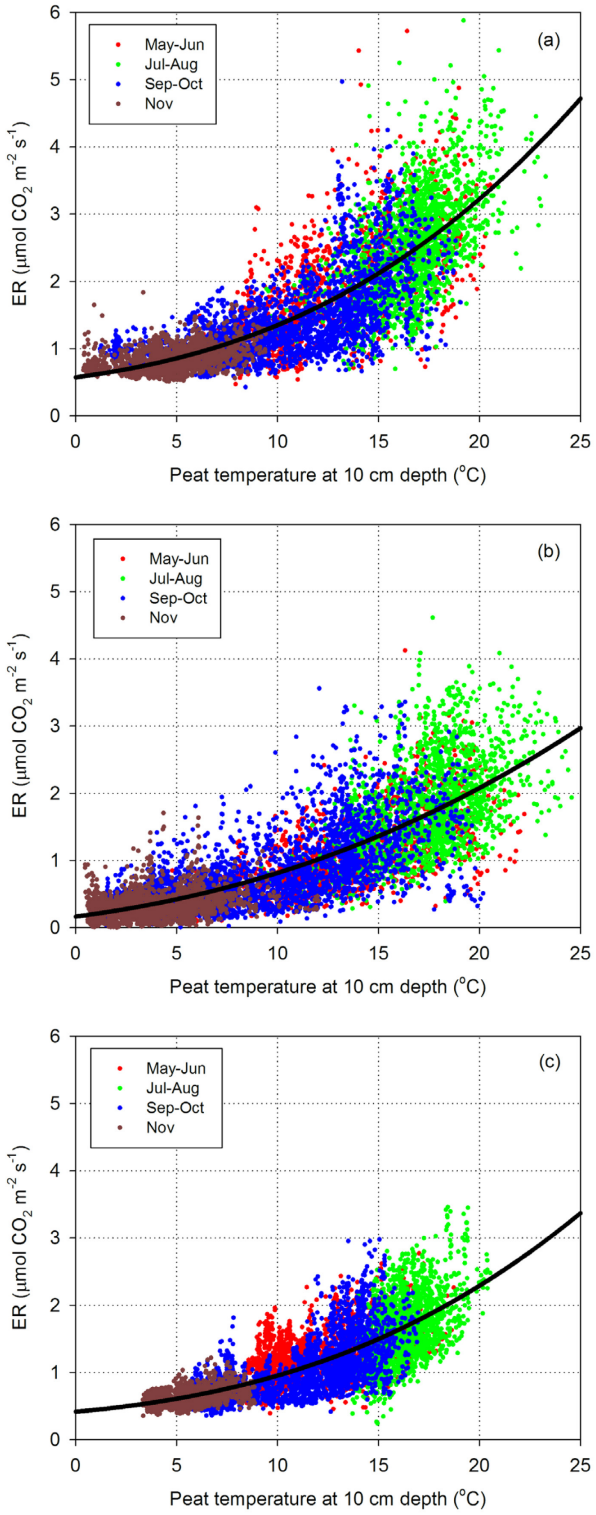


Figure 5.9. Monthly variations of (a) apparent quantum yield (µmol CO_2 µmol^{-1} PAR), (b) maximum gross photosynthesis (P_{max}, µmol CO_2 m^{-2} s^{-1}), and (c) P_{max} normalized by green area (µmol CO_2 VGA unit^{-1} s^{-1}) in the three plant communities. Error bar indicates ± 1 standard error of the parameter estimate.

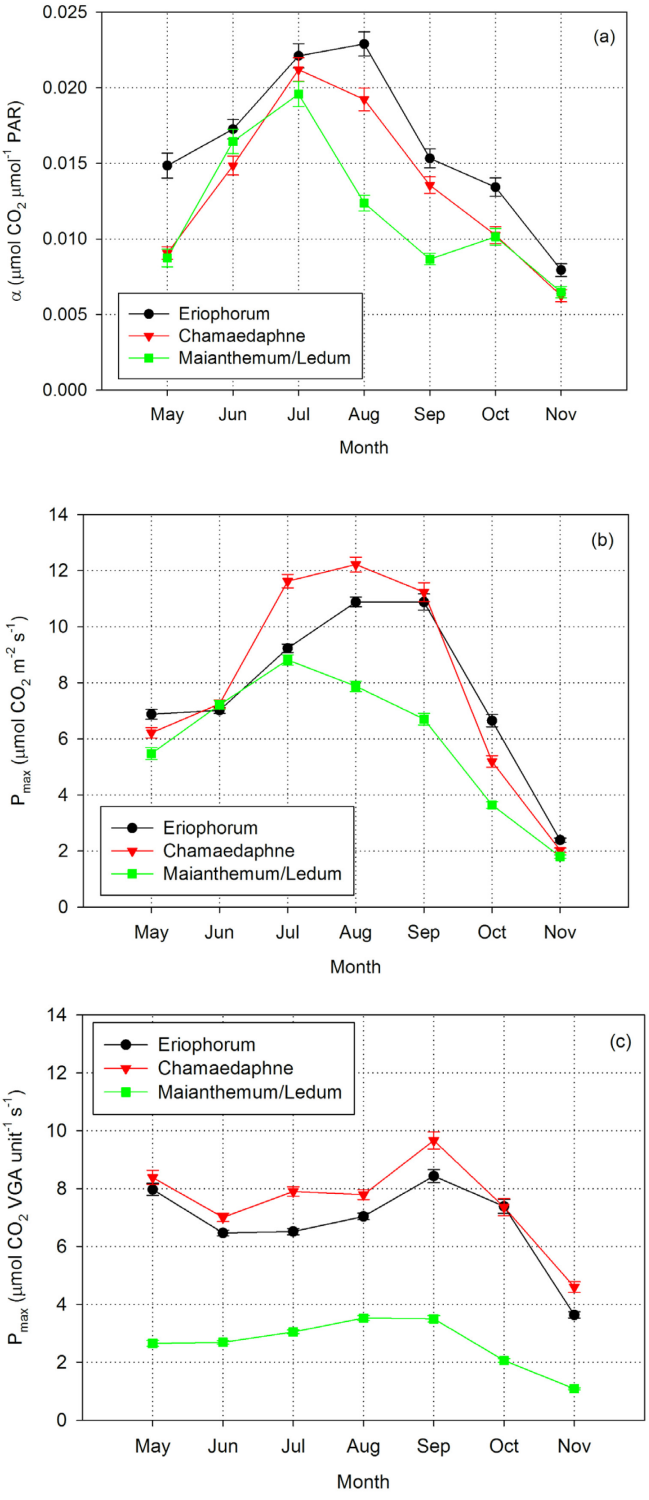


Table 5.1. Vascular plant species, mean water table depth, peat temperature at 10 cm depth, and peak vascular green area index (VGA) for the 9 autochambers in 2009.

Chamber	Vascular plant species[a]	Water table depth[b] (cm)	Peat temperature[b] (°C)	Peak VGA (m^2 m^{-2})
Eriophorum-dominated				
1	Ev, Vm, Lg, Ka	-24.8	11.9	0.82
4	Ev, Lg, Cc, Ka	-18.8	12.1	1.35
7	Ev, Cc, Mt, Lg	-19.2	12.4	1.13
Chamaedaphne-dominated				
3	Cc, Vm, Mt, Lg	-29.3	12.5	1.52
5	Cc, Lg, Vm	-35.4	11.9	1.12
6	Cc, Vm	-37.3	12.8	1.56
Maianthemum/Ledum-dominated				
8	Mt, Lg	-19.5	11.8	2.09
9	Lg, Mt, Ka	-24.0	12.2	0.47
10	Mt, Lg	-20.0	12.1	2.00

Cc: *Chamaedaphne calyculata*, Ev: *Eriophorum vaginatum*, Ka: *Kalmia angustifolia*, Lg: *Ledum groenlandicum*, Mt: *Maianthemum trifolium*, Vm: *Vaccinium myrtilloides*.

[a]In descending order of peak VGA. Only species with peak VGA > 0.1 m^2 m^{-2} are included.

[b]Averaged over the whole measurement period (DOY 142-334).

Table 5.2. Mean daily peat temperature at 10 cm depth, water table depth and VGA for three plant communities by time period.

	Peat Temp. (ºC)	Water table (cm)	VGA (m^2 m^{-2})
May-Jun (N=120)			
Eriophorum	12.9 a	-24.4 a	0.54 a
	(0.29)	(0.38)	(0.02)
Chamaedaphne	14.1 b	-37.8 b	0.71 b
	(0.31)	(0.46)	(0.02)
Maianthemum/Ledum	11.9 c	-25.0 a	0.99 c
	(0.22)	(0.41)	(0.06)
Jul-Aug (N=186)			
Eriophorum	16.8 a	-18.9 a	0.99 a
	(0.13)	(0.30)	(0.02)
Chamaedaphne	17.8 b	-31.6 b	1.27 b
	(0.16)	(0.33)	(0.02)
Maianthemum/Ledum	16.3 c	-18.6 a	1.02 a
	(0.09)	(0.28)	(0.05)
Sep-Oct (N=183)			
Eriophorum	10.6 ab	-21.5 a	0.60 a
	(0.26)	(0.31)	(0.02)
Chamaedaphne	10.1 a	-34.9 b	0.68 b
	(0.31)	(0.40)	(0.02)
Maianthemum/Ledum	11.0 b	-22.2 a	0.30 c
	(0.21)	(0.31)	(0.01)
Nov (N=90)			
Eriophorum	4.8 a	-19.4 a	0.17 a
	(0.18)	(0.34)	(0.01)
Chamaedaphne	3.7 b	-32.1 b	0.19 b
	(0.20)	(0.40)	(0.01)
Maianthemum/Ledum	5.6 c	-19.4 a	0.11 c
	(0.12)	(0.24)	(0.01)

Different letters denote significant difference between plant communities (p<0.05).

Table 5.3. Intercept and dummy variable coefficients of the parameterized GEP and ER models based on the full data set in 2009.

Model	Intercept	Coefficient for *Eriophorum* community	Coefficient for *Maianthemum/Ledum* community	R^2	*N*
GEP	-0.05	0.44 **	-0.58 **	0.72	36396
ER	-0.38	0.39 **	-0.04 **	0.69	23816

** Significant difference of the dummy variable coefficient from zero (p<0.01).

R^2: Coefficient of determination, *N*: Number of data points.

Table 5.4. Parameter estimates of the gross ecosystem production model for three vascular plant communities at the Mer Bleue bog.

Plant community	α (μmol CO_2 μmol^{-1} PAR)	P_{max} (μmol m^{-2} s^{-1} VGA unit^{-1})	T_{opt} (ºC)	T_{tol} (ºC)	s (m^2 m^{-2})	R^2	SEE	N
Eriophorum	0.015 a	7.80 a	14.4 a	19.2 a	0.49 a	0.77	1.94	11605
	(0.0002)	(0.138)	(0.31)	(0.46)	(0.016)			
Chamaedaphne	0.013 b	8.42 b	15.8 b	19.3 a	0.25 b	0.76	2.26	12209
	(0.0002)	(0.150)	(0.37)	(0.58)	(0.015)			
Maianthemum/	0.006 c	3.28 c	18.2 c	13.3 b	1.54 c	0.69	2.06	12582
Ledum	(0.0001)	(0.061)	(0.14)	(0.22)	(0.036)			

Different letters denote significant difference in parameter estimate between plant communities (p<0.05).

Values in parentheses are standard errors of the parameter estimates.

R^2: Coefficient of determination, SEE: standard error of estimate, N: Number of data points.

Table 5.5. Parameter estimates of the ecosystem respiration model for three vascular plant communities at the Mer Bleue bog.

Plant community	R_{10} (μmol m^{-2} s^{-1})	E_0 (K)	b (cm^{-1})	v (μmol m^{-2} s^{-1} VGA unit $^{-1}$)	R^2	SEE	*N*
Eriophorum	0.56 a	392.3 a	0.023 a	0.36 a	0.72	0.25	7812
	(0.022)	(4.36)	(0.0011)	(0.033)			
Chamaedaphne	0.64 b	321.8 b	0.014 b	-0.10 b	0.70	0.20	7980
	(0.021)	(2.93)	(0.0007)	(0.025)			
Maianthemum/	0.36 c	401.8 a	0.025 a	0.27 c	0.71	0.11	8024
Ledum	(0.008)	(4.64)	(0.0008)	(0.008)			

Different letters denote significant difference in parameter estimate between plant communities (p<0.05).

Values in parentheses are standard errors of the parameter estimates.

R^2: Coefficient of determination, SEE: standard error of estimate, *N*: Number of data points.

Table 5.6. Results of F-test comparing the overall GEP and ER models between vascular plant communities.

Model	*Eriophorum vs. Chamaedaphne*		*Eriophorum vs. Maianthemum/Ledum*		*Chamaedaphne vs. Maianthemum/Ledum*	
	F value	P value	F value	P value	F value	P value
GEP	247.1	<0.001	917.5	<0.001	679.3	<0.001
ER	690.8	<0.001	1149.8	<0.001	140.2	<0.001

Chapter 6

The Spatial and Temporal Relationships Between CO_2 and CH_4 Exchange in a Temperate Ombrotrophic Peatland

Context within Thesis

Chapters 4 and 5 have examined the spatial and temporal variability of CO_2 and CH_4 fluxes, and factors that relate to these gas exchanges at the plant community level at Mer Bleue bog. In this chapter, I will focus on investigating the linkage between CO_2 and CH_4 fluxes across space and time to evaluate whether there is a substrate-based coupling between plant production and CH_4 emissions. I will determine the spatial relationships between the two using manual chamber measurements at 18 sites that cover three different categories. I will also take advantage of the availability of high temporal resolution autochamber data and employ cross-correlation analysis to determine the time lag and relationship between GEP and CH_4 flux at different time scales.

6.1 Abstract

We investigate the relationships between CO_2 and CH_4 fluxes across space and time at a temperate ombrotrophic bog in Canada to assess the coupling between plant production and CH_4 emissions. Based on periodic manual chamber measurements, we show that seasonal mean maximum net ecosystem CO_2 exchange (NEE_{max}) and CH_4 flux were tightly related across the 18 sites grouped in three categories. NEE_{max} was a good predictor of the spatial variations in CH_4 flux among *Eriophorum* and lawn sites (r^2 = 0.61 to 0.88), yet the inclusion of hummock sites considerably weakened the overall relationship (r^2 = 0.30 to 0.60). Also, we observed large interannual variability in the NEE_{max}-CH_4 relationship at the *Eriophorum* and lawn sites, with a lower regression slope in 2010 that had a seasonal mean water table 8 cm lower than in 2009. Results of cross-correlation of instantaneous gross ecosystem production (GEP) and CH_4 flux from the autochambers show a moderate relationship in the *Eriophorum* community at a lag of 9 to 12 hours, suggesting a rapid turnover of recent photosynthate for methanogenesis. On the other hand, we found in two *Maianthemum*-dominated chambers that the temperature-independent residuals of daily mean CH_4 flux lagged behind GEP by 18 to 26 days at the seasonal scale. The lagged correlations between GEP and CH_4 flux by month were particularly strong in the late growing season in the *Eriophorum* and *Maianthemum/Ledum* communities, probably due to a change in the allocation pattern of recently fixed carbon as plants entered senescence. Our findings demonstrate the presence of spatial and temporal coupling of plant production and CH_4 emissions in this bog, which varies with species composition, water table position, and plant phenology.

6.2 Introduction

Peatlands in the boreal and subarctic regions contain between 270 to 370 Pg carbon (C) in peat (Turunen *et al.*, 2002), which comprises 12 to 16% of C contained globally in the top 3 m of soils (Jobbágy and Jackson, 2000). These estimates are even higher when peatlands containing permafrost and at higher latitudes are included (McGuire *et al.*, 2009; Tarnocai *et al.*, 2009). While northern peatlands have been consistently sequestering C for millennia (Frolking and Roulet, 2007), they are also a significant global source of methane (CH_4) gas, releasing 20 to 38 Tg of CH_4 to the atmosphere annually (Bartlett and Harriss, 1993; Mikaloff Fletcher *et al.*, 2004). The emissions of CH_4 from northern peatlands play a role in affecting the net ecosystem C balance (Nilsson *et al.*, 2008; Roulet *et al.*, 2007), as well as a climate radiative forcing impact (Frolking *et al.*, 2006). In view of the importance of northern peatlands in CH_4 cycling, an understanding of the spatial and temporal controls of CH_4 flux is essential for accurately predicting the response of peatland CH_4 emissions to natural and anthropogenic perturbations.

Previous studies have found water table position as a dominant control of the spatial variability of seasonal mean CH_4 flux (Moore *et al.*, 2011), while peat temperature governs the seasonal variations of CH_4 emissions in northern peatlands (Jackowicz-Korczyski *et al.*, 2010; Laine *et al.*, 2007b). Meanwhile, vascular plant productivity can also influence peatland CH_4 emissions through various processes coupled with the production, oxidation, and transport of CH_4 gas (Joabsson *et al.*, 1999a). Numerous studies have reported a relationship between seasonal mean net ecosystem exchange of CO_2 (NEE) and CH_4 emissions across a range of wetland types (Whiting and Chanton, 1993), and across sites within a peatland (Alm *et al.*, 1997; Bellisario *et al.*, 1999). Positive relationships have also been found spatially between CH_4 flux and gross primary production (GPP) (Ström and Christensen, 2007; Ström *et al.*, 2012), as well as sedge biomass in peatlands (Bellisario *et al.*, 1999; Marinier *et al.*, 2004; Pelletier *et al.*, 2007). The higher CH_4 flux associated with the higher plant productivity

has been attributed to a greater supply of organic substrate from belowground tissues for methanogenesis (King *et al.*, 2002; Ström and Christensen, 2007), an enhanced plant-mediated transport of CH_4 to the atmosphere via aerenchymatous tissues (Joabsson and Christensen, 2001), an interrelationship between NEE and environmental conditions (Joabsson *et al.*, 1999a), or a combination of the above. On the other hand, some studies observed a negative relationship between NEE and CH_4 flux, which could be related to a difference in rhizospheric CH_4 oxidation (Ström *et al.*, 2005), water table, and plant biomass (Waddington and Roulet, 1996). Thus, the coupling of plant productivity and CH_4 emissions at the plant community level may be confounded by other factors including species composition (Öquist and Svensson, 2002) and microtopography (Waddington *et al.*, 1996).

Plant productivity has been found to correlate with CH_4 flux from peatlands over the season, with the strength of relationship varied depending on water table depth and weather conditions (Christensen *et al.*, 2000; Joabsson and Christensen, 2001). These studies employed a simple correlation analysis of the NEE-CH_4 relationship that assumes implicitly an instantaneous response of CH_4 flux to changes in plant productivity. Yet, if plant production enhances CH_4 flux through an increased substrate supply to methanogens, there should be a lag in the response of CH_4 emissions due to the time needed for the translocation of recent photosynthate to belowground tissues, exudation of soluble organics from roots to the rhizosphere, and fermentation of organic compounds to acetate for methanogenesis (Kuzyakov and Gavrichkova, 2010; Öquist and Svensson, 2002; Whiting and Chanton, 1992). Pulse labelling of ^{14}C of tundra mesocosms have shown that photosynthate-derived CH_4 could be emitted within 2 hours, with a maximum ^{14}C activity being reached within a week of labelling (King and Reeburgh, 2002; King *et al.*, 2002). Nevertheless, there is still a paucity of studies done in a field setting on the temporal NEE-CH_4 relationship and the time lag of methanogenic response to photosynthetic activity among vascular plant communities in northern peatlands.

The coupling of plant productivity and CH_4 flux can also be studied by conducting time series analysis on a high temporal resolution flux data set, which has the advantage of being able to quantify the time lag as well as the amplitude of changes in CH_4 flux response to photosynthetic activity (Kuzyakov and Gavrichkova, 2010). Cross-correlation analysis has been recently applied to investigate the time lag of soil CO_2 efflux to photosynthesis in a number of forest and grassland ecosystems (Stoy *et al.*, 2007; Vargas *et al.*, 2010), as well as the time lag of CH_4 emission to variations in temperature and water table in a boreal peatland (Kettunen *et al.*, 1996). Meanwhile, no attempt has yet been made to determine the lag time and temporal correlation between plant production and CH_4 flux in an ombrotrophic bog with cross-correlation analysis.

The objectives of our study are to: (1) examine the relationship between seasonal mean CO_2 and CH_4 exchange across a range of sites at the Mer Bleue bog, and (2) determine the temporal correlation and time lag between photosynthetic activity and CH_4 emission at multiple time scales for three different peatland vascular plant communities.

6.3 Methods

6.3.1 Site Description

Mer Bleue peatland is a 28 km^2 ombrotrophic bog located near Ottawa, Canada (45.41ºN, 75.52ºW). This region has a cool continental climate, with a mean annual temperature of 6.0 ± 0.8 ºC and mean annual precipitation of 944 mm (1971-2000 climate normals) (Environment Canada, 2011). Field measurements were made at a dome-shaped bog in the northwest part of this peatland. Peat depth reaches about 5 to 6 m near the centre of the bog, and is shallower (<0.3 m) near the beaver pond margin (Roulet *et al.*, 2007). The surface of this peatland is completely covered by *Sphagnum* moss (*Sphagnum angustifolium*, *Sphagnum capillifolium*, *Sphagnum fallax*, *Sphagnum magellanicum*) and the vascular plant cover is dominated by low growing ericaceous evergreen shrubs (*Chamaedaphne calyculata*, *Ledum groenlandicum*,

Kalmia angustifolia), with an occasional mix of deciduous shrub (*Vaccinium myrtilloides*), sedge (*Eriophorum vaginatum*) and forb (*Maianthemum trifolium*). This bog is relatively dry, with a mean growing season (May to October) water table depth from the top of hummock of 42.7 cm over 1998-2008 (Teklemariam *et al.*, 2010), 33.5 cm in 2009 and 40.8 cm in 2010 (Humphreys, pers. comm.). It has a hummock-lawn microtopography, with a mean difference of 17 cm in elevation between the hummock and lawn surfaces (Wilson, 2012).

6.3.2 Manual Chamber Measurements

We conducted manual chamber measurements of CO_2 and CH_4 fluxes at 18 sites at the Mer Bleue bog, capturing the broad range of water table and vegetation observed at the peatland (Table 6.1). These sites were classified into three different categories, including *Eriophorum*, hummocks and lawns, depending on the dominant vascular species and mean water table position. Flux measurements were made on sunny days at 1- to 5-week intervals from 26 May to 17 September in 2009 and May 13 to August 31 in 2010. For NEE measurements, we used a clear, closed dynamic chamber (27 cm in diameter, 25 cm in height) equipped with a fan for air mixing and water-circulating coils for cooling. The chamber was placed on permanently installed collars for 3 minutes and CO_2 concentration in the chamber headspace was recorded by an infra-red gas analyzer (EGM-4, PP Systems, MA, USA) every 10 seconds in the first minute and every 30 seconds in the last 2 minutes. At each location, we first measured maximum NEE (NEE_{max}) at photosynthetically active radiation (PAR) greater than 1000 μmol photons m^{-2} s^{-1}, followed by a second round of measurement with the chamber covered with black cloth to measure ecosystem respiration (ER) in darkness.

For CH_4 flux measurements, we placed an opaque, static chamber (27 cm in diameter, headspace volume of 18 L) on the collar for a total of 25 minutes, while sampling the air in the chamber headspace every 5 minutes through a septum and stopcock. The gas samples were stored in 10-mL syringes and brought

back to the laboratory for analysis of CH_4 concentration within 24 hours with a gas chromatograph (Mini II, Shimadzu Scientific Instruments, MD, USA) equipped with a flame ionization detector. Following chamber flux measurements, peat temperature at 10 cm depth and water table position were measured immediately at each collar location.

6.3.3 Autochamber System

We installed nine autochambers at the Mer Bleue bog within a 15-m radius about 50 m south of the eddy covariance tower. These included three replicates each representing plant communities dominated by *Eriophorum*, *Chamaedaphne*, and *Maianthemum/Ledum* respectively while covering a range of water table and leaf area (Table 6.2). The dynamic, closed autochamber consisted of a transparent Plexiglas dome fitted to a PVC cylinder with a hinged aluminum frame. The near semi-spherical dome had a height of 20.5 cm and the PVC cylinder had an internal diameter of 52 cm, a thickness of 1 cm and a height of 38.5 cm. Each autochamber covered a surface area of 0.21 m^2. The PVC cylinders were inserted 16 to 31 cm deep into the peat, leaving about 7 to 22 cm above the peat surface, but below the height of the top of the shrubs. A small brushless fan within the dome mixed the air in the chamber headspace and a coiled 50-cm long open-ended vent tube on the dome top ensured equilibration of pressure between the inside and outside of chamber during flux measurements.

Chamber selection, measurement timing and data acquisition of the autochamber system were controlled by a datalogger (CR23X, Campbell Scientific, UT, USA). A pneumatic cylinder assembly (Model BFT-173-DB, Bimba Manufacturing, IL, USA) connected to an oil-free air compressor (Model CPFAC2600P, Porter Cable, TN, USA) opened and closed the chamber domes. Sampling tubes (Synflex 1300, 4.3 mm i.d., Saint-Gobain Performance Plastics, NJ, USA) connected to the gas inlet and outlet located at the top of chamber dome led to a sampling manifold controlled by solenoid valves. Concentrations of CO_2 and CH_4 were measured by a closed-path infrared gas analyzer (LI-6262, LI-COR,

NE, USA) and a fast methane analyzer based on off-axis integrated cavity output spectroscopy (DLT-100, Los Gatos Research, CA, USA), respectively. After passing through the gas analyzers, air was re-circulated back to the chambers at a flow rate of 3.5 L min^{-1} by an AC linear pump (Model DDL, Gast Manufacturing, MI, USA). The datalogger, pump, and gas analyzers were all placed inside temperature-controlled housings.

The autochamber system was in operation between 22 May and 7 December in 2009 and between 26 March and 5 December in 2010. Prior to 6 July 2010, the autochambers were programmed to close sequentially to measure gas fluxes for 2.5 minutes to provide one measured flux for each chamber every 30 minutes between 0200 and 2400 h daily. From 6 July 2010 onwards, the chamber deployment period was increased to 15 minutes, and one flux measurement was made every three hours per chamber. Analog outputs from the gas analyzers were sampled at 1 Hz by the datalogger, averaged every 5 seconds, and downloaded automatically to a PC located in a hut on site. All high frequency data were retained for flux processing. We also continuously measured water table depth at each chamber location with a capacitance water level probe, peat temperature with a thermocouple at 10 cm depth inside each chamber and at 40 cm depth of a lawn location, and averaged them half-hourly.

6.3.4 Data Analysis

We calculated CO_2 and CH_4 fluxes based on the slope of linear regression of gas concentration in the chamber headspace against time, taking into account the chamber volume and surface area covered. We rejected CH_4 fluxes measured by the manual chambers when the initial concentration was high (> 5 ppmv) or the pattern of the concentration trace was poor. This led to the removal of 1.7 to 1.9% of measured CH_4 fluxes in the two years of measurement. For the calculation of NEE_{max} from manual chambers, only the concentration trace in the first 30 seconds was used in the regression if the slope appeared to flatten out after this initial period, as this might indicate the plants inside the chamber were under

stress under high temperature and moisture conditions. Moreover, we calculated the maximum rate of photosynthesis (GEP_{max}) for each chamber as the difference between NEE_{max} and ER measured in full light and darkness, respectively.

We calculated CO_2 and CH_4 effluxes from the autochambers based on regression of the concentration trace over a period of 1.5 minutes, after discarding the data in the initial 45 seconds and 12.75 minutes for a chamber deployment period of 2.5 and 15 minutes, respectively. For the calculation of CO_2 uptake rate, the initial 45 seconds of concentration data were removed regardless of the chamber deployment period. Fluxes were accepted only if $r^2 > 0.9$, except when CH_4 flux measured with a 15-minute deployment period was ≤ 39 μmol m^{-2} hr^{-1} then a r^2 threshold of 0.7 was used due to both lower flux magnitude and sensitivity of analyzer signal output. Poor quality flux data obtained during periods of equipment failure and system maintenance were also discarded from analysis. These quality control procedures led to the removal of 3 to 17% and all CO_2 fluxes and 2 to 28% of all CH_4 fluxes collected for a given chamber. To minimize the turbulence-related measurement bias associated with a chamber deployment period of 2.5 minutes, correction of CO_2 efflux and filtering of CH_4 flux by friction velocity were done following the protocol of Lai *et al.* (2012). We gap-filled missing half-hourly NEE, gross ecosystem production (GEP) and ER following the procedures described in Chapter 5 of this thesis. Because of the strong diel variability of CO_2 flux, we produced time series data of daily mean NEE, GEP and ER based on the gap-filled half-hourly values, while daily mean CH_4 fluxes were calculated using only the available measured values. We used the atmospheric sign convention for NEE and CH_4 flux, with a positive value indicating a net release by peatland or a net gain by the atmosphere. Meanwhile, we denoted both GEP and ER as positive values. GEP during the daytime (i.e. PAR > 0) was determined as ER - NEE, while at night (i.e. PAR = 0), GEP was set to zero and ER was equivalent to the measured CO_2 flux.

6.3.5 Statistical Analysis

We conducted a linear regression analysis to determine the relationships between NEE_{max}, GEP_{max} and CH_4 flux across the 18 collar locations. We applied a cross-correlation analysis on the time series of the residuals of instantaneous CO_2 flux (including NEE, GEP and ER) and CH_4 flux measured between 17 August and 15 September in 2010 in three autochambers (Chambers 3, 7 and 10) with each representing a different plant community to investigate the relationship and time lag between the two fluxes at the fine temporal scale of one day. Fluxes from these three chambers over the said 30-day period were selected because the data coverage was most complete (> 90%), and the temporal variations in environmental conditions were small (standard deviation of peat temperature: 1.3-2.5ºC, standard deviation of water table: 3.1-3.6 cm). To eliminate the effect of temperature on diel variations of gas exchange rates, we conducted a linear regression of CO_2 and CH_4 fluxes against peat temperatures at a depth of 10 cm and 40 cm, respectively, for each day and then calculated the residuals as the difference between the measured and modelled fluxes. We used temperature at a greater depth for CH_4 since methanogenesis only occurred in the anaerobic peat below the water table. The residuals obtained were then used in the final cross-correlation analysis.

We determined the cross-correlation between daily mean peat temperature at 40 cm depth and CH_4 flux to investigate the temperature effects on seasonal change in CH_4 emissions. In addition, we examined the relationship between photosynthetic activity and CH_4 emission at the seasonal scale by conducting a cross-correlation analysis on the time series of the residuals of daily mean GEP and CH_4 flux between May and October 2009. Due to an uncharacteristically wet summer, water table remained high over this period and hence was expected to have limited influence on the seasonal variability of gas fluxes. To eliminate the spurious temperature effects on the GEP-CH_4 relationship, we conducted a linear regression between GEP and peat temperature at 10 cm depth, and a non-linear regression between CH_4 flux and peat temperature at 40 cm depth with an exponential function for the whole period, followed by calculating the residuals of

GEP and CH_4 flux as the difference between measured and modelled values. Further, we conducted cross-correlation analysis on the residuals of daily GEP and CH_4 flux by month to determine if the temporal relationship varied seasonally. We only focused on positive correlations that were in agreement with the hypothesis of a substrate-based coupling of CH_4 emissions with photosynthetic activity.

6.4 Results

6.4.1 Relationships Between CO_2 and CH_4 Fluxes Across Sites

Figures 6.1a and 6.1b show the relationship between seasonal mean NEE_{max} and CH_4 emission across the 18 locations at the Mer Bleue bog in 2009 and 2010, respectively. Overall, NEE_{max} was significantly and negatively correlated with CH_4 flux in both years (r = -0.77 and -0.55, $p < 0.05$), indicating a higher CH_4 emission associated with a higher photosynthetic CO_2 uptake (i.e. more negative NEE_{max}). If hummock sites were excluded from the regression analysis, the r^2 values of the overall NEE_{max}-CH_4 relationship improved from 0.60 to 0.88 in 2009, and from 0.30 to 0.61 in 2010 ($p < 0.01$). Sites dominated by *Eriophorum vaginatum* had much higher NEE_{max} and CH_4 fluxes than other shrub or herb dominated sites at hummocks and lawns. NEE_{max} alone was able to explain 99% of the spatial variations in CH_4 flux among sites dominated by *Eriophorum* in 2009 ($p < 0.1$), but the relationship was insignificant in 2010 (p = 0.24). While there were no significant relationships between NEE_{max} and CH_4 flux among the lawn sites, we found NEE_{max} accounting for 49% of the variations in CH_4 emission among hummock sites in 2010 ($p < 0.1$). Moreover, we generally observed a steeper slope of increase in CH_4 flux with increasing magnitude of NEE_{max} in 2009 than in 2010, regardless of the vegetation types. The hummocks had the smallest slopes among the three plant types, with an increase of only 0.003 mmol m^{-2} hr^{-1} of CH_4 flux per unit increase in NEE_{max}.

Similarly, seasonal mean GEP_{max} and CH_4 flux were significantly correlated across the 18 sites in 2009 and 2010 (r = 0.79 and 0.61, $p < 0.01$)

(Figures 6.2a and 6.2b). When looking at the three site categories separately, we found GEP_{max} accounting for over 98% of the spatial variations in CH_4 flux among the *Eriophorum* locations ($p < 0.1$). The hummocks again had the lowest rate of increase in CH_4 flux with GEP_{max} in both years. At lawn sites, CH_4 fluxes were highly variable even though seasonal mean GEP_{max} were within a narrow range of 20 mmol m^{-2} hr^{-1} among the 7 locations. We observed a significant decrease in the slope of CH_4 flux against GEP_{max} by over 70% for both *Eriophorum* and lawn sites in the drier 2010 compared to the wetter 2009, in spite of a small difference in seasonal mean water table of only 8 cm between the two years (Table 6.1).

6.4.2 Relationships Between CO_2 and CH_4 Fluxes Over Time

Based on the instantaneous fluxes measured over a 30-day period in the summer of 2010, we identified the largest negative cross-correlation coefficient (σ) of -0.31 between CH_4 flux and NEE at a time lag of 12 hours for the *Eriophorum* chamber (Figure 6.3a). The correlation between the two fluxes at a lag of 9 hours was about the same at σ = -0.29 ($p < 0.05$). For the *Maianthemum/Ledum* chamber, the relationship between NEE and CH_4 flux was not significant except at zero lag when a small σ = -0.16 was obtained. No significant correlation was found at any lag periods for the *Chamaedaphne* chamber ($p > 0.05$). We found very similar patterns of change in σ with lag time between CH_4 flux and GEP, except the sign was opposite (Figure 6.3b). A maximum σ = 0.30 ($p < 0.05$) occurred when CH_4 flux lagged 12 hours behind GEP in the *Eriophorum* chamber. The cross-correlations between ER and CH_4 flux were overall poor and insignificant at any lags across the three plant communities (Figure 6.3c).

The results of cross-correlation analysis of daily average peat temperature at 40 cm depth and CH_4 flux in 2009 show that the two variables were highly coupled with no time lags (Figure 6.4). We found maximum σ values of 0.76-0.80 in the *Eriophorum* chambers, 0.49-0.60 in the *Chamaedaphne* chambers, and 0.63-0.74 in the *Maianthemum/Ledum* chambers ($p < 0.05$). The correlation

between peat temperature and CH_4 flux decreased consistently with increasing lag time for all the three communities.

On a seasonal time scale, daily mean GEP was positively correlated with CH_4 flux with maximum σ values in the range of 0.25-0.59, 0.35-0.37, and 0.34-0.55 in the *Eriophorum*, *Chamaedaphne*, and *Maianthemum/Ledum* chambers, respectively (data not shown). Yet, after correcting for the effects of temperature, the residuals of daily mean GEP and CH_4 flux were in general weakly and insignificantly correlated in the *Eriophorum* chambers ($\sigma < 0.2$, $p > 0.05$) (Figure 6.5a). Similarly in the *Chamaedaphne* chambers, the relationships between the two fluxes were mostly insignificant, except in one of the chambers where σ rose to a small peak of 0.25 (Figure 6.5b). However, we observed significant σ values of 0.43 and 0.50 at lags of 18 and 26 days in the two chambers dominated by *Maianthemum* ($p < 0.05$) (filled circles and triangles, Figure 6.5c), while the other chamber dominated by *Ledum* had no significant correlation between CH_4 flux and gross photosynthesis (open circles, Figure 6.5c). When the cross-correlation analysis was conducted by month, we observed significant relationships between GEP and CH_4 flux in two of the *Eriophorum* chambers in September, with maximum σ of 0.37 and 0.50 being reached within a lag of two days (Figure 6.6a). In August, the correlations between GEP and CH_4 flux were significant in all three *Maianthemum/Ledum* chambers ($p < 0.05$), attaining the largest σ values ranging between 0.32 and 0.60 with a lag of 10-13 days (Figure 6.6b).

6.5 Discussion

6.5.1 Relationships Between CO_2 and CH_4 Fluxes Across Sites

Based on our periodic manual chamber flux measurements at 18 locations at the Mer Bleue bog, we found an overall significant relationship between seasonal mean NEE_{max} and CH_4 flux, as well as between GEP_{max} and CH_4 flux in the two years of study (Figures 6.1 and 6.2). The positive correlation between CO_2 uptake and CH_4 emission observed across space was in agreement with the results reported by others in northern peatlands and tundra (Alm *et al.*, 1997;

Bellisario *et al.*, 1999; Ström and Christensen, 2007; Ström *et al.*, 2012; Whiting and Chanton, 1992). This could partly be attributed to the stimulation of CH_4 production by an increased supply of labile organic carbon to the rhizosphere via root exudation and turnover arising from plant production. Shaded experimental plots in the wet sedge tundra with reduced NEE were shown to have a significantly lower formation rate of acetate, a precursor of methanogenesis, in *Eriophorum* root microcosms (Ström *et al.*, 2003), and subsequently decreased CH_4 production potential in the surface peat and total CH_4 emissions (Joabsson and Christensen, 2001). In addition, CH_4 emissions could be enhanced by plant-mediated transport of CH_4 in aerenchymatous species, with the transport capacity being a function of shoot and root densities that are directly reflected in NEE (Joabsson and Christensen, 2001; Öquist and Svensson, 2002). Waddington *et al.* (1996) observed a greater CH_4 flux from unclipped *Eriophorum* sites that had lower porewater CH_4 concentrations, which suggests a rapid removal of CH_4 from porewater by plant-mediated transport via the internal air space of sedges to the atmosphere. By isolating plant shoots from peat, Dorodnikov *et al.* (2011) determined that plant-mediated transport could contribute to 31 to 38% of the total CH_4 flux from *Eriophorum vaginatum* mesocosms.

When the three site categories were considered individually, the NEE_{max}-CH_4 and GEP_{max}-CH_4 relationships could be quite different among them. Correlations were very strong in the *Eriophorum* sites indicating a tight coupling of plant productivity and CH_4 fluxes within the community. Sedges are generally very efficient in photosynthetic activity (Leppälä *et al.*, 2008), and *Eriophorum* in particular has a root exudation rate 7 times higher than *Carex* and *Juncus* sedges (Ström *et al.*, 2005), thus providing conditions favourable for acetoclastic methanogenesis. Contrastingly, variations in CH_4 flux across lawn sites were poorly explained by plant production ($r^2 \leq 0.15$, $p \geq 0.40$). The coefficients of variation were much larger for CH_4 flux than NEE_{max} (~57% *vs.* 28%), which suggest the presence of other factors than plant productivity in governing CH_4 emissions. We found that ebullition captured in a few sampling events led to some

of the highest seasonal mean CH_4 fluxes obtained at lawn sites, adding further complexity to the analysis. NEE_{max} could serve as a good predictor of CH_4 flux accounting for 61 to 88% of the spatial variations when *Eriophorum* and lawn sites were pooled together, but the percentage variance explained by NEE_{max} decreased substantially when hummocks were included. The NEE-CH_4 relationship was very different in the hummocks, with a considerably lower rate of increase in CH_4 flux with CO_2 uptake compared to the other two site categories. This was likely due to the low water table position in hummocks that enhanced CH_4 oxidation in the peat profile and subsequently reduced net CH_4 emissions to the atmosphere (Moore *et al.*, 2011). Hummocks at Mer Bleue are dominated by ericaceous shrubs that have roots not well-adapted to anoxic conditions (Murphy and Moore, 2010), thus most of the exudates released from shrub roots would not be made available for methanogens below the water table. Whiting and Chanton (1993) found a strong correlation between mean net ecosystem production and mean CH_4 emissions across a latitudinal gradient of water-saturated wetlands, yet other studies have reported no NEE-CH_4 relationships in the dry, shrub-dominated ridge sites of a Swedish peatland (Waddington *et al.*, 1996), and in the Minnesota bog sites with low water tables (Chanton *et al.*, 1995). Our findings support these previous results and suggest that microtopography should be taken into account in relating plant productivity to CH_4 flux in dry, ombrotrophic peatlands.

We observed a large interannual variability of the spatial relationships between seasonal mean CO_2 and CH_4 fluxes in the two years of measurements. The hummock water table between May and September in 2010 was lower (average: -42.7 *vs.* -33.9 cm) and varied to a greater extent (range: 32.1 *vs.* 14.9 cm) than in 2009. This resulted in a significant decrease in the slope of CH_4 flux against NEE_{max} or GEP_{max} in the *Eriophorum* and lawn sites in 2010 with a drier summer, indicating a greater sensitivity of CH_4 flux to drought than CO_2 exchange. We observed a much smaller change in the regression slope in the hummock sites between 2009 and 2010, probably because CH_4 production was already low in the wetter year. Waddington *et al.* (1996) found a strong positive

correlation between mean daily NEE and CH_4 flux at the sedge-dominated lawn sites after combining data in two growing seasons. No information on the climate or water table was provided for comparison between the two years, though the lawns they studied were known to have water tables very close to the surface. In contrast, lawn sites at Mer Bleue have a much lower mean water table (Table 6.1), and hence water table in a dry year is more likely to drop below the rooting depth and has a greater effect on CH_4 flux. Consideration of interannual variability in water table position especially at sites that are wetter and have shallow-rooted species is thus essential in any attempt to estimate CH_4 emissions in ombrotrophic bogs as a function of plant productivity.

6.5.2 Relationships Between CO_2 and CH_4 Fluxes Over Time

We expect CH_4 flux to lag behind photosynthetic CO_2 uptake for a certain period if recent plant photosynthate serves as a substrate for microbial CH_4 production. Using instantaneous fluxes measured intensively by autochambers over a 30-day period, we identified a time lag of 9-12 hours of CH_4 fluxes behind NEE in the *Eriophorum* community with a moderate cross-correlation coefficient of -0.31 (Figure 6.3a). This agrees well with a lag of 6-12 hours found in a sedge-dominated boreal fen based on intensive manual chamber measurements over a 24-hour period (Waddington *et al.*, 1996), and a lag of 2-24 hours for the first appearance of $^{14}CH_4$ after pulse labelling of ^{14}C in sedge tundra mesocosms (King and Reeburgh, 2002; King *et al.*, 2002). Addition of ^{14}C-acetate at 9 cm depth in a peat monolith demonstrates a lag time of 4 hours for CH_4 emissions following isotopic labelling (Ström *et al.*, 2003), which implies a probable delay of 5-8 hours for recently fixed C to translocate from photosynthesizing tissues to the rhizosphere for methanogenesis at our site. All these results combine to suggest that *Eriophorum* has a rapid turnover of recent photosynthate. It has been suggested that a continuous input of labile organic acids is essential to sustain acetoclastic methanogenesis in an *Eriophorum*-dominated Arctic fen, given the hourly rate of root exudation can only support not more than 1.5 hours of CH_4 flux (Ström *et al.*, 2012). In contrast, as would be expected if this argument is

correct, we found very weak or insignificant relationships between NEE and CH_4 at any lags over a temporal scale of one day in the *Chamaedaphne* and *Maianthemum/Ledum* communities. This was likely due to the dominance of CH_4 oxidation associated with a low water table (Bubier and Moore, 1994), the more recently fixed carbon being retained in the shoot tissues rather than translocated belowground in the long-lived evergreen *Chamaedaphne* shrubs (Ward *et al.*, 2009), and the majority of exudation from *Chamaedaphne* being unable to reach the CH_4 production zone as shrub roots only grow above the water table (Murphy and Moore, 2010). For the *Maianthemum/Ledum* community, the lack of NEE-CH_4 relationship over the short-term might be partly related to a low rate of photosynthetic CO_2 uptake by forbs per unit leaf area (Leppälä *et al.*, 2008) and a difference in plant physiology and morphology that lead to a slower turnover of recent photosynthate. Since the forb *M. trifolium* has a substantially larger fraction of live biomass found in roots belowground compared to the sedge *E. vaginatum* (Moore *et al.*, 2011), *M. trifolium* might prefer keeping a greater portion of recent photosynthate in roots for growth rather than leaking out labile organic compounds rapidly to the rhizosphere.

We found that peat temperature was the most dominant control of the seasonal variations of daily mean CH_4 flux for all three plant communities (Figure 6.4). The maximum cross-correlation coefficients obtained between peat temperature and CH_4 flux were consistently and considerably stronger than those between GEP and CH_4 flux. Peat temperature had an immediate and positive effect on CH_4 emissions with the strongest relationships (σ = 0.49 to 0.80) observed at zero time lags. Kettunen *et al.* (1996) also observed in a boreal fen a strong correlation between changes in temperature at 20 and 50 cm depths and CH_4 flux within a lag of 2 days. We attribute this rapid temperature response in CH_4 flux to enhanced microbial activity, with CH_4 production by methanogens being more sensitive to a temperature rise than CH_4 oxidation by methanotrophs as shown by incubation of peat soils (Dunfield *et al.*, 1993). Our results further highlight the importance of accounting for confounding temperature effects when

using correlation analysis of gas fluxes to investigate the possible substrate control on CH_4 emissions.

When residuals of daily mean GEP and CH_4 flux independent of peat temperature were used in the cross-correlation analysis, we found significant, but moderate relationships (σ = 0.43 to 0.50) in two *Maianthemum*-dominated chambers at a lag of 18 to 26 days over the season (Figure 6.5c). It has been shown in a grass-dominated ecosystem that peak root production lagged behind leaf production by 15 days (Steinaker and Wilson, 2008). The seasonal lag of CH_4 flux in the *Maianthemum* chambers might similarly be partly related to a delayed response of root production, and hence substrate supply via root exudation and turnover, to plant production. Quantification of root phenology and turnover using mini-rhizotrons, and determination of the time taken for the transfer of photosynthate to roots using ^{14}C pulse labelling are further needed to explain the lags we observed in *Maianthemum*. Meanwhile, it is clear that the coupling between GEP and CH_4 flux is species-specific, with significant relationships found in the two *Maianthemum* chambers but not the one dominated by *Ledum* shrub. We did not observe a significant GEP-CH_4 relationship in the *Eriophorum* community (Figure 6.5a), which suggests a stronger plant-mediated substrate control at the hourly than seasonal scale. Decomposition of organic matter in peat could be an important carbon source for methanogenesis, given that only 0.03 to 0.1% of ^{14}C assimilated by *Eriophorum* is being released into the atmosphere as $^{14}CH_4$ (Dorodnikov *et al.*, 2011; King and Reeburgh, 2002). While King *et al.* (2002) estimated that over 75% of mean CH_4 emissions from wet sedge tundra originated from recent photosynthate, this might be an overestimate since the measurement was done in a laboratory setting in which water table was always kept at a high level. Moreover, environmental stress could lead to short-term increase in the translocation of carbon to roots (King and Reeburgh, 2002) and release of non-structural carbohydrate to peat (Joabsson *et al.*, 1999b), making it potentially more difficult to detect a consistent relationship between GEP and CH_4 flux in *Eriophorum* over a longer time period.

When determining the GEP-CH_4 relationship by month, we observed particularly strong correlations in August and September for *Maianthemum/Ledum* and *Eriophorum* communities, respectively (Figure 6.6). *M. trifolium* has a short life span with senescence beginning in July, while *Eriophorum* reaches maximum vascular green area in August. It has been shown in a subarctic peatland that a greater proportion of recently assimilated carbon is being allocated in the belowground compartments in August-September than in June-July (Olsrud and Christensen, 2004, 2011). In addition, plant roots can release organic compounds into the rhizosphere as a result of cell degeneration upon senescence (Jones *et al.*, 2009). These changes in allocation and phenology can together enhance the availability of labile substrate to methanogens, leading to a stronger coupling of GEP-CH_4 in the late growing season.

Our cross-correlation analysis demonstrates different lagged relationships between CH_4 flux and plant productivity at a bog, depending on the type of vascular plant community and the time scale of analysis. Hence, the correlation between NEE and CH_4 emissions observed in previous studies (e.g. Bellisario *et al.*, 1999; Whiting and Chanton, 1993) might be partly caused by an artefact of averaging data over time and/or space that reduces some of the variance associated with the individual fluxes. For example, when correlating seasonal mean NEE with CH_4 flux, the lag effects shown by the *Eriophorum* community at the hourly scale and *Maianthemum/Ledum* community at the seasonal scale in our study would likely be masked. Retaining the fine scale detail of individual fluxes is important for the understanding of peatland CH_4 dynamics and modelling of the time series of CH_4 flux. In the LPJ-WHyMe methane model, root exudation from graminoids is simulated as a fixed fraction of net primary production with a monthly time step (Wania *et al.*, 2010). This would miss out the short time lag of CH_4 flux that we observed from the *Eriophorum* community on a scale of hours, and might lead to bias in flux estimation if forb is included in future versions of the model while ignoring the relatively long time lag as shown in the *Maianthemum/Ledum* community. We acknowledge the limitation of cross-

correlation analysis in investigating time lags and correlations at the seasonal scale, since it does not take into account the influence of non-stationary phenomena (e.g. hot spells). Wavelet analysis could be useful to overcome this issue by using a window size that varies as a function of frequency. It has been recently applied to explore the temporal correlation between photosynthesis and CO_2 efflux in forest and grassland ecosystems (Vargas *et al.*, 2011).

6.6 Conclusions

We demonstrated an overall strong relationship between seasonal mean NEE_{max}, GEP_{max}, and CH_4 flux across the 18 sites at the Mer Bleue bog, yet the rate of increase in CH_4 flux with CO_2 uptake was considerably lower among the hummocks than the *Eriophorum* and lawn locations. Moreover, we observed an interannual variability in the NEE_{max}-CH_4 relationship, with a significant decrease in the regression slope especially in the *Eriophorum* and lawn sites in 2010 with a drier summer. These results highlight the importance of microtopography and water table position in affecting the coupling of plant production and CH_4 emissions across space.

We found a moderate correlation between instantaneous GEP and CH_4 flux in the *Eriophorum* community at a lag of 9 to 12 hours, indicating a rapid turnover of recently fixed carbon for CH_4 production. At the seasonal scale, residuals of daily mean CH_4 flux was significantly correlated with GEP in the two *Maianthemum*-dominated chambers at a lag of 18 to 26 days, which might be related to a slower transfer of photosynthate belowground and delayed root response to plant production. Moreover, we observed particularly strong GEP-CH_4 relationships in the late growing season in both *Eriophorum* and *Maianthemum/Ledum* communities, probably due to changes in plant phenology and the allocation pattern of assimilated carbon. Our findings suggest that the substrate-based response of CH_4 flux to plant production in this ombrotrophic bog varies depending on the species composition and phenology of vascular plants.

Figure 6.1. The relationships between seasonal mean NEE_{max} and CH_4 flux across 18 locations at the Mer Bleue bog in (a) 2009 and (b) 2010. The overall regression equations (shown in solid line) in 2009 and 2010 were CH_4 flux = -0.243 - 0.041NEE_{max} (r^2 = 0.60, p < 0.001) and CH_4 flux = -0.010 - 0.006NEE_{max} (r^2 = 0.30, p = 0.02), respectively.

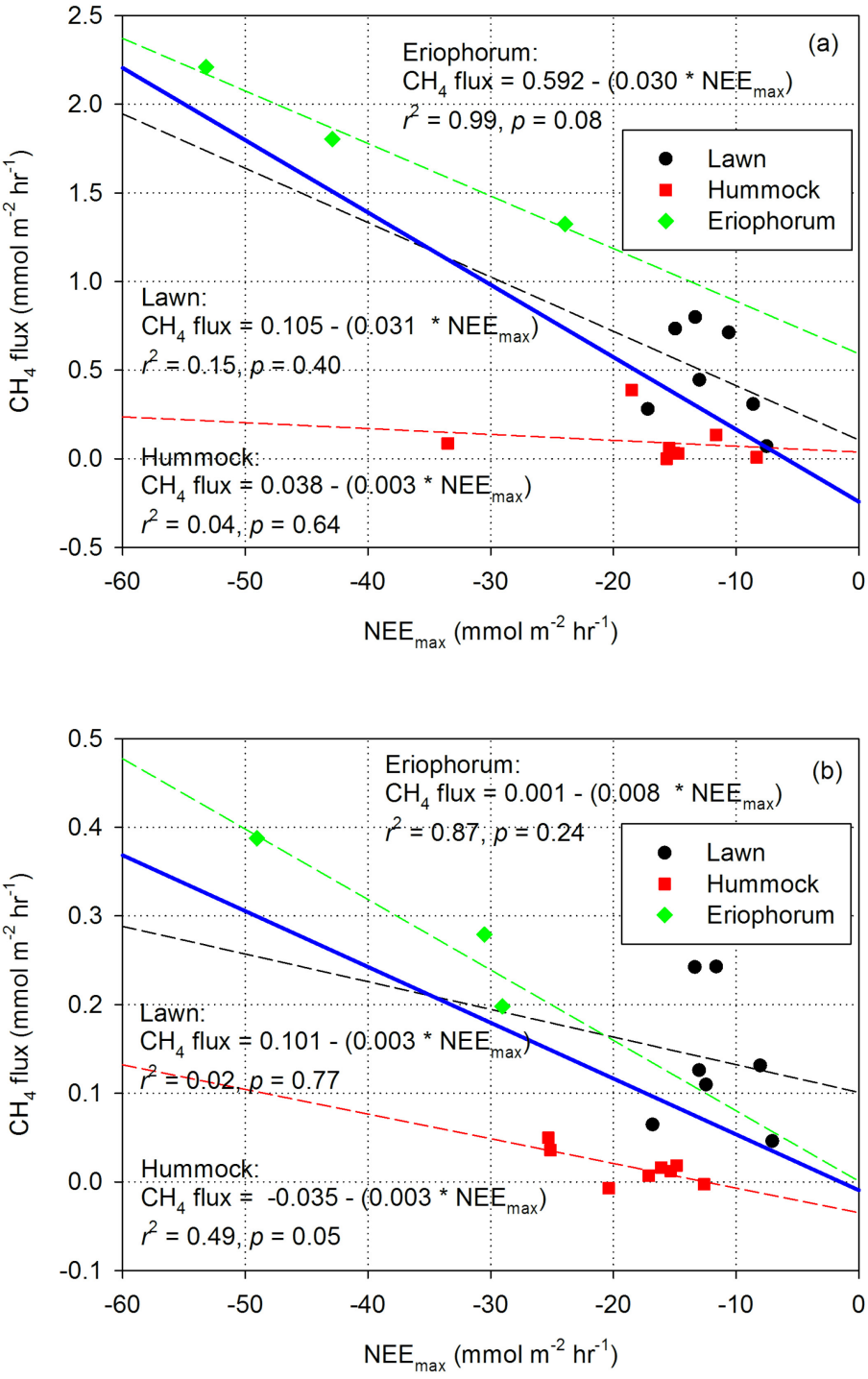


Figure 6.2. The relationships between seasonal mean GEP_{max} and CH_4 flux across 18 locations at the Mer Bleue bog in (a) 2009 and (b) 2010. The overall regression equations (shown in solid line) in 2009 and 2010 were CH_4 flux = -0.303 + 0.020GEP_{max} (r^2 = 0.62, p < 0.001) and CH_4 flux = -0.023 + 0.003GEP_{max} (r^2 = 0.37, p < 0.01), respectively.

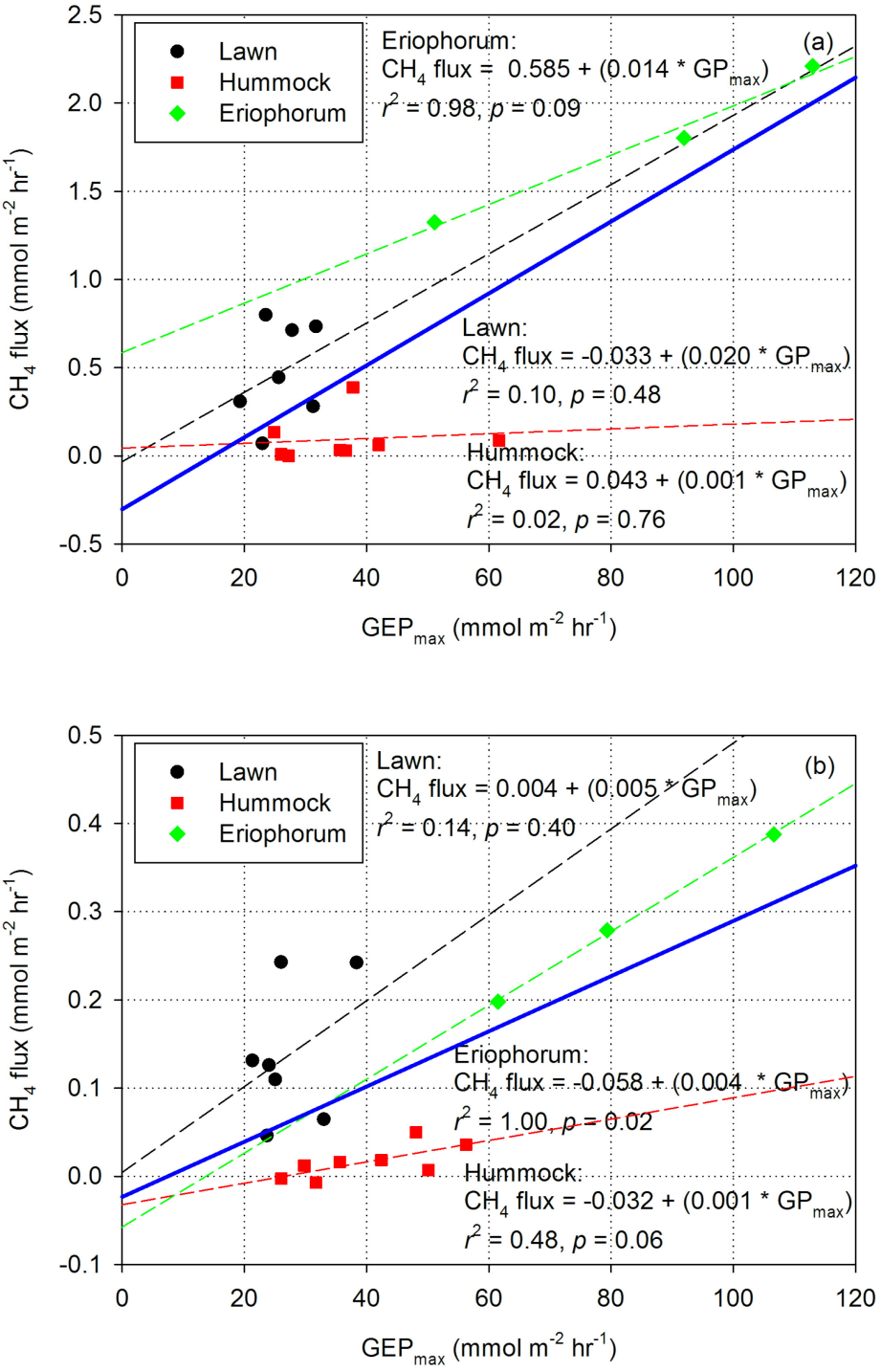


Figure 6.3. Cross-correlation between residuals of instantaneous CH_4 flux and (a) NEE, (b) GEP, and (c) ER for three vascular plant communities during a 30-day period in August-September 2010. The dashed lines represent the thresholds within which a cross-correlation coefficient is not significantly different from zero ($p > 0.05$). The lag time represents the number of hours that CH_4 flux lags behind the CO_2 flux.

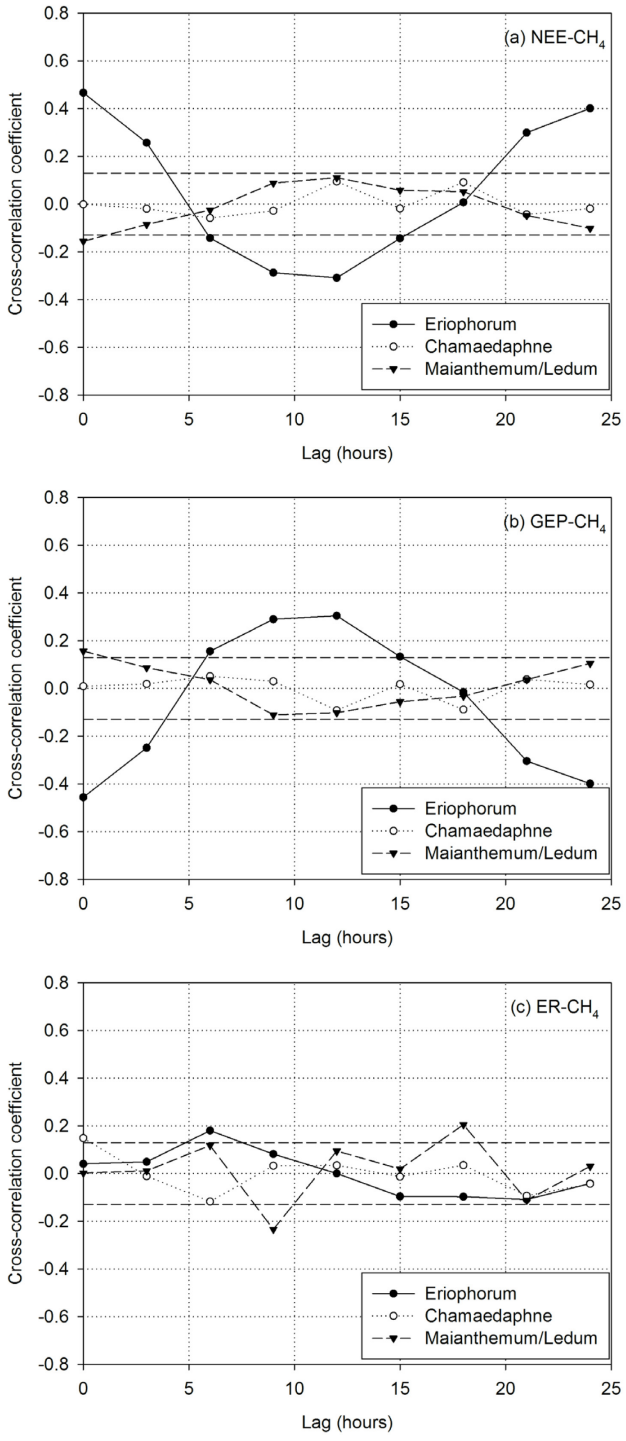


Figure 6.4. Cross-correlation between daily average CH_4 flux and peat temperature from triplicate (a) *Eriophorum*-, (b) *Chamaedaphne*-, and (c) *Maianthemum/Ledum*-dominated autochambers for May-October 2009. The dashed lines represent the thresholds within which a cross-correlation coefficient is not significantly different from zero ($p > 0.05$).

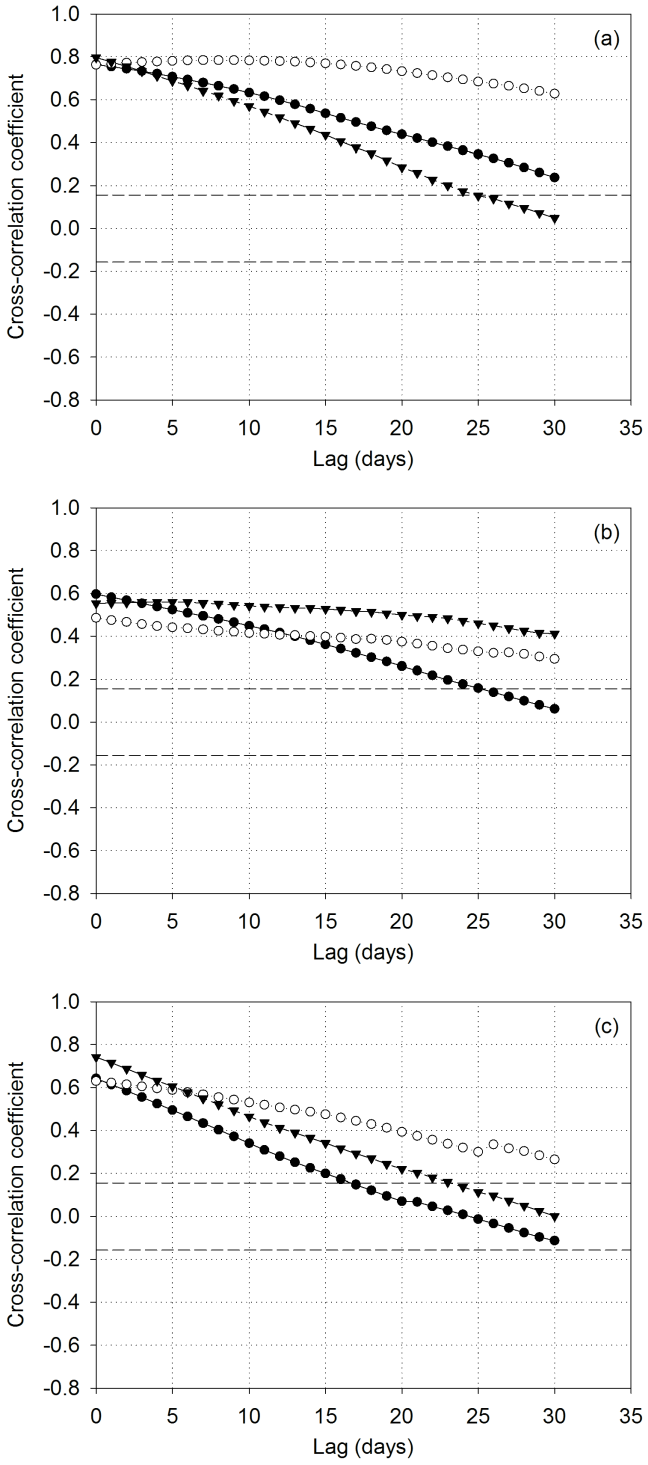


Figure 6.5. Cross-correlation between residuals of daily average CH_4 flux and GEP from triplicate (a) *Eriophorum*-, (b) *Chamaedaphne*-, and (c) *Maianthemum/Ledum*-dominated autochambers for May-October 2009. The dashed lines represent the thresholds within which a cross-correlation coefficient is not significantly different from zero ($p > 0.05$).

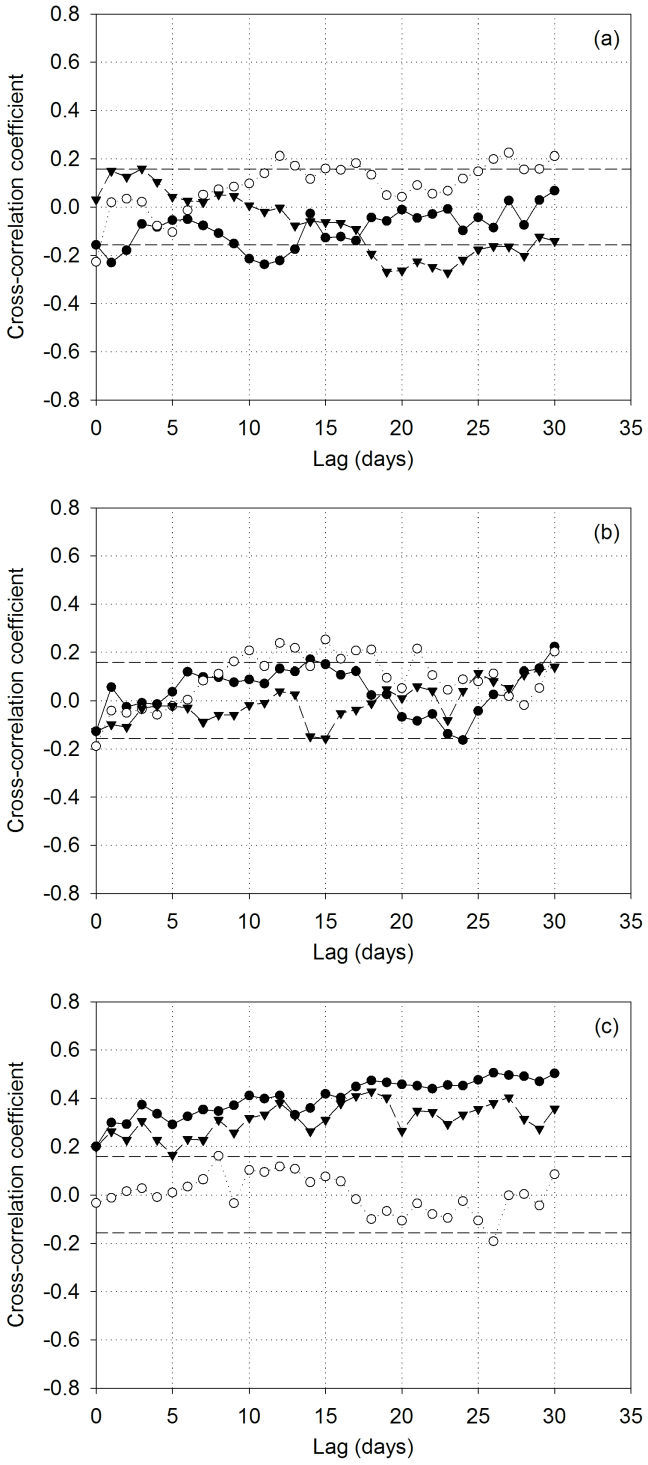


Figure 6.6. Cross-correlation between residuals of daily average CH_4 flux and GEP from triplicate (a) *Eriophorum*-dominated autochambers for September 2009, and (b) *Maianthemum/Ledum*-dominated autochambers for August 2009. The dashed lines represent the thresholds within which a cross-correlation coefficient is not significantly different from zero ($p > 0.05$).

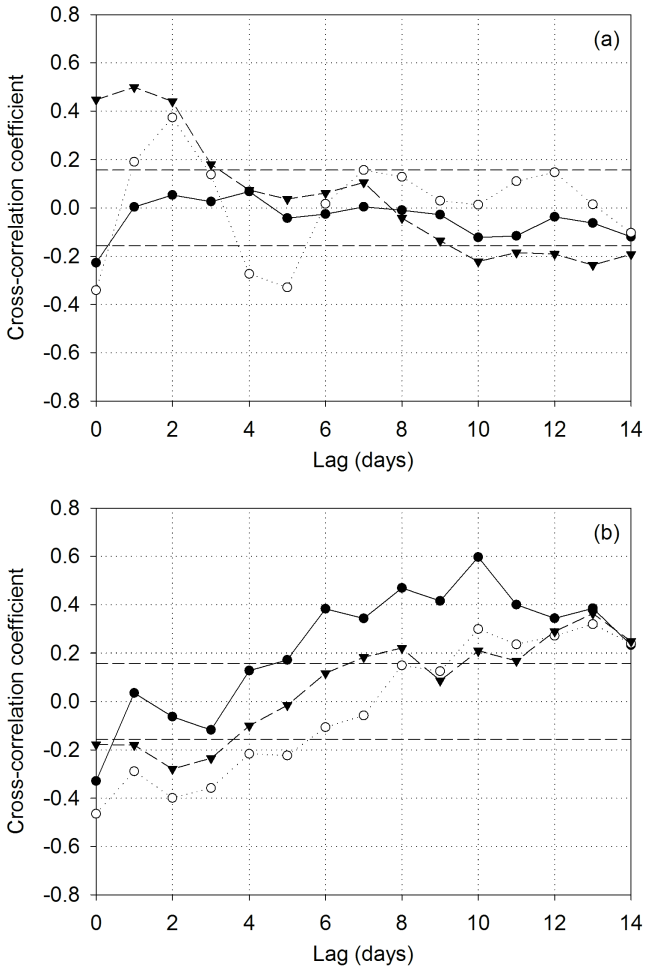


Table 6.1. Vascular plant species and seasonal mean water table depth (May-September) for the 18 manual chamber measurement locations in 2009 and 2010.

Chamber	Vascular plant species	2009 water table depth (cm)	2010 water table depth (cm)
Sedge			
1	Ev, Lg	-19.4	-27.4
3	Ev, Vm	-16.3	-24.2
4	Ev, Lg	-14.3	-22.2
Lawns			
2	Vm, Ka	-12.4	-20.4
5	Lg, Ka	-16.8	-24.7
7	Lg, Mt	-16.4	-24.4
8	Mt	-7.3	-15.2
9	Mt	-12.1	-20.0
10	Mt, Ka	-12.8	-20.7
12	Mt	-10.8	-18.7
Hummocks			
6	Lg, Ka	-21.9	-29.9
11	Vm, Ka	-31.8	-39.7
13	Vm, Ka	-20.6	-28.5
14	Lg, Mt	-18.8	-26.7
15	Cc	-20.3	-28.2
16	Lg	-19.4	-27.4
17	Cc	-21.6	-29.5
18	Cc, Vm	-34.3	-42.2

Cc: *Chamaedaphne calyculata*, Ev: *Eriophorum vaginatum*, Ka: *Kalmia angustifolia*,

Lg: *Ledum groenlandicum*, Mt: *Maianthemum trifolium*, Vm: *Vaccinium myrtilloides*.

Table 6.2. Vascular plant species, mean water table depth, peat temperature at 10 cm depth, and peak vascular green area index (VGA) for the 9 autochambers in 2009.

Chamber	Vascular plant species	Water table depth[a] (cm)	Peat temperature[a] (°C)	Peak VGA (m^2 m^{-2})
Eriophorum-dominated				
1	Ev, Vm, Lg, Ka	-24.8	11.9	0.82
4	Ev, Lg, Cc, Ka	-18.8	12.1	1.35
7	Ev, Cc, Mt, Lg	-19.2	12.4	1.13
Chamaedaphne-dominated				
3	Cc, Vm, Mt, Lg	-29.3	12.5	1.52
5	Cc, Lg, Vm	-35.4	11.9	1.12
6	Cc, Vm	-37.3	12.8	1.56
Maianthemum/Ledum-dominated				
8	Mt, Lg	-19.5	11.8	2.09
9	Lg, Mt, Ka	-24.0	12.2	0.47
10	Mt, Lg	-20.0	12.1	2.00

Cc: *Chamaedaphne calyculata*, Ev: *Eriophorum vaginatum*, Ka: *Kalmia angustifolia*, Lg: *Ledum groenlandicum*, Mt: *Maianthemum trifolium*, Vm: *Vaccinium myrtilloides*.

[a]Averaged between DOY 142 and 334.

Chapter 7

Summary, Conclusions, and Directions for Future Research

7.1 Summary of Findings and Original Contributions

Northern peatlands are highly heterogeneous in their physical, chemical and biological characteristics at a scale length as short as a few meters. To accurately predict the response of peatland C exchange to climate variability and anthropogenic perturbations, an understanding of the relationships between gas fluxes and environmental and biotic correlates at the level of fundamental functional units, i.e. the plant community or microtopographic level, is required. The majority of studies on community level gas exchange in peatlands has employed manual chambers that have a limited sampling frequency owing to labour and time constraints. In this study, I used an autochamber system to measure C gas fluxes at a sub-daily time scale from three vascular plant communities at the Mer Bleue bog. By using this high temporal resolution data set, the first ever collected in an ombrotrophic peatland, my Ph.D. research aimed to quantify community level CO_2 and CH_4 fluxes from this bog, and determine how gas exchange relates to environmental and biotic factors across time and space.

My first objective was to examine the effects of atmospheric turbulence and chamber deployment period on autochamber CO_2 and CH_4 fluxes. I observed that gas fluxes obtained by closed chambers with a short deployment period of 2.5 minutes were strongly related to atmospheric turbulence conditions prior to chamber deployment. As a result, the CH_4 flux and the nighttime CO_2 efflux were underestimated by 9-57% and 13-21%, respectively, in turbulent conditions, but overestimated by ~100% in stable conditions. Flux underestimation was caused by effects of wind flushing and pressure pumping that reduced the transient gas concentration gradient in surface peat as shown by CO_2 profile in the peat. By extending the chamber deployment period to 30 minutes, I further found that the turbulence-related measurement artefact affected the chamber headspace concentration during the first 13 minutes of chamber closure, while gas fluxes

determined beyond this initial period could be used to estimate the biological gas production rate. My findings are unique in that they suggest that when closed chambers are deployed for only a short duration in ombrotrophic bogs or other ecosystems with very porous and well aerated substrate, the fluxes obtained may not represent the actual rate of gas exchange across soils and the atmosphere. The measurement bias observed in this study would not have been detected with manual chambers that monitor headspace gas concentration at a much lower temporal resolution. Also, the tendency to use manual chambers only during the daytime limits the range of turbulence conditions for which fluxes are obtained.

My second objective was to determine the variability of CH_4 flux, as well as the influence of environmental and biotic factors, over the season among three vascular plant communities at the bog. The *Eriophorum* community was a CH_4 emission hotspot, with seasonal mean CH_4 fluxes 1.4 to 5.5 times higher than the *Maianthemum/Ledum* and *Chamaedaphne* communities. While covering only 3% and 27% of the peatland area, *Eriophorum* and *Maianthemum/Ledum* communities contributed to 8 to 11% and 47%, respectively, of total CH_4 emissions from the bog. This demonstrates that plant communities with small coverage could have a disproportionate effect on the ecosystem level CH_4 flux that would be measured by eddy covariance, and introduce additional complexity in upscaling peatland CH_4 flux on top of the non-linear spatial relationships with water table. Also, I observed a 55 to 60% decrease in mean summer CH_4 emissions from the *Maianthemum/Ledum* and *Chamaedaphne* communities in the drier 2010 with a mean water table 5.5 to 9.0 cm lower than in 2009. CH_4 flux had a significant and positive relationship with peat temperature over time with a correlation coefficient > 0.4, only when water table was less than 20, 30, and 40 cm below the peat surface for *Maianthemum/Ledum*, *Chamaedaphne*, and *Eriophorum* communities, respectively, which I related, in part, to variations in plant rooting depth and thus the ability to sustain CH_4 flux in dry conditions. This is an important and new finding made possible to detect only by the availability of high temporal resolution data that show quantitatively the threshold of water table

depth for temperature to predominantly control the temporal changes in community level CH_4 flux. This further suggests that regression models of CH_4 flux based on periodic manual chamber measurements may not be applicable for the actual emissions at a finer temporal scale. Simulation of peatland CH_4 emissions over time has to take into account this interaction of temperature and water table that varies among plant communities.

My third objective was to investigate the temporal controls of CO_2 exchange, and compare the photosynthetic and respiratory responses to changing environmental and biotic factors among three vascular plant communities at the bog. I found significant differences in the overall parameterized GEP and ER models among all three communities, based on over 19,000 measurements of NEE in each community. This is the first study to show the uniqueness of the three separate communities. This has important implications for the modelling of peatland CO_2 exchanges and the interpretation of eddy covariance observations that are a spatially integrated NEE. Eddy covariance NEE results from an unknown combination of the functionally different vascular plant communities dominated by distinct growth forms. The *Eriophorum* community was most efficient in CO_2 uptake at lower light levels with a significantly higher effective quantum yield in the GEP model than the other two communities. The rate of linear increase in GEP with vascular green area index (VGA) was much lower in the *Maianthemum/Ledum* community that might be related to the higher specific leaf area of *Maianthemum* forb leaves. Further, another unique result is that the seasonal variability of P_{max} was greatly reduced when it was normalized by the monthly mean green area, showing that the temporal variations in community level P_{max} are governed primarily by changes in green area rather than changes in photosynthetic capacity per unit green area. My results suggest that simulation of CO_2 exchange from peatland plant communities could be improved by considering changes in phenological development of plants over the season.

My fourth objective was to assess the linkage between CO_2 and CH_4

exchange across space, as well as the correlation and time lag between photosynthetic activity and CH_4 fluxes at different temporal scales in three plant communities at the bog. Based on manual chamber measurements across 18 sites grouped in three categories, seasonal mean NEE_{max} was found to strongly correlate with CH_4 flux at the Mer Bleue bog. While NEE_{max} well described the spatial variations in CH_4 flux among *Eriophorum* and lawn sites, the overall relationship was considerably weaker following the inclusion of hummocks. This shows that the coupling of plant production and CH_4 emissions found by Whiting and Chanton (1993) across a range of flooded wetlands is only valid among peatland sites that are wetter or dominated by sedges, but not at drier, shrub-dominated sites where the influence of lower water tables are common. Moreover, I observed large interannual variability in the NEE_{max}-CH_4 relationship at the *Eriophorum* and lawn sites, with a lower rate of CH_4 flux increase with NEE_{max} in 2010 when the mean water table was 8 cm lower than in 2009. Furthermore, I made an original contribution by conducting a cross-correlation analysis on CO_2 and CH_4 fluxes measured simultaneously from peatland plant communities with a high temporal resolution to explore the coupling between plant production and CH_4 flux over time. CH_4 flux lagged behind photosynthesis at a lag of 9 to 12 hours in the *Eriophorum* community, indicating a rapid turnover of photosynthate by sedges for CH_4 production, while *Maianthemum*-dominated community had a longer lag of 18 to 26 days for CH_4 emissions. My findings indicate that the effect of plant productivity on peatland CH_4 fluxes varies depending on the water table position, dominant vascular plant species, and time scale of analysis.

My Ph.D. research aims to fill the knowledge gap of the temporal variations and controls of CO_2 and CH_4 exchange in ombrotrophic peatlands at the plant community level. This knowledge is important because the chamber fluxes provide insights to interpreting the observations of ecosystem level gas fluxes measured by the eddy covariance method, which alone do not provide mechanistic details of the flux components in a heterogeneous footprint. Overall, the results of my study demonstrate that the influence of environmental and biotic

factors on the spatial and temporal variations of CO_2 and CH_4 fluxes at the Mer Bleue bog is complex and differs among plant communities. The spatial heterogeneity in water table and plant species composition, together with the functional divergence of C gas exchange among plant communities, present challenges of simulating peatland CO_2 and CH_4 exchange at the ecosystem scale. Our results suggest that C gas fluxes in this bog is best modelled by taking into account the three plant communities dominated by different growth forms separately as each of them represent a distinct plant functional type. Moreover, our findings show that it will be difficult to interpret the temporal variability of ecosystem level gas fluxes obtained by the eddy covariance system in peatlands using only a common set of measurements of environmental and biotic parameters. The variability of C gas exchange response at the plant community level should be considered in simulating or explaining the overall CO_2 and CH_4 fluxes in ombrotrophic bogs.

7.2 Prospects for Future Research

Based on my findings in this study, I propose research that should be pursued to improve our understanding of C dynamics in northern peatlands. While the chamber method has the advantage of providing mechanistic details about gas exchange at the plant community level, it is important to be aware of any possible measurement artefacts and be able to assess the reliability of flux estimates obtained by chambers under various deployment conditions. Results will not be accurate or meaningful if the analysis is done based on some biased data. I suggest exploring the effect of atmospheric turbulence and chamber deployment period on gas fluxes measured by closed chambers in other northern peatland sites with different peat porosity and water table. I hypothesize that turbulence-related measurement artefact will be more significant at sites with very porous and well aerated peat (e.g. bogs) than at sites with denser peat and a higher water table (e.g. fens), as a higher air-filled peat porosity facilitates mass flow of gas from pore space to the atmosphere. I also hypothesize that the time duration required for fluxes measured in windy conditions to reach a stable level will be longer for a

closed chamber with no fan compared to one equipped with a fan, since there is a greater difference in headspace turbulence before and during chamber deployment. Moreover, CO_2 and CH_4 concentrations in the headspace of manual chambers should be measured at high frequency (e.g. 1 Hz) over a sufficiently long deployment period (e.g. 30 minutes) to investigate the pattern of concentration trace over a range of turbulence conditions. I hypothesize that the headspace gas concentration in manual closed chambers will similarly be affected in the initial period by turbulence as in autochambers, and will be detected when high frequency samples are obtained.

Given the different responses of CO_2 and CH_4 exchange to changing environmental conditions shown among the three plant communities dominated by evergreen shrub, sedge and forb, the next step is to test whether the CO_2 and CH_4 fluxes measured at the plant community level by autochambers can be upscaled to provide a reasonable flux estimate at the ecosystem scale. I hypothesize that the upscaled fluxes of CO_2 and CH_4 from the three plant communities will be different from the measurements obtained by the eddy covariance tower at the instantaneous scale, since eddy covariance can capture the mass flow of gas into the atmosphere in windy conditions while the closed chambers cannot. However, I hypothesize that the upscaled chamber fluxes and tower fluxes will agree well at the daily or longer time scale, implying that the three communities can adequately capture the spatial heterogeneity of CO_2 and CH_4 exchange in ombrotrophic bogs, since plant communities integrate the environmental drivers of gas exchange.

Simulation of CO_2 exchange over time requires the parameterization of photosynthesis and respiration models for each plant functional type. While I found significant differences in the GEP and ER responses to changing environmental conditions among three plant communities in the wet 2009, it is not known whether this functional divergence will also exist in a drier year. I hypothesize that the three plant communities will keep functioning differently

with respect to CO_2 exchange in a drier year, but the parameters of the GEP and ER models will be different with water table exerting a stronger control as compared to a wetter year. Moreover, the CO_2 exchange response for the understory *Sphagnum* moss in peatlands deserves further investigation in field studies, as vascular plants and moss are expected to behave differently within a community. In my GEP model, the contribution of moss to the overall GEP was estimated as a parameter while the estimated P_{max} represented the combined effect of moss and vascular plants. Light response curves have recently been established for *Sphagnum* at the Mer Bleue bog based on laboratory experiments (Chong *et al.*, 2012), as well as for sub-arctic bryophytes based on field measurements of NEE (Street *et al.*, 2012). A combination of lab- and field-based studies should be further made on moss CO_2 exchange in northern peatlands with considerations given to the effects of different *Sphagnum* species.

Ebullition is one of the CH_4 transport mechanisms in northern peatlands, and is least understood due to the difficulty in quantifying the episodic release of gas bubbles. The high temporal resolution CH_4 flux data obtained by autochambers provides a good opportunity to investigate the occurrence of ebullition events in peatlands. Goodrich et al. (2011) have attempted to estimate CH_4 ebullition in a temperate poor fen based on nonlinearity in CH_4 concentration time series in the headspace of autochambers. There is a possibility to apply similar protocols to identify ebullition events from my autochambers at a bog site using the longer deployment period of 15 minutes in the summer of 2010. I hypothesize that ebullition will occur less frequently in a bog than in a fen, as a low water table will promote oxidation of CH_4 in micro-bubbles and reduce the effects of wind in loosening the bubbles adhered on the water surface.

Last, but not least, the coupling of plant production and CH_4 emissions should be further investigated using wavelet analysis on the high temporal resolution CO_2 and CH_4 fluxes measured by the autochambers at the Mer Bleue bog. Existing CH_4 models simulate the influence of plant production on CH_4

emissions using a function of fixed fraction of net primary production, while assuming there is no time lags between the two processes (Walter *et al.*, 2001; Wania *et al.*, 2010). Wavelet analysis is capable of identifying spectral properties of time series that contain non-stationary phenomena, and have been used to investigate the temporal relationships between photosynthesis and soil CO_2 efflux in forest ecosystems (Vargas *et al.*, 2011). Application of this time series technique may yield interesting information regarding the temporal relationship between photosynthesis and CH_4 flux in peatlands. Pulse labelling of ^{14}C should also be conducted to examine the contribution of recent photosynthate to CH_4 emissions from plant communities dominated by different vascular species, as existing studies have mostly focused on sedges only.

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