Effect of Plant Functional Type on Methane Dynamics in a Restored Minerotrophic Peatland

Maria Strack*[1, 2], Kisa Mwakanyamale [1,3], Golnoush Hassanpour Fard[1], Melanie Bird[1,4], Vicky Bérubé[5] and Line Rochefort[5]

[1]Department of Geography, University of Calgary, Alberta, Canada

[2]Department of Geography and Environmental Management, University of Waterloo, Ontario, Canada

[3] now at: Illinois State Geological Survey, University of Illinois at Urbana-Champaign, Champaign, IL

[4] now at: NAIT Boreal Research Institute, Peace River, Canada

[5] Department of Plant Sciences and Peatland Ecology Research Group, Laval University, Québec, Canada.

*Corresponding author

mstrack@uwaterloo.ca

Phone: +1 519-888-4567 x30164; Fax: +1 519-746-0658

Keywords: CH_4, *Carex aquatilis,* fen, *Myrica gale, Tomenthypnum nitens,*

Abstract

Background and Aims: Peatland methane (CH_4) fluxes may vary between plant types; however, in mixed communities, the specific role of each species is difficult to distinguish. The goal of this study was to determine the individual and interacting effect of moss, graminoid and shrub plant functional types on CH_4 dynamics of experimentally planted plots in a rewetted minerotrophic peatland

Methods: We measured CH_4 flux, pore water CH_4 concentration and CH_4 production and oxidation potential in pure stands of reintroduced *Tomenthypnum nitens* (Hedw.) Loeske, *Carex aquatilis* Wahlenb, or *Myrica gale* L., as well as mixtures of *T. nitens* + *C. aquatilis* and *T. nitens* + *M. gale*. Methane flux was also measured on bare peat plots.

Results: The presence of both the graminoid *C. aquatilis* and the shrub *M. gale* resulted in the highest CH_4 production potential in near surface peat (10 cm). The presence of moss (*T. nitens*) and *C. aquatilis* significantly increased CH_4 oxidation potential. Water table position was a significant control on CH_4 flux, but the presence of *C. aquatilis* maintained higher flux even at dry plots. Plots including *C. aquatilis* had significantly lower pore water CH_4 concentration at 30 cm depth, likely reflecting CH_4 oxidation and transport.

Conclusions: Management of restored sites aiming to reduce CH_4 flux should focus on hydrology, i.e. water table position. The presence of graminoids enhances CH_4 flux, while moss presence may result in lower CH_4 emission.

Introduction

Peatlands are wetlands characterized by accumulation of soil organic matter as peat. The waterlogged environment in peatlands creates anoxic conditions that significantly reduce the decomposition rate and contribute to accumulation and storage of the carbon-rich organic matter (Gorham, 1991). As litter continues to deposit, previous layers become buried in the waterlogged peat profile, where decomposition occurs very slowly through anaerobic processes, releasing some carbon (C) in the form of methane (CH_4). Production of CH_4 through methanogenesis within the peat profile has turned peatlands into an important (annual release of 46 Tg CH_4-C to the atmosphere) global CH_4 source (Gorham, 1991; Lai, 2009). Once anoxic conditions have been met, the rate of methanogenesis within the peat profile is primarily controlled by microbial populations (methanogens), temperature, and substrate quantity and quality (Lai, 2009).

Methane emissions to the atmosphere result from a balance between CH_4 production and CH_4 oxidation. Different plant species in peatlands greatly influence CH_4 dynamics in terms of production (by providing substrate), consumption and emissions (Ström *et al*., 2005; Kao-Kniffin *et al*., 2010; Koelbener *et al*., 2010; Wang *et al*., 2013; Bhullar *et al*., 2014). Herbaceous vegetation enhances CH_4 production by providing a labile substrate directly in the anoxic zone where methanogenesis occurs (Saarnio and Silvola, 1999; Ström *et al.*, 2003). Old peat and certain types of vegetation (e.g. bryophytes) are more recalcitrant to decomposition, whereas many vascular plants can provide fresh and easily decomposable litter and root exudates for methanogenesis (Ström *et al*., 2005). Using a plant removal experiment in an ombrotrophic peatland, Robroek *et al*. (2015) observed only small changes in peat organic chemistry, but an indication that graminoid removal reduced the polysaccharide content; however, the microbial community changed significantly with removal of both graminoids and ericoid shrubs with potential methane production (PMP) significantly lower when graminoids were removed.

In the presence of oxic conditions, some of the produced CH_4 is consumed (oxidized) by another set of microbes (methanotrophs) for growth and maintenance (Lai, 2009). Residence time of CH_4 in the anoxic and oxic zones affects the quantity of CH_4 released to the atmosphere (Olefeldt *et al*., 2013). Plant aerenchyma (porous gas exchange tissues), can also transport oxygen from the atmosphere down to the anoxic peat layer, where radial oxygen loss (ROL) from roots may cause local oxidation of CH_4 to CO_2 (Arah and Stephen, 1998; Dannenberg and Conrad, 1999; Ström *et al*., 2005; Fritz *et al*., 2011). Removal of graminoids from lawns of an ombrotrophic bog reduced copies of some genes associated with methanotrophs, while a similar effect was observed at hummocks when both graminoids and ericoid shrubs were removed (Robroek *et al*., 2015).

Previous studies have also reported on the symbiotic relationship between mosses (e.g., *Sphagnum* spp., *Scorpidium scorpioides*) with methanotrophic bacteria, which allows oxidation of CH_4 that leads to a reduction in CH_4 emissions to the atmosphere (e.g., Liebner *et al*. 2011; Larmola *et al*., 2010). This within-plant oxidation of CH_4 has been observed in boreal (e.g. Basiliko *et al*., 2004) and in arctic regions, where submerged brown moss oxidized CH_4 at rates that are 100 times higher than reported values for bulk soil (Liebner *et al*., 2011). Moss associated CH_4 oxidation increases with temperature (van Winden *et al*., 2012) and for *Sphagnum* is greater in species growing in wetter locations (Basiliko *et al*., 2004).

Whereas, oxidation of CH_4 by vascular plants due to ROL in the anoxic zone reduces CH_4 flux, the same plant aerenchymatous roots and stems (especially of graminoids (Bellisario *et al*., 1999; Schimel, 1995)), can act as a conduit to transfer CH_4 from the anoxic production zone to the atmosphere, bypassing oxidation in the oxic zone above the water table (Ström *et al*., 2005;

Bellisario *et al*., 1999). The relative importance of each of these plant-mediated effects will result in the local impact of plant presence on CH_4 fluxes. While many studies have reported a positive correlation between plant cover, biomass or productivity and CH_4 flux (e.g. Whiting and Chanton, 1993; Waddington *et al*., 1996; Couwenberg and Fritz, 2012), in other cases, the presence of particular plant species may reduce CH_4 emission (Bhullar *et al*., 2013; Fritz *et al*., 2011). In general, the presence of graminoids has often been reported to result in higher CH_4 flux (e.g., Marinier *et al*., 2004; Couwenberg and Fritz, 2012; Ward *et al*., 2013) and it has been suggested that vegetation type can be used as a proxy for greenhouse gas flux, including CH_4 flux, in peatlands (Bubier, 1995; Couwenberg *et al*., 2011).

As the climate changes, the composition of plant functional types (PFTs) within a peatland has the potential to shift in response to changing environmental characteristics (e.g., Strack *et al*., 2006; Kuiper *et al*., 2014; Dieleman *et al*., 2015; Moor *et al*., 2015). Industrial extraction of peat for horticulture also modifies the cover and composition of plant species from that which occurs in undisturbed peatlands, and hence changes CH_4 dynamics in these disturbed sites (Tuittila *et al*., 2000; Waddington and Day, 2007; Dias *et al*., 2010). The degradation of natural peatland functions after industrial extraction of peat converts the peatlands to a persistent source of CO_2 to the atmosphere (Waddington *et al*., 2002), while reducing CH_4 emissions to very low levels on drained peat fields (Waddington and Price, 2000). Studies have also shown that ecological restoration after peat extraction may cause peatlands to return to sources of CH_4 of a magnitude similar to natural peatlands (Waddington and Day, 2007; Cooper *et al*., 2014; Vanselow-Algan *et al*., 2015).

Although restoration is practiced as a post-extraction management strategy to reestablish the extracted site as a functioning peatland ecosystem (Waddington and Price, 2000), current restoration planning in North America does not specifically consider the role of plant diversity in restoring natural functions of peatlands (Rochefort *et al.*, 2003; González and Rochefort, 2014). There is reason to believe that, the manipulation of plant diversity is effective for achieving and enhancing restoration objectives (Díaz *et al*., 2009). For example, Kivimaki *et al*. (2007) suggested that C uptake in a restored peatland was enhanced when graminoids grew in association with moss compared to graminoids growing alone. In order to increase understanding of the possible feedback mechanisms that plant diversity might have on peatland greenhouse gas exchange, and evaluate the fulfillment of the goal of peatland restoration initiatives following peat extraction, it is of vital importance to understand (1) how individual plant species affect CH_4 dynamics in restored peatland ecosystems, and (2) whether these effects change depending on the composition of the community in which the species is growing. Reliable knowledge of the impact of plant diversity and PFT on CH_4 dynamics could inform guidelines and policies for post-extraction management of peatlands by the peat industry.

Several studies have investigated the role of plant communities or PFT in peatland CH_4 dynamics by either targeting specific naturally occurring assemblages (e.g., Armstrong *et al*., 2015) or conducting plant removal studies (e.g., Ward *et al*., 2013; Robroek *et al*., 2015). The difficulty with the former approach is that particular species tend to dominate in specific hydrological conditions, which also drive CH_4 dynamics and can be difficult to tease apart from plant type. In plant removal studies, legacy impacts of the removed plants on soil chemistry and microbial community may make it difficult to determine specific plant effects (*e.g*., Robroek *et* *al.*, 2015) unless the plant removal is continued for many years. Moreover, removal of a canopy of graminoids and/or shrubs reduces shading of the underlying moss, resulting in moisture stress (*e.g.*, McNeil and Waddington, 2003) making it difficult to understand the role of moss in an intact community. Planting experiments on cutover peatlands can overcome many of these issues. Species composition can be controlled during planting, the same combinations planted along existing hydrological gradients at the site, and PFTs added to a relatively uniform residual peat layer. Therefore, the specific impacts of each PFT on CH_4 dynamics can be more clearly identified. Accordingly, the primary purpose of this project was to investigate the effects of common peatland PFTs (both in monoculture and in combination) on CH_4 dynamics in a restored minerotrophic peatland. We focus specifically on species representing a range of PFTs – moss, graminoid and shrub and a combination of these plant types, to determine the effect on: (1) CH_4 fluxes, (2) pore water CH_4 concentrations, (3) CH_4 production potential, and (4) CH_4 oxidation potential. To address these questions we used both field and laboratory techniques to study moss, graminoid, shrub, and a combination of moss and graminoid, and moss and shrub plots, planted in 2009 in a restored minerotrophic peatland in Quebec, Canada.

Study Site

The study was conducted at Bic Saint-Fabien (BSF) peatland (48.322°N, 68.833°W), which is located in the St. Lawrence Lowlands, approximately 25 km west of Rimouski, Quebec, Canada (Figure 1). Mean annual precipitation based on 1981-2010 measurements from the Rimouski meteorological station is 959 mm, 28% of which falls as snow (data available: http://climate.weather.gc.ca/climate_normals/). The growing season between May-September receives on average 434 mm of rain. Average daily temperatures are -11 °C and 18 °C in

January and July, respectively. The area consists of both natural and disturbed (extracted) peatland (Figure 1).

The restored portion of the peatland consists of 15 ha, which was utilized for horticultural peat extraction from 1946 to 2000. This portion was initially a raised bog, which was extracted down to its minerotrophic peat layer and residual peat conditions of the site now resemble that of a fen with peat pH of 5.0-5.3 and specific electrical conductivity of 93-145 µs cm^{-1}. Remnant peat thickness varies between 1.6 and 3.5 m (Ketcheson *et al*., 2012). This extracted section of the BSF peatland is characterized by a moderately-decomposed peat (von Post H5-H6) consisting of moss and sedge remains with varying degrees of spontaneous recolonization by plants, and ruderal species such as cattails (*Typha* spp.) in former ditches that largely remain filled with water. The vast majority of the easternmost part of the site remained bare until 2010 when an assortment of restoration actions was implemented, including rewetting (creation of berms to redistribute more uniformly the water over the site, birch cuttings, ditch blocking and peat surface reprofiling). The central section was used for a biodiversity-control experiment in which various plant species representative of various PFTs common in fens in the region (V. Bérubé, unpublished data) have been planted.

The assessment of CH_4 dynamics of the different planted communities was carried out within a blocked design with each planting treatment replicated at a random location within each of three blocks. The blocks were created within three adjacent peat fields and each block varied in hydrology due to differences in water table that existed across the site. We investigated CH_4 dynamics with one closed chamber (see description below) per treatment and per block (5 planting treatments x 3 blocks for a total of 15 plots for the following functional plant type treatment: 1) *Tomenthypnum nitens* (Hedw.) Loeske (moss), 2) *Carex aquatilis* Wahlenb. (graminoid), 3) *Myrica gale* L. (shrub), 4) *T. nitens + C. aquatilis* and 5) *T. nitens + M. gale* planted together. Each experimental unit measured 3 m x 3 m. Plants were collected from an undisturbed fen (donor site) in May 2009, and planted in May and June of the same year at the study site. Mosses were spread at a density of 1:5 (1 m^2 from donor site spread over 5 m^2 at the study area) while *C. aquatilis* plants were planted every 20 cm for a total of 240 plants per plot and *M. gale* were planted every 30 cm for a total of 121 plants per plot. By 2011 and 2012 when the study was conducted, plants were well-established and few bare peat areas remained within or between the planted study blocks. As such, it was difficult to establish bare peat areas within the same hydrologic conditions as the vegetated study plots. Methane flux was measured on small bare areas in other areas of the site (Figure 1), but samples were not collected there for pore water or CH_4 production and oxidation potential incubations as contamination by root exudates from nearby plants was likely, particularly by 2012.

Methods

Environmental Conditions

Field measurements were conducted during the growing seasons of 2011 (May-August) and 2012 (May-September), two and three years after planting. A meteorological station located on the extracted site (Figure 1) continuously recorded water table elevation (*WT*, cm; Solinst levelogger). Soil surface temperature and air temperature were measured using thermocouples connected to a data logger (Campbell Scientific, CR10X). Measurements were taken every minute and averaged over 30-minute intervals in 2011 and 20-minute intervals in 2012 from May to August. Additionally, three probes (Onset HOBOware Pro) recorded soil surface temperature at three locations (one in each of block 1, 3, 4) at 30 min intervals in 2012.

Potential Methane Production and Oxidation

Peat cores (10 cm x 10 cm x 50 cm deep) for the laboratory study were extracted from within each experimental unit in September 2012. The cores were subdivided in 10 cm sections and were frozen until sample incubation in January 2013. Subsamples (10 - 11 g wet weight) were collected from each of the peat cores after thawing for 48 hours, and added to 125 mL glass incubation jars. Two subsamples at depths of 0 - 10 cm to represent the layer of fresh litter deposition, and two at 40 - 50 cm depth for the permanently saturated zone from each of the 15 experimental units. After 24 hrs of acclimation, the samples were incubated at 20 °C over a period of 72 hrs. Anoxic and oxic conditions were used during incubation to determine potential methane production (PMP) and oxidation (PMO), respectively.

For the oxic experiment, the peat samples were left in jars without lids during the acclimation period (24 hrs). After acclimation, lids equipped with septa were placed on the jars and 20 mL of CH_4 standard (≈2.235 μmol CH_4) was injected. For the anoxic experiment, the peat samples in the incubation jars were saturated with distilled water to make a slurry and the samples were left without lids to acclimate at room temperature (20 °C). The saturated samples were then flushed with N_2 for 15 min and sealed in a glove bag. At 12 hr intervals, gas samples were collected from headspace of both oxic and anoxic jars, and injected into pre-evacuated vials. Nitrogen was injected to maintain pressure within the jars. Anoxic samples were mechanically agitated for 10 minutes prior to sampling to mix the entrapped gases within the peat pore spaces and the jar headspace. The collected gas samples were analyzed for CH_4 concentration using a Varian Gas Chromatograph 3800 (GC) with flame ionization detector at 250 °C. Standards, of known CH_4 concentration, were also analyzed to check for instrumental error and ensure quality control. PMP and PMO rates were determined from the linear increase or decrease in concentration of CH_4 within the jars over the incubation period after correcting for dilution by N_2.

Methane Flux Measurements

The closed chamber technique was used for CH_4 flux measurements (e.g., Alm *et al*., 2007). Steel collars (60 cm x 60 cm x 15 cm deep; sample plots) were installed within each experimental unit at the beginning of May 2011. Opaque steel chambers (60 cm x 60 cm x 30 cm) were placed on top of collars to create a closed system, and the grooves of the collar were filled with water to ensure an airtight seal. Bare peat CH_4 flux was measured with smaller plots (26 cm diameter) and chambers (13 L) due to the limited amount of bare peat remaining on site post restoration. Each chamber was equipped with a battery-operated fan to mix the headspace. Four 20 mL gas samples were taken from the headspace at regular intervals after chamber closure (7, 15, 25, 35 min) using a syringe equipped with a three-way valve. Methane fluxes were conducted weekly during the two growing seasons. Ambient air samples were also collected on each day of flux measurements to be used as the initial measure of CH_4 concentration, i.e., 0 min (Mahmood and Strack, 2011). All samples were stored in pre-evacuated Exetainers (Labco Ltd.) and analyzed on the gas chromatograph described above within 2 months of collection. Laboratory tests with standards injected into Exetainers indicate sample integrity for at least 4 months.

The instantaneous flux was calculated as the linear change in CH_4 concentration in the headspace over time. If the pattern of concentration did not consistently increase or decrease over time or jumped suddenly indicating potential ebullition, the flux value was not used except in cases where the slope was not significantly different from zero indicating a non-detectable, low flux. This resulted in loss of 5% of the data.

Environmental variables were also monitored during CH_4 flux measurements, including air temperature inside the chamber, WT elevation in a well adjacent to each collar, and soil temperature at 2, 5, 10, 15, 20, 25, and 30 cm depths. Temperature measurements were recorded using thermocouple thermometers.

Vegetation Volume Measurements

A 'Fuel Rule' visual obstruction method adapted from Davies *et al*. (2008), was used to estimate the aboveground biomass in the form of vegetation volume (*VV*) within the CH_4 flux collars biweekly. The Fuel Rule is a 2 m long measuring stick that is 2.5 cm wide and painted with alternating white and red bands. One face has bands 10 cm high whereas the reverse has two bandwidths of 2 and 5 cm starting at opposite ends and running half its length. Each set of bands is labeled with numbers. In this method, visual obstruction of this banded measurement stick by plants was used to estimate vegetation volume based on a combination of vegetation height and its density. To take a reading, the Fuel Rule was placed vertically in the middle of a collar and pressed down through the moss and litter layer until it reached the more compact cutover peat below ground. The user, while standing at arm's length, visually estimated the percentage of each band obscured by vegetation. When vegetation was tall enough, at least five bands were obstructed; hence, an appropriate scale was chosen based on the height of the vegetation at each collar (Mahmood and Strack, 2011). The data was entered into the PObscured computer program (available at: http://www.firebeaters.org.uk) to determine *VV* as described by Davies *et al*. (2008). Vegetation volume of the vascular species plots was modeled over the growing season by applying Gaussian curve-fitting (Equation 1), adapted from Riutta et al., (2007) to the 10-13 measured values:

$$VV = VVmax * \exp[(\frac{JD-JDmax}{b})]^2 \quad [1]$$

Where *VVmax* is the maximum *VV* during the season, *JD* is the Julian day (days of a year numbered from 1 to 365), *JDmax* is the timing of *VVmax* and *b* is the width of the Gaussian curve. The Gaussian curve fit the data well with adjusted R^2 between 0.32 and 0.88. As moss cover varied little over the season, a mean value of *VVmax* was used for *T. nitens* plots, resulting largely on the height of the moss above the cutover surface.

Pore Water Methane Concentration

Pore water samplers consisted of a 20 cm length of 2.5 cm inner diameter PVC pipe, closed at both ends, slotted at the middle 10 cm, and covered in Nitex screening to prevent clogging (see Strack *et al*., 2004). These samplers were installed, centered at 30 cm depth, for each sample plot in May 2012. To evaluate variation of CH_4 concentration with depth, additional samplers centered at 50 cm and 75 cm were installed at each plot within the block with the intermediate *WT*. A sampling tube fitted with a three-way valve was inserted at one end of the sampler and extended above the surface of the peat to allow for collection of water samples. Once in the ground, samplers were allowed to equilibrate for a week, and then left in place throughout the study. Pore water samples were collected from May to September 2012. After each sample collection, the samplers were filled with water and the valve closed to prevent air from entering the tube. CH_4 concentration from the water samples were then determined using headspace analysis after equilibration with ambient air in the field (Mahmood and Strack, 2011).

Data Analysis

The effect of planting treatment, year and environmental factors contributing to variation in field measured CH_4 fluxes and pore water CH_4 concentrations at 30 cm were evaluated in R (R Core Team, 2013) with mixed effects models using the package nlme (Pinheiro *et al*. 2014). Planting treatment and year were considered in a linear mixed effects model including $\log_{10}(CH_4 \text{ flux})$ or pore water concentration as the independent variable, planting treatment, year and planting treatment x year interaction as a fixed factors and sample plot as a random factor to account for the repeated measures nature of the data. Similar models were used to evaluate difference in water table (*WT*) and vegetation volume (*VV*) between planting treatments and years. To investigate specific environmental controls on CH_4 dynamics, additional linear mixed effect models considered seasonal mean $\log_{10}(CH_4 \text{ flux})$ or pore water concentration as the independent variable, seasonal mean *WT*, maximum *VV* (*VVmax*; see equation 1), and PFT presence and all two-way interactions as fixed effects, and plot as a random effect. Factors that were insignificant were removed from the model one at a time, starting with the least significant, until the final model was found. Non-significant individual factors were retained in the model when they occurred in a significant interaction term. Residuals were inspected visually for normality and heterogeneity.

In order to evaluate treatment effects on PMP and PMO rates a general linear model was used that included planting treatment, depth of core sample and planting treatment x depth as categorical fixed effects. If a factor significantly explained the variation in the data, a Tukey pairwise comparison was conducted using the package multcomp (Hothorn *et al*., 2008). Groups were considered significantly different if $p < 0.05$. A general linear model was also used (gls in the nlme package) to investigate whether the presence of each PFT, depth and the interaction between PFT and depth were significant for explaining variation in PMP and PMO rates. The final models were determined as described above, by dropping non-significant factors one at a time starting with the least significant.

Results

Potential methane production and oxidation

Measured potential CH_4 production (PMP) was 0.067 – 0.20 nmol g dry peat^{-1} hr^{-1}, being generally greater in surface (0-10 cm deep) peat samples than at depth (40-50 cm). There was a significant effect of depth (Table 1; $F_{1,18} = 33.7$, $p<0.0001$) and a significant planting treatment-depth interaction (Table 1; $F_{4,18} = 3.26$, $p=0.036$) for explaining variation in PMP. In the shallow peat, PMP was significantly greater at *C. aquatilis* monoculture plots than at *T. nitens* monoculture plots. All planting treatments had significantly greater PMP in shallow peat than deep peat except *T. nitens* monoculture plots, where there was no significant effect of depth (Figure 2a). Planting treatment alone did not significantly explain variation in PMP (Table 1; $F_{4,18} = 0.91$, $p=0.50$). Depth was the only significant factor accounting for variation in PMP in a linear model that also considered the presence of each PFT (Table 2).

Measured potential CH_4 oxidation (PMO) was 2.8 – 5.9 nmol g dry peat^{-1} hr^{-1}. Planting treatment explained a significant portion of the variation in PMO (Table 1; $F_{4,20}$ = 3.33, p=0.030), although there was also a significant planting treatment-depth interaction (Table 1; $F_{4,20}$ = 3.84, p=0.018). PMO was significantly greater in shallow peat compared to deep peat for *C.aquatilis* - *T.nitens* mixed plots, but did not vary significantly with depth at any other plot type. Considering the presence of each PFT on PMO indicated that the presence of moss (Table 2; $F_{1,25}$=7.39, p=0.012) significantly increased PMO, and there was a significant interaction between depth and graminoid presence ($F_{1,25}$ = 8.48, p=0.0075) whereby PMO was significantly greater in shallow peat than deep peat only in plots that included the graminoid *C. aquatilis* (Figure 2b).

Environmental conditions and methane fluxes

The water table was significantly shallower in 2011 than 2012 (Table 3; $F_{1,13}$=31.8, p=0.0001), although it did not vary significantly between the planting treatments ($F_{4,13}$=0.35, p=0.87). Maximum vegetation volume (*VVmax*) was greater in 2012 compared to 2011 (Table 3; $F_{1,10}$=16.13, p=0.0025) except at *T. nitens* only plots that did not vary over time, resulting in a significant planting treatment-year interaction ($F_{4,10}$=8.28, p=0.0033). There were differences in *VVmax* between planting treatments (Table 3; $F_{4,10}$=8.27, p=0.0033) with *C. aquatilis* and *C. aquatilis-T. nitens* plots having greater *VVmax* than all other planting treatments, which were not different from each other.

Mean (standard deviation) CH_4 flux was 4.2 (7.1), and 9.7 (11.6) mg CH_4 m^{-2} d^{-1} in 2011 and 2012, respectively. There was no significant difference in flux between the years ($F_{1,13}$=0.02, p=0.90) or between the various planting treatments ($F_{5,13}$=1.14, p=0.39) and no significant planting treatment-year interaction ($F_{5,13}$ = 1.14, p=0.39). Results from the linear mixed model (Table 2) indicate that *WT* and an interaction between *WT* and graminoid presence were significant factors explaining spatial variability in CH_4 flux. Plots with shallower *WT* had greater CH_4 flux, but this relationship was not significant when the graminoid *C. aquatilis* was present (Figure 3a). CH_4 flux was also positively related to *VVmax* when considered individually (Figure 3b; $F_{1,18}$ =9.08 , p= 0.0075), but this factor was not significant in the model when *WT* and graminoid presence were included (Table 2).

Pore water CH_4 concentration

Average pore water CH_4 concentration at 30 cm depth was 1.5 to 294 µM. There was no significant difference in CH_4 concentration between planting treatments (Figure 4a, $F_{4,10}$=1.49, p=0.27). However, the presence of graminoids was related to significantly lower pore water concentration (Table 2, $F_{1,12}$=8.08, p=0.015). *WT* was also significantly related to 30 cm pore water CH_4 concentration, with deeper *WT* corresponding to lower concentration (Table 2).

Depth profiles of pore water CH_4 concentration had relatively consistent patterns across measured study plots (Figure 4b). Concentration generally increased from 30 cm, was highest at 50 cm depth across all planting treatments, with a decreasing trend to 75 cm.

Discussion

Measured CH_4 flux and pore water CH_4 concentrations in the present study were recorded only during May to September, representing spring to early autumn; this misses processes occurring throughout most of autumn and winter, but as the study focused on differences between the

PFTs, any main difference in growing season effects will be evident. While our measured values for pore water CH_4 concentration and potential CH_4 production and oxidation rates were within the range reported previously in literature for restored peatlands, CH_4 flux was on the low end of reported values. Mean CH_4 flux across the sample plots was 4.2 – 9.7 mg CH_4 m^{-2} d^{-1}, below the median rates of 23.0 and 37.1 mg CH_4 m^{-2} d^{-1} from northern bogs and fens, respectively (Olefeldt *et al*., 2013). However, the rates from the present study are similar to mean fluxes reported from restored bog fields of 0.1 to 23.4 mg CH_4 m^{-2} d^{-1} (Waddington and Day, 2007; Strack and Zuback, 2013). Although substrate limitation may play a role in the lower values from restored areas compared to natural bogs (e.g., Basiliko *et al*., 2007), low fluxes also correspond to deeper average *WT* position, as values over 300 mg CH_4 m^{-2} d^{-1} have been reported from flooded restored areas (e.g., Waddington and Day, 2007; Strack *et al*., 2014; Beyer and Höper, 2015). As reported widely in literature (e.g., Roulet and Moore, 1993; Couwenberg and Fritz, 2012; Strack *et al*., 2014) we observed a significant positive relationship between *WT* and CH_4 flux across our study plots, and relatively dry conditions in two of the three study blocks (mean seasonal *WT* of -16 and -18 cm) may have contributed to the low measured emissions.

Previous studies have reported that peat extraction reduces rates of PMP and PMO by exposing deep, highly decomposed peat layers, but that these rates recover relatively quickly following restoration (Basiliko *et al*., 2007; Waddington and Day, 2007). Our range of PMP values (0.066 – 0.20 nmol (g dry peat)$^{-1}$ hr^{-1}) and PMO (2.8-5.9 nmol (g dry peat)$^{-1}$ d^{-1}) are similar to ranges reported by Dunfield *et al*. (1993) of 0.25-0.42 nmol (g dry peat)$^{-1}$ hr^{-1} and 2.9-4.0 nmol (g dry peat)$^{-1}$ hr^{-1} for PMP and PMO, respectively across a range of undisturbed peatlands, suggesting that microbial production and oxidation recover quickly once plants are established.

Our measured pore water concentrations of 1.5 - 294 µM fall within the relatively wide range of the few studies that report CH_4 concentration from restored peatlands; reported values include 0 – 160 µM and 150 – 345 µM at restored fields and ditches (Waddington and Day, 2007) and ~0 to 750 µM at spontaneously revegetated areas of the present study site (Mahmood and Strack, 2011). Pore water CH_4 concentration at undisturbed peatlands has a similar range of values (e.g., Clymo and Pearce, 1995; Waddington and Roulet, 1997; Strack and Waddington, 2008), although local concentrations of up to 7000 µM have been reported (Chasar *et al*., 2000). Given the wide range of pore water values reported in literature, it is unsurprising that the present study falls within it, but the observation of values towards the higher end of the range at several plots provides further evidence that rates of CH_4 production recovers quickly post-restoration.

Plant controls on CH_4 production

In this study, while CH_4 emission and pore water concentration were correlated to water table position, PFT was also a significant factor for variation in rates of CH_4 production and consumption. Once anaerobic conditions are met, the quality and supply of the substrate is the major factor in CH_4 production; lower CH_4 emissions from bogs compared to fens is likely linked to lower lability of substrate in the former (Bridgham *et al*. 2013). Significantly higher PMP rates were observed in the shallower (0-10 cm) peat (Figure 2a), where fresh inputs from the planted vegetation are more likely to be located. Potential CH_4 production decreased in older peat at the 40 - 50 cm depth (Figure 2a), as at this depth labile substrates are depleted (e.g., Clymo and Bryant, 2008). This reduction in PMP with depth was reflected in pore water CH_4

concentration; although highest at 50 cm depth, CH_4 concentration declined sharply by 75 cm likely due to lack of fresh substrate.

Furthermore, the difference between PMP in surface and deeper peat was significant in the presence of graminoids and shrubs, but not when moss grew alone, highlighting the importance of vascular plant litter and root exudates as a substrate source for CH_4 production. Similarly, Robroek *et al*. (2015) report lower rates of PMP following graminoid removal considering data across both lawns and hummocks in an ombrotrophic peatland. Decomposition of graminoids and other vascular plants is relatively fast compared to other PFTs (e.g., moss; Graf and Rochefort, 2009), resulting in high CH_4 production rates (Bohdálková *et al*., 2013). This highlights the importance of plant-microbial interactions in driving the rate of PMP under various PFTs (Robroek *et al*., 2015). The higher rates of PMP associated with vascular plants observed in the present study likely contributed to the higher measured rates of CH_4 flux from plots containing graminoids and shrubs compared to plots containing moss alone and bare plots (Table 3), and the significant positive relationship between *VV* and CH_4 flux (Figure 3b).

Plant effects on CH_4 oxidation

As indicated by our laboratory incubation, PMO rates varied between plot types with the highest value at *C. aquatilis + T. nitens* mixed plots. There was no significant effect of depth, as PMO decreased with depth at some plot types and increased with depth at others. Across all plots and depths the presence of both moss and graminoids increased PMO. As the graminoid *C. aquatilis* has aerenchymous tissue (Bellisario *et al*., 1999; Joabsson *et al*., 1999; Tuitilla *et al*., 2000) it can transport oxygen to depth in peat and promote oxidation through radial oxygen loss (Bellisario *et* *al*., 1999; Joabsson *et al*., 1999). In fact, Popp *et al*. (2000) report that up to 30% of CH_4 was oxidized in a fen dominated by *C. aquatilis* and *Carex rostrata*. Oxidation in the rhizosphere may explain the significantly lower pore water CH_4 concentration observed in the presence of *C. aquatilis* (Figure 4; Table 2). In contrast, Robroek *et al.* (2015) report significantly lower PMO in the presence of graminoid and ericoid shrubs compared to plots from which they were removed, a response mediated by changes to the microbial community. The different response to the presence of vascular plants between the two studies may be due to species differences and peat quality. In the present study, substrate limitation in the residual cutover peat deposit likely limits CH_4 production in the absence of plants, resulting in little CH_4 available for methanotrophs and thus low rates of PMO unless plants are present.

The presence of both *Sphagnum* and brown moss has been shown to enhance rates of CH_4 oxidation in wetlands due to the presence of symbiotic methanotrophic bacteria living within moss cells (e.g. Larmola *et al*., 2010; Liebner *et al*., 2011). Observations of higher observed PMO from plots containing the moss *T. nitens* in the present study are consistent with these findings. In contrast, if higher rates of CH_4 oxidation in the presence of *T. nitens* were caused by methanotrophs living in association with the moss itself, we would expect a decline in PMO with depth, but observed no clear pattern. Therefore, while this study presents some evidence that the presence of moss on restored peatlands may reduce CH_4 emissions by enhancing CH_4 oxidation, further research is needed to determine the specific importance of CH_4 oxidation associated with *T. nitens* in these ecosystems.

Plant effects on CH_4 flux

Although the flux of CH_4 was consistently higher in the presence of the vascular plants *C. aquatilis* and *M. gale*, we found no significant difference in flux between planting treatments. However, variability in CH_4 flux between sample plots was high, likely due to hydrologic differences across the site, and this masked differences between PFTs. Plant functional type has been shown in many peatland studies to explain variation in CH_4 flux, generally with highest fluxes from graminoid dominated plots (*e.g*., Ward *et al*., 2013; Armstrong *et al*., 2015), leading to the suggestion that greenhouse gas fluxes could be estimated based on vegetation type (Couwenberg *et al*., 2011). Higher fluxes in the presence of graminoids have also been reported for restored peatlands (e.g., Tuittila *et al*. 2000, Bohdalkova *et al*. 2013, Wilson *et al*. 2007), though this may partially be due to the fact that graminoids often grow preferentially in wetter areas (Mahmood and Strack, 2011). We found a significant interaction of graminoid presence with *WT*; there was no significant effect of *WT* on CH_4 flux when graminoids were present. Because of this, CH_4 flux was enhanced at dry sites by the presence of the graminoid *C. aquatilis*, but may be slightly reduced at wet sites (Figure 3a). This pattern results from the combined effect *C. aquatilis* has on CH_4 production, oxidation and transport.

If PMP rates are indicators of the corresponding belowground pore water CH_4 concentration, we would expect plots with graminoids and shrubs to have the highest CH_4 concentration. Contrary to our expectations, both graminoid monoculture and polyculture (*C. aquatilis + T. nitens*) plots had the lowest CH_4 concentration at 30 cm depth. According to Strack and Waddington (2008), the pore water CH_4 stock at a particular point in the peatland will be controlled by the difference between the rate of CH_4 addition to that point via production and transfer, and the rate of CH_4 loss via oxidation, translocation or emission. Therefore, despite substrate input that resulted in high rates of CH_4 production, loss of CH_4 to oxidation and transport must reduce the residence time of CH_4 in the presence of *C. aquatilis*, limiting the size of the pore water pool. The fact that CH_4 flux remained high in these plots suggests that *C. aquatilis'* role in venting CH_4 to the atmosphere outweighs oxidation. Green and Baird (2012) also observed that the presence of graminoids was associated with lower pore water CH_4 concentration, but higher total flux.

While aerenchyma and the potential to oxygenate the root zone have been reported for the shrub *M. gale* (e.g. Cronk and Fennessey, 2001), our data did not indicate a significant reduction in the pore water CH_4 pool in the presence of *M. gale*, nor were PMO rates increased in peat from *M. gale* plots. Therefore, while it is possible that *M. gale* also enhances oxidation and transport of CH_4, its main effect on CH_4 dynamics appears to be substrate provision that increases CH_4 production, but while not significantly enhancing flux.

Conclusions

In general, both physical (temperature, water table, etc.) and biological (plant species, microbes, etc.) properties are important controls on CH_4 dynamics in peatlands, including those restored post-extraction. We investigated the specific role of plant species from different peatland functional types (PFTs), *Tomenthypnum nitens* (moss), *Carex aquatilis* (graminoid) and *Myrica gale* (shrub) on CH_4 dynamics in a restored minerotrophic peatland. Water table (*WT*) was the dominant control on spatial variability in CH_4 flux. Although flux was not significantly different between planting treatments, the presence of easily degradable vascular plants contributed to the enhanced CH_4 production. The significant interaction between the presence of graminoids and *WT* position for describing variation in CH_4 flux indicates that plant-mediated transport by graminoids contributes to higher CH_4 emission, particularly at dry plots. In contrast, significantly higher rates of potential methane oxidation and low pore water CH_4 pools at plots with graminoids indicate that this species also contributes to rhizospheric CH_4 oxidation that may help to reduce flux at inundated sites. The moss *T. nitens* may also enhance CH_4 oxidation, although more research is needed to confirm the extent of this effect.

Since CH_4 is a potent greenhouse gas, peatland restoration projects with a goal of creating a greenhouse gas sink often aim to minimize CH_4 emissions. As *WT* was an important control on flux, managers should primarily consider targeting local hydrological conditions to minimize CH_4 emissions. Mosses may help to reduce CH_4 flux by enhancing oxidation, while vascular plants provide substrate that enhances CH_4 production in the residual cutover peat. Although graminoids (*C. aquatilis* in the present study) also encourage some CH_4 oxidation below the water table, enhanced CH_4 transport will likely increase emission even at drier locations. Promoting colonization by shrubs instead of graminoids in these areas would likely reduce CH_4 flux. However, when making management decisions to reduce CH_4 flux, consideration should also be given to the effects of PFTs in CO_2 dynamics as vascular plants make important contributions to CO_2 uptake (e.g. Strack *et al*., 2014) and organic matter accumulation (Andersen *et al*., 2013) at restored sites. Moreover, successional changes following restoration should also be considered as introduced species might not persist in the restored ecosystem if hydrochemical conditions are not favourable for their establishment, or when conditions change over time as the system develops (e.g., González et al., 2014). Integrating understanding of these ecohydrological controls on peatland greenhouse gas exchange will help to improve restoration planning and management.

Acknowledgements

Funding was provided by the Industrial Research Chair in Peatland Management to LR funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) supported by the Canadian Sphagnum Peat Moss Association and its members. Dr. Martin Brummell and two anonymous reviewers provided useful comments on the manuscript. We are grateful for field assistance provided by Elena Farries, Sarah Scarlett, Magnus Keith, Marie-Eve Gauthier and Torben Russo.

References

Alm J, Shurpali NJ, Tuittila E-S, Laurila T, Maljanen M, Saarnio S, Minkkinen K (2007) Methods for determining emission factors for the use of peat and peatlands - flux measurement and modeling. Boreal Environ Res 12: 85-100.

Andersen R, Pouliot R, Rochefort L (2013) Above-ground net primary production from vascular plants shifts the balance towards organic matter accumulation in restored *Sphagnum* bogs. Wetlands 33: 811-821.

Arah JRM, Stephen KD (1998) Model of the processes leading to methane emission from peatland. Atmos Environ 32: 3257-3264.

Armstrong A, Waldron S, Ostle NJ, Richardson H, Whitaker J (2015) Biotic and abiotic factors interact to regulate northern peatland carbon cycling. Ecosystems 18: 1395-1409.

Basiliko NR, Knowles R, Moore TR (2004) Roles of moss species and habitat in methane consumption potential in a northern peatland. Wetlands 24: 178-185.

Basiliko N, Blodau C, Roehm C, Bengtson P, Moore TR (2007) Regulation of decomposition and methane dynamics across natural, commercially mined, and restored northern peatlands. Ecosystems 10: 1148-1165.

Bellisario LM, Bubier JL, Moore TR, Chanton JP (1999) Controls on CH_4 emissions from a northern peatland. Global Biogeochem Cycles 13: 81-91.

Bhullar GS, Edwards PJ, Venterink HO (2013) Variation in the plant-mediated methane transport and its importance for methane emission from intact wetland peat mesocosms. J Plant Ecol 6: 298-304.

Bhullar GS, Edwards PJ, Venterink HO (2014) Influence of different plant apecies on methane emissions from soil in a restored Swiss wetland. PLoS ONE 9: e89588, doi:10.1371/journal.pone.0089588

Bohdálková L, Curík J, Kubena AA, Buzek F (2013) Dynamics of methane fluxes from two peat bogs in the Ore Mountains, Czech Republic. Plant Soil Environ 59: 14-21.

Bridgham SD, Cadillo-Quiroz H, Keller JK, Zhuang Q (2013) Methane emission from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. Global Change Biol 19: 1325-1346.

Bubier JL (1995) The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. J Ecol 83: 403-420.

Chasar LS, Chanton JP, Glaser PH, Siegel DI (2000) Methane concentration and stable isotope distribution as evidence of rhizospheric processes: Comparison of a fen and bog in the Glacial Lake Agassiz peatland complex. Annals of Botany 86: 655-663.

Clymo RS, Bryant CL (2008) Diffusion and mass flow of dissolved carbon dioxide, methane, and dissolved organic carbon in a 7-m deep raised peat bog. Geochim Cosmochim Ac 72: 2048-2066.

Clymo RS, Pearce DME (1995) Methane and carbon dioxide production in, transport through, and efflux from a peatland, Philos T R Soc A 351: 249-259.

Cooper, M.D.A., Evans, C. D., Zielinski, P., Levy, P. E., Gray, A., Peacock, M, Norris D, Fenner N and Freeman C (2014) Infilled Ditches are Hotspots of Landscape Methane Flux Following Peatland Rewetting. Ecosystems 17: 1227–1241 DOI: 10.1007/s10021-014-9791-3.

Couwenberg J, Fritz C (2012) Towards developing IPCC methane ‘emission factors’ for peatlands (organic soils). Mires and Peat 10: 3.

Couwenberg J, Thiele A, Tanneberger F, Augustin J, Bärisch S, Dubovik D, Liashchynskaya N, Michaelis D, Minke M, Skuratovich A, Joosten H (2011) Assessing greenhouse gas emissions from peatlands using vegetation as a proxy. Hydrobiologia 674: 67-89.

Cronk JK, Fennesey MS (2001) Wetland Plants: Biology and Ecology. Lewis Publishers, Boca Raton.

Dannenberg S, Conrad R (1999) Effect of rice plants on methane production and rhizospheric metabolism in paddy soil. Biogeochemistry 45: 53-71.

Davies G, Hamilton A, Smith A, Legg C (2008) Using visual obstruction to estimate heathland fuel load and structure. Int J Wildland Fire 17: 380-389.

Dias ATC, Hoorens B, van Logtestijn RSP, Vermaat JE, Aerts R (2010) Plant species composition can be used as a proxy to predict methane emissions in peatland ecosystems after land-use change. Ecosystems 13: 526-538.

Díaz S, Hector A, Wardle DA (2009) Biodiversity in forest carbon sequestration initiatives: not just a side benefit. Current Opinion in Environmental Sustainability 1: 55-60.

Dieleman CM, Branfireun BA, McLaughlin JW, Lindo ZE (2015) Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. Global Change Biol 21: 388–395.

Dunfield PF, Knowles R, Dumont R, Moore TR (1993) Methane production and consumption in temperate and subarctice peat soils: Response to temperature and pH. Soil Biol Biochem 25: 321-326.

Fritz C, Pancotto VA, Elzeng JTM, Visser EJW, Grootjans AP, Pol A, Iturraspe R, Roelofs JGM, Smolders AJP (2011) Zero methane emission bogs: extreme rhizospheric oxygenation by cushion plants in Patagonia. New Phytologist 190: 398-408.

González, E, Rochefort L (2014) Drivers of success in 53 cutover bogs restored by a moss layer transfer technique. Ecological Engineering 68: 279-290.

González E, Rochefort L, Boudreau S, Poulin M (2014) Combining indicator species and key environmental and management factors to predict restoration success of degraded ecosystems. Ecological Indicators 46: 156-166.

Gorham E (1991) Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecol Appl, 1: 182-195.

Graf M, Rochefort L (2009) Examining the peat-accumulating potential of fen vegetation in the context of fen restoration of harvested peatlands. Écoscience 16: 158-166.

Green SM, Baird AJ (2012) A mesocosm study of the role of the sedge *Eriophorum angustifolium* in the efflux of methane – including that due to episodic ebullition – from peatlands. Plant Soil 351: 207-218.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346-363.

Joabsson A, Christensen TR, Wallen B, (1999) Vascular plant controls on methane emissions from northern peat forming wetlands. Trends Ecol Evol 14: 385–388.

Kao-Kniffin J, Freyre DS, Balser TC (2010) Methane dynamics across wetland plant species. Aquat Bot, 93: 107-113.

Ketcheson SJ, Whittington PN, Price JS (2012) The effect of peatland harvesting on snow accumulation, ablation and snow surface energy balance. Hydrol Process 26: 2592-2600.

Kivimäki SK, Yli-petäys M, Tuittila E-S (2007) Carbon sink function of sedge and *Sphagnum* patches in a restored cut-away peatland: increased functional diversity leads to higher production. J Appl Ecol 45: 921-929.

Koelbener A, Ström L, Edwards PJ, Venterink HO (2010) Plant species from mesotrophic wetlands cause relatively high methane emissions from peat soil. Plant Soil 326: 147–158.

Kuiper JJ, Mooij WM, Bragazza L, Robroek BJM (2014) Plant functional types define magnitude of drought response in peatland CO_2 exchange. Ecology 95: 123–131.

Lai DYF (2009) Methane dynamics in northern peatlands: A review. Pedosphere 19: 409-421.

Larmola T, Tuittila E-S, Tiirola M, Nykänen H, Martikainen PJ, Yrjälä K, Tuomivirta T, Fritze H (2010) The role of *Sphagnum* mosses in the methane cycling of a boreal mire. Ecology 91: 2356-2365.

Liebner S, Zeyer J, Wagner D, Schubert C, Pfeiffer E-M, Knoblauch C (2011) Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra. J Ecol 99: 914-922.

Mahmood MS, Strack M (2011) Methane dynamics of recolonized cutover minerotrophic peatland: Implications for restoration. Ecol Eng 37: 1859–1868.

Marinier M, Glatzel S, Moore T (2004) The role of cotton-grass (*Eriophorum vaginatum*) in the exchange of CO_2 and CH_4 at two restored peatlands, eastern Canada. Écoscience 11: 141-149.

McNeil P, Waddington JM (2003) Moisture controls on *Sphagnum* growth and CO_2 exchange on a cutover bog. J App Ecol 40: 354-367.

Moor H, Hylander K, Norberg J (2015) Predicting climate change effects on wetland ecosystem services using species distribution modeling and plant functional traits. Ambio 44: S113-S126.

Moore TR, Roulet NT (1993) Methane flux – water-table relations in northern wetlands. Geophys Res Lett 20: 587-590.

Olefeldt D, Turetsky MR, Crill PM, McGuire AD (2013) Environmental and physical controls on northern terrestrial methane emissions across permafrost zones. Global Change Biol 19: 589-603.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2014) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-117, URL http://CRAN.R-project.org/package=nlme.

Popp TJ, Chanton JP, Whiting GJ, Grant N (2000) Evaluation of methane oxidation in the rhizosphere of a Carex dominated fen in central Alberta, Canada. Biogeochemistry 51: 259-281.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; http://www.R-project.org/.

Riutta T, Laine J, Tuittila E-S (2007) Sensitivity of CO_2 exchange of fen ecosystem components to water level variation. Ecosystems 10: 718-733.

Robroek BJM, Jassey VEJ, Kox MAR, Berendsen RL, Mills RTE, Cecillon L, Puissant J, Meima-Franke M, Bakker PAHM, Bodelier PLE (2015) Peatland vascular plant functional types affect methane dynamics by altering microbial community structure. J Ecol 103: 925–934

Rochefort L, Quinty F, Campeau S, Johnson K, Malterer T (2003) North American approach to the restoration of *Sphagnum* dominated peatlands. Wetl Ecol Manag 11: 3-20.

Saarnio S, Silvola J (1999) Effects of increased CO_2 and N on CH_4 efflux from a boreal mire: a growth chamber experiment. Oecologia 119: 349-356.

Schimel JP (1995) Plant-transport and methane production as controls on methane flux from arctic wet meadow tundra. Biogeochemistry 28: 183-200.

Strack M, Waddington JM (2008) Spatio-temporal variability in peatland subsurface methane dynamics. J Geophys Res 113: G02010, doi:10.1029/2007JG000472.

Strack M, Zuback YCA (2013) Annual carbon balance of a peatland 10 yr following restoration. Biogeosciences 10: 2885-2896.

Strack M, Waddington JM, Tuittila E-S (2004) Effect of water table drawdown on northern peatland methane dynamics: Implications for climate change. Global Biogeochem Cycles 18: GB4003, doi:10.1029/2003GB002209.

Strack M, Waller MF, Waddington JM (2006) Sedge succession and peatland methane dynamics: A potential feedback to climate change. Ecosystems 9: 278-287.

Strack M, Keith AM, Xu B (2014) Growing season carbon dioxide and methane exchange at a restored peatland on the Western Boreal Plain. Ecol Eng 64: 231-239.

Ström L, Ekberg A, Mastepanov M, Christensen TR (2003) The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Glob Change Biol 9: 1185-1192.

Ström L, Mastepanov M, Christensen TR (2005) Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. Biogeochemistry 75: 65–82.

Tuitilla E-S, Komulainen V-M, Vasander H, Nykänen H, Martikainen PJ, Laine J (2000) Methane dynamics of a restored cut-away peatland. Glob Change Biol 6: 569–581.

Van Winden JL, Reichart G-J, McNamara NP, Benthien A, Damasté JSS (2012) Temperature-induced increase in methane release from peat bogs: a mesocosm experiment. PLoS ONE 7: e39614, doi: 10.1371/journal.pone.0039614.

Vanselow-Algan M, Schmidt SR, Greven M, Fiencke C, Kutzbach L, Pfeiffer E-M (2015) High methane emissions dominated annual greenhouse gas balances 30 years after bog rewetting. Biogeosciences 12: 4361-4371.

Waddington JM, Day SM (2007) Methane emissions from a peatland following restoration. J Geophys Res 112: G03018, doi: 10.1029/2007JG000400.

Waddington JM, Price JS (2000) Effect of peatland drainage, harvesting, and restoration on atmospheric water and carbon exchange. Phys Geogr 21: 433-451.

Waddington JM, Roulet NT (1997) Groundwater flow and dissolved carbon movement in a boreal peatland. J Hydrol 191: 122-138.

Waddington JM, Roulet NT, Swanson RV (1996) Water table control for CH_4 emission enhancement by vascular plants in boreal peatlands. J Geophys Res 101: 22775-22785.

Waddington JM, Warner KD, Kennedy GW (2002) Cutover peatlands: A persistent source of atmospheric CO_2. Global Biogeochem Cy 16: 1002, doi: 10.1029/2001GB001398.

Wang Y, Yang H, Ye C, Chen X, Xie B, Huang C, Zhang J, Xu M (2013) Effects of plant species on soil microbial processes and CH_4 emission from constructed wetlands. Environ Poll 174: 273-278.

Ward SE, Ostle NJ, Oakley S, Quirk H, Henrys PA, Bardgett RD (2013) Warming effects on greenhouse gas fluxes in a peatland are modulated by vegetation composition. Ecology Letters 16: 1285-1293.

Whiting GJ, Chanton JP (1993) Primary production control of methane emission from wetlands. Nature 364: 794-795.

Wilson D, Alm J, Laine J, Byrne KA, Farrell EP, Tuittila E-S (2007) Rewetting of cutaway peatlands: Are we re-creating hot spots of methane emissions. Restor Ecol 17: 796-806.

Table 1: Results of the linear model investigating variation in potential methane production and oxidation between planting treatments and depth

		PMP		PMO	
Source	**df**	**F**	**p**	**F**	**p**
Planting treatment	4	0.910	0.50	3.33	0.030
Depth	1	33.7	<0.0001	2.23	0.15
Planting treatment x depth	4	3.26	0.036	3.84	0.018
Intercept	1	107	<0.0001	120	<0.0001

Table 2: Significant factors in linear models describing variation in methane production, oxidation, flux and pore water concentration at 30 cm

Independent variable	Factor	F	p
Potential CH_4 production[a]	Depth	$F_{1,26} = 53.3$	<0.0001
	Intercept	$F_{1,26} = 237.5$	<0.0001
Potential CH_4 oxidation[a]	Depth	$F_{1,25} = 0.13$	0.72
	Graminoid	$F_{1,25} = 2.7$	0.12
	Moss	$F_{1,25} = 7.4$	0.012
	Depth x Graminoid	$F_{1,25} = 8.5$	0.0075
	Intercept	$F_{1,25} = 220.1$	<0.0001
CH_4 flux[b]	Water table	$F_{1,17} = 15.3$	0.0011
	Graminoid	$F_{1,17} = 0.42$	0.53
	Water table x Graminoid	$F_{1,17} = 7.8$	0.012
	Intercept	$F_{1,17} = 101.7$	<0.0001
Pore water CH_4 concentration (30 cm depth)	Water table	$F_{1,12} = 12.3$	0.0043
	Graminoid	$F_{1,12} = 8.1$	0.015
	Intercept	$F_{1,12} = 43.4$	<0.0001

a. results from a general linear model. Full model included depth (categorical), presence of graminoid (*C. aquatilis*), moss (*T. nitens*) and shrub (*M. gale*), and interaction of presence of each with depth. Factors were removed from the model sequentially starting with the least significant. Individual factors were retained in the model if their interaction was significant

b. results of a linear mixed effects model with plot as a random factor. Seasonal mean values were used. Full model included water table, maximum vegetation volume, presence of graminoid (*C. aquatilis*), moss (*T. nitens*) and shrub (*M. gale*) and interaction of each species with water table and volume. Final model chosen as described in (a).

c. results from a general linear model considering seasonal mean pore water concentration. Full model included water table, maximum vegetation volume, presence of graminoid (*C. aquatilis*), moss (*T. nitens*) and shrub (*M. gale*) and interaction of each species with water table and volume. Final model chosen as described in (a).

Table 3: Water table position, vegetation volume and methane flux[a]

Planting treatment	Year	Water table (cm)	Vegetation volume	CH_4 flux ($mg\ CH_4\ m^{-2}\ d^{-1}$)
Graminoid	2011	-10.6 (8.0)	21.4 (16.7)	4.3 (6.1)
(*C. aquatilis*)	2012	-18.3 (8.8)	33.4 (16.1)	13.8 (3.0)
Gram. + moss	2011	-9.7 (7.7)	33.3 (10.4)	6.1 (4.1)
(*C. aquatilis + T. nitens*)	2012	-16.9 (9.2)	43.1 (2.5)	13.8 (0.7)
Shrub	2011	-6.1 (8.3)	20.6 (7.0)	9.0 (12.2)
(*M. gale*)	2012	-12.3 (11.7)	12.2 (1.7)	14.3 (25.3)
Shrub + moss	2011	-9.7 (9.8)	19.6 (7.2)	-1.3 (3.0)
(*M. gale +T. nitens*)	2012	-15.5 (10.9)	16.8 (10.0)	5.0 (7.7)
Moss	2011	-7.9 (8.5)	1.8 (1.1)	2.7 (7.4)
(*T. nitens)*	2012	-16.0 (9.9)	1.8 (1.1)	1.7 (5.3)
Bare	2011	-11.3 (5.9)	0	0.63 (2.6)
	2012	-18.8 (3.6)	0	0.36 (2.7)

a. values for water table and CH_4 flux are the mean (standard deviation) of the seasonal mean at each plot, while vegetation volume is the mean (standard deviation) of the maximum vegetation volume as estimated by the Gaussian curve (Equation 1) fit to the field measured data.

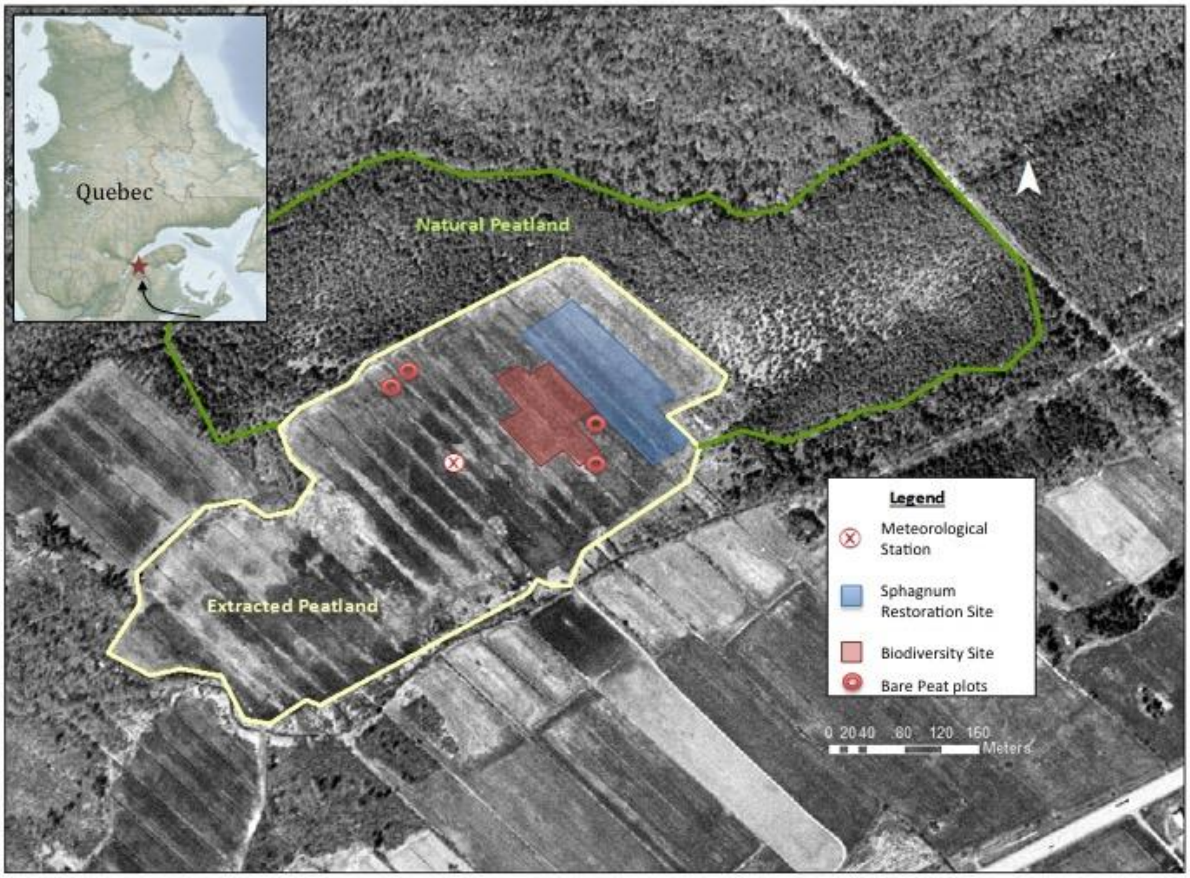

Figure 1. Aerial view of the Bic Saint-Fabien peatland, showing the disturbed and natural peatlands. Aside from bare plots for flux measurement, the study was conducted in the section restored with biodiversity plantings, one replicate in each of the adjacent peat fields.

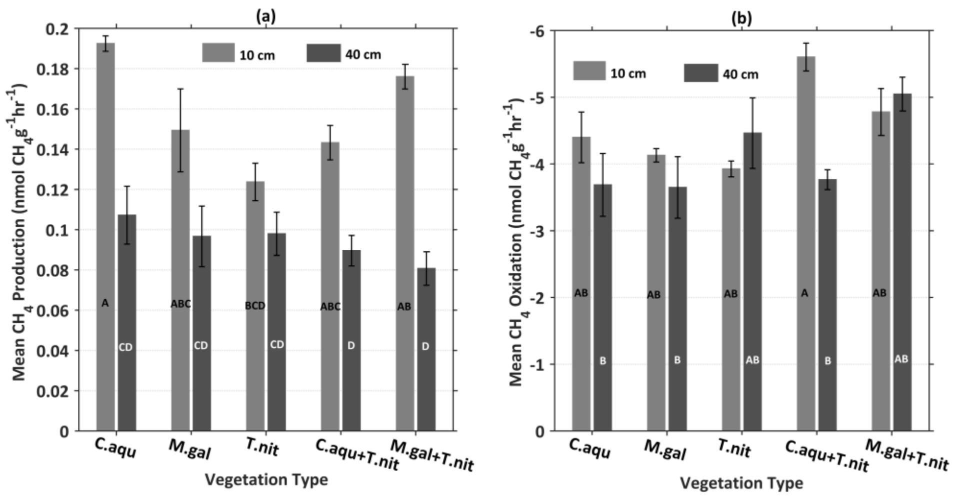

Figure 2. Potential CH_4 (a) production under anoxic conditions and (b) oxidation under oxic conditions, at two depths 0-10 cm and 40-50 cm across five planting treatments. Bars that do not share a letter are significantly different (p-value <0.05). Error bars represent standard error between triplicate cores. C. aqu = sedge, *Carex aquatilis*; M. gal = shrub, *Myrica gale*; T. nit = moss, *Tomenthypnum nitens*.

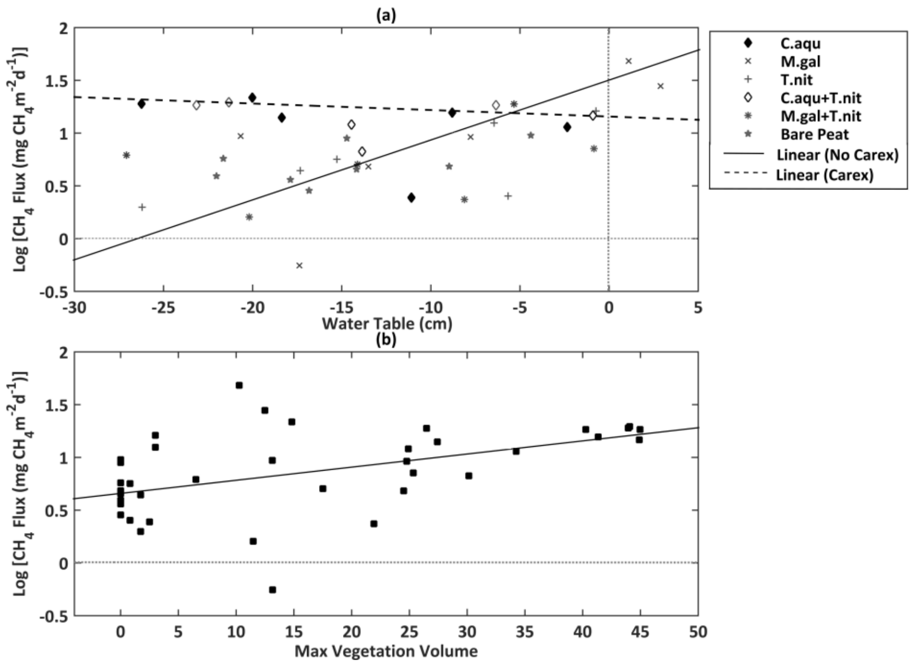

Figure 3. (a) Seasonal mean CH_4 flux vs. *WT* with and without the sedge *Carex aquatilis*. (b) Seasonal mean CH_4 flux vs. maximum vegetation volume. C. aqu = sedge, *Carex aquatilis*, M. gal = shrub, *Myrica gale*, T. nit = moss, *Tomenthypnum nitens*.

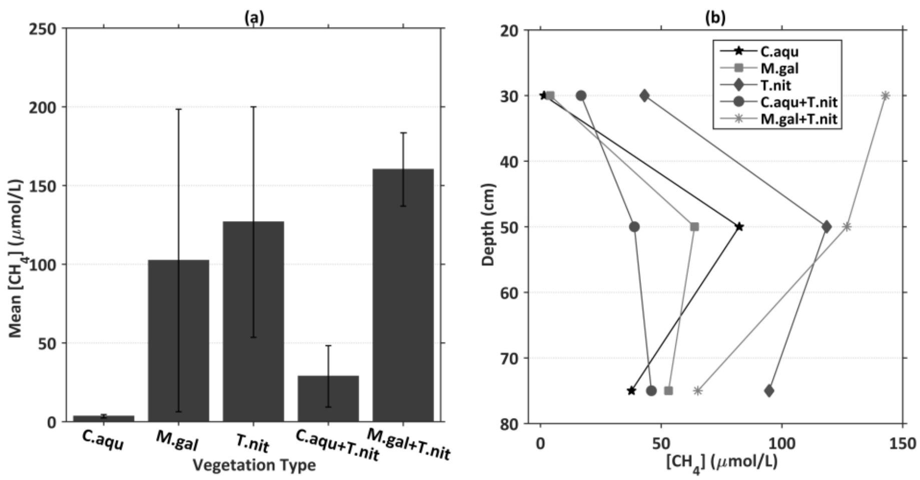

Figure 4. (a) Average seasonal pore water CH_4 concentration at 30 cm depth monitored in the growing season of 2012. The bars represent seasonal averages obtained by taking mean of the mean of triplicate sampling plots. Error bars represent standard error of the concentration from the triplicates. (b) Pore water CH_4 concentration from the intermediate wetness block at 30, 50 and 75 cm depth monitored in the growing season of 2012. The values represent seasonal averages at each respective depth. Error bars are omitted for clarity. C. aqu = sedge, *Carex aquatilis*, M. gal = shrub, *Myrica gale*, T. nit = moss, *Tomenthypnum nitens*.