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Methane dynamics of recolonized cutover minerotrophic peatland: Implications for restoration

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ABSTRACT

In North America, mulching of vacuum-harvested sites combined with blocking of the drainage system is widely used for peatland restoration to accelerate Sphagnum establishment. However, peat extraction in fen peatlands or exposure of deeper minerotrophic peat layers results in soil chemistry that is less suitable for re-establishment of Sphagnum moss. In this situation, restoration of plant species characteristic of minerotrophic peatlands is desirable to return the site to a carbon accumulating system. In these cases, it may be worthwhile to maintain spontaneously revegetating species as part of restoration if they provide desirable ecosystem functions. We studied the role of six spontaneously recolonizing vegetation communities for methane (CH₄) emissions and pore water CH₄ concentration for two growing seasons (2008 and 2009) at an abandoned minerotrophic peatland in southeastern Quebec. We then compared the results with bare peat and adjacent natural fen vegetation. Communities dominated by Eriophorum vaginatum, Carex aquatilis and Typha latifolia had CH4 flux an order of magnitude greater than other cutover vegetation types and natural sites. In contrast, Scirpus atrocinctus and Equisetum arvense had CH4 emission rates lower than natural hollow vegetation. We found seasonal average water table and vegetation volume had significant correlation with CH₄ flux. Water table and soil temperature were significantly correlated with CH₄ flux at plots where the water table was near or above the surface. Pore water CH₄ concentration suggests that CH₄ is being produced at the cutover peatland and that low measured fluxes likely result from substantial oxidation of CH₄ in the unsaturated zone. Understanding ecosystem functions of spontaneously recolonizing species on cutover fens can be used to help make decisions about the inclusion of these communities for future restoration measures.

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1. Introduction

Peatlands can be found all over the world, covering 5–8% of the world's land and freshwater surface (IPCC, 2000). Peatlands play important roles in the global cycling of carbon (C) as they are net sinks of atmospheric carbon dioxide (CO₂) and a large source of atmospheric methane (CH₄) (Baird et al., 2009). In Canada, ~24 000 ha of peatlands have been drained for peat extraction activities for horticultural use with 14 000 ha currently in production (Environment Canada, 2010). The impact of horticultural peat extraction on the peatland ecosystem is severe as it involves changes to the hydrological conditions (Van Seters and Price, 2001), complete removal of vegetation (Rochefort et al., 2003) and extraction of a thick layer of soil usually occurring over a period of several decades (Waddington and Price, 2000). After cessation of peat extraction, the remaining cutover surfaces are net sources of C to the atmosphere as the residual peat gradually decomposes (Tuittila et al., 1999; Waddington et al., 2002).

The restoration of abandoned cutover peatlands has recently been encouraged as a land-use management practice especially to reduce C emissions (Kivimäki et al., 2008; Yli-Petäys et al., 2007; Waddington et al., 2010). In North America, peatland restoration has focused on bogs, whose water supply comes solely from precipitation, as opposed to fens (minerotrophic peatlands) where water supply consists of ground/surface water and precipitation (Charman, 2002). The North American approach to bog restoration involves introduction of diaspores and mulching of harvested sites with blocking the drainage to accelerate Sphagnum establishment (Rochefort et al., 2003). However, in fens, establishment of Sphagnum may not be the goal due to hydrochemical conditions (Wind-Mulder and Vitt, 2000). The European fen restoration technique is likely not appropriate for North American fen restoration, as the goals, desired end-states and use of peatlands are different (Graf and Rochefort, 2008). In Europe many peatland areas are used for intensive agriculture while in North America most peatland management is related to horticultural peat extraction (Graf





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Fig. 1. The Bic-St. Fabien peatland study site. The cutover site is surrounded by natural minerotrophic peatlands to the northeast (beyond the dotted line), but here it only shows the portion of the natural fen where study collars are located.

and Rochefort, 2008). The desired end-states following restoration are semi-natural fen state or extensive agriculture, and natural fen state, in Europe and North America, respectively (Graf and Rochefort, 2008). Thus, the main goal of European fen restoration is associated with high plant diversity and successful reintroduction of rare species (Graf and Rochefort, 2008 and references therein), whereas in North America the focus is on the return of the peatland's ecosystem functions such as peat accumulation, vegetation structure, nutrient cycling, diplotelmic hydrological layer and C sink function (Rochefort, 2000).

Establishment of vascular vegetation following extraction is also generally more extensive on cutover fens than that observed on cutover bogs (Graf et al., 2008). The presence of vascular plants might be important, as it has been found that the growth of *Sphagnum* (Tuittila et al., 2000b) and brown mosses (Graf and Rochefort, 2008) is dependent on the presence of these plant species at the early stage of restoration. Restoration of cutover fens has been limited, due to lack of knowledge regarding target vegetation communities for re-establishment, and the impacts of revegetated species on the C flux rate. Spontaneously recolonizing species resulting from natural succession could play an important role in ecosystem recovery if they have the potential to act as C sink, as they are more stable and cost less than active, imposed restoration strategies (Bradshaw, 2000; Prach et al., 2001).

CH₄ is a greenhouse gas with 25 times the global warming potential of CO_2 on a 100-year time scale (IPCC, 2007). CH₄ concentrations have been increasing by 7.0 parts per billion (ppb) per year from pre-industrial revolution concentrations (IPCC, 2007). Anthropogenic sources of CH₄ account for 60% of methane emissions while natural sources produce the rest (IPCC, 2007). Among the anthropogenic and natural sources, wetlands encompass the largest single source of CH₄ to the atmosphere (IPCC, 2007). Vegetation influences CH₄ fluxes by supplying substrate for methanogenesis and through plant-mediated transport of CH₄ from the soil to the atmosphere. The presence of vascular vegetation in peatlands has been found to increase CH₄ emissions (Shannon and White, 1994; Shannon et al., 1996; Waddington et al., 1996). Many studies have observed significant relationships between plant productivity or C assimilation and CH₄ flux (Joabsson and Christensen, 2001; King et al., 2002; Whiting and Chanton, 1993; Whiting et al., 1991). Van den Pol-Van Dasselaar

et al. (1999) found that plant residues in the peat surface (from 0 to 5 cm depth) contributed up to 70% of the total CH₄ production capacity of the peat, indicating that plants are crucial to the formation of substrate for methanogenesis. The plant species composition of a wetland also affects the CH₄ fluxes through the amount of CH₄ transportation and the substrate production (Shannon et al., 1996). Given the importance of CH₄ to peatland greenhouse gas budgets and the strong link between vascular vegetation and CH₄ fluxes, it is critical to better understand the role of spontaneously recolonizing vascular species in cutover fen CH₄ dynamics to inform decisions about the inclusion of these species in restoration efforts.

The overall objective of our research is to identify suitable recolonizing fen species for minerotrophic peatland restoration. In this study we investigate the CH_4 flux and pore water CH_4 pool of spontaneously recolonizing species of a cutover fen. Our specific objectives are to: (1) determine the effect of extraction and recolonization on CH_4 flux and (2) investigate relationships between CH_4 flux and temperature, water table and vegetation biomass.

2. Methods

2.1. Study site

The study was conducted in the Bic Saint-Fabien (BSF) peatland (48°18'N, 68°52'W), which is located approximately 25 km west of Rimouski, Quebec, Canada (Fig. 1). The undisturbed part of the peatland, a moderately rich fen with an average peat depth of 4.5 m, is dominated by Eastern White Cedar (Thuja occidentalis) in the forested part, with the lower moss layer dominated by brown mosses including Campylium stellatum, Drepanocladus spp., and Tomenthypnum nitens. In the specific area of the fen investigated, hummocks are dominated by Sphagnum fuscum and cover less than 50% of the ground surface. Shrubs are also found on hummocks and include species such as Chamaedaphne calyculata, Kalmia angustifolia, and Ledum groenlandicum. Sedges, such as Trichophorum cespitosum, Tricophorum alpinum, Carex interior, Carex prairea and small herbs, including, Valerianna uliginosa, Menyanthes trifoliata, Sanguisorba canadensis, Parnassia glauca and Tofieldia glutinosa, dominated on the hollows. Some hollow areas also had substantial shrub cover consisting of mainly Myrica gale.

The extracted portion of the peatland has been mined for horticultural peat since 1946, with the vacuum extraction technique employed since 1970. Most of the site has been abandoned during the last few decades, and spontaneous recolonization has occurred in some sections. The present harvested portion of BSF is about 22 ha. The south-west one-third of the harvested site has been naturally revegetated by marsh-like vegetation with ruderal species. The remaining two-third has had limited recovery of vegetation, resulting in large regions of bare peat, interspersed with vegetation patches, consisting of a limited number of vascular species. This section will be the focus of large-scale restoration efforts and will be referred to as the cutover site in this study. Overall, on the cutover site, moss cover is very low (<1%). Dominant species in the cutover site are Scirpus atrocinctus, Scirpus cyperinus, Equisetum arvense, Calamagrostis canadensis, Eriophorum vaginatum, Salix spp., Eupatorium maculatum, Spiraea latifolia, Hypericum virginicum, Carex aquatilis and in ditches Typha latifolia.

2.2. CH₄ flux measurement

The study was conducted during two growing seasons in 2008 (June-August) and 2009 (May-August). The samples were collected 4-8 times for recolonizing and natural vegetation but only one time for bare peats in 2008 and 13 times for vegetation and 12 times for bare peats in 2009. Following a preliminary survey of vegetation communities at the cutover peatland at BSF in 2008, five recolonizing communities, primarily consisting of one dominant species, were chosen for study. These are: S. atrocinctus (Sci_atr), E. arvense (Equ_arv), C. canadensis (Cal_can), E. vaginatum (Eri_vag), and C. aquatilis (Car_aqu). T. latifolia (Typ_lat) was added in 2009 as it was observed to dominate in ditches which continue to cover a large area at the cutover site. Triplicate plots were established in each vegetation type. Four plots were established on bare peat (P) at the cutover site and studied in both seasons. Six plots were also studied in the natural (N) fen adjacent to the cutover site and arranged to be representative of the hydrologic gradient at the site with three plots on low-lying hollows (Nhol) and three plots at higher, drier hummocks (Nhum). Three more plots were added in 2009 to study the shrub vegetation (Nshrub) common in some hollows at the natural site.

To determine CH₄ flux the closed chamber method was used (Alm et al., 2007). A permanent 60 cm \times 60 cm or a round (diameter = 30 cm) collar with a groove for water sealing was installed in the peat. The smaller round collars were used only for bare peat sites. The sleeve of the collar extended 20 cm in soil, which is usually below the rooting zone (Laiho and Finér, 1996). For CH₄ gas sampling an opaque steel chamber (60 cm \times 60 cm \times 30 cm) was placed upon the collar and sealed by adding water in the groove. For measuring the bare peat CH₄ flux, a round chamber (12.7 cm³) was used. Since fluxes from bare cutover peat are generally very low (Waddington and Day, 2007) the small volume of these chambers allowed for better detection of small changes in CH₄ concentration in the headspace. All the chambers were equipped with a battery-operated fan to mix the chamber headspace air.

Four 20 mL gas samples were collected from the chamber headspace with three-way stopcock syringes at 7, 15, 25, and 35 min after chamber closure. The samples were then transferred to evacuated Exetainers (Labco Ltd., UK). Samples were sent back to the Department of Geography, University of Calgary, for analysis. Air temperature inside the chamber was also measured at the same time the gas samples were collected using a thermocouple thermometer (VWR Int., USA). Two ambient air samples were collected for each day of flux measurement to use as the CH₄ concentration at the beginning of sample collection (i.e. 0 min). The gas samples were analyzed for CH₄ concentration using a Varian Gas Chromatograph 3800 (GC) with flame ionization detector. To calibrate for any potential instrumental errors, known standards were measured at the beginning and end of an eight-sample analysis pattern. The flux was calculated as the linear change in CH_4 concentration in the headspace over time.

At the time of each flux measurement, environmental variables were also measured. Water table was measured in a well adjacent to each collar constructed from 2.5 cm inner diameter (i.d.) plastic pipe. At depths of 2, 5, 10, 15, 20, 25, and 30 cm soil temperatures (°C) were measured close to the collar using thermocouple thermometers.

2.3. Pore water CH₄ concentration

Pore water CH₄ samples were collected weekly in 2009 from May to August. Pore water depth profiles were collected from 50 cm. 75 cm and 125 cm depth for each vegetation type and bare peat except for Equ_arv and Nshrub. All other collars except Nshrub had samplers installed at 50 cm depth. Pore water was collected using samplers, consisting of a 20 cm length of 2.5 cm i.d. plastic pipe slotted at the middle 10 cm, covered in Nitex screening to prevent clogging, and sealed at both ends with stoppers (see Strack et al., 2004). The stopper at one end contained a central hole through which a sampling tube had been fitted. At the other end of the tubing a three-way valve was inserted and sealed with household adhesive. Samplers were inserted vertically to the appropriate depth in the peat in the middle of May, with the sampling tube extending from the top end of the sampler to the peatland surface to allow water collection. Samplers were then left in place throughout the study. The entire sampler was filled with water and the valve closed between sampling dates to prevent air from travelling to the sampling depth.

To collect a pore water sample, 60 mL of water was removed from the sampler to flush it and then a sample of 5–20 mL was collected by connecting a sampling syringe. After that 20 mL of ambient air was added with the sample and shaken for ~5 min to allow equilibration of dissolved gases into the headspace in the syringe. The air sample was then transferred in a pre-evacuated Exetainer (Labco Ltd., UK). Both the time of water sample collection and equilibration was noted to find the equilibration temperature from meteorological data. Samples were returned to the laboratory and analyzed for CH₄ concentration on the Varian GC.

2.4. Vegetation measurement

A visual obstruction method developed by Davies et al. (2008), known as the 'Fuel Rule', was used to estimate volume of vegetation (a calculated index) in CH₄ flux sampling collars. A statistically significant relationship was found between vegetation volume determined with this method and destructively harvested biomass for the BSF peatland (Strack and Srivastava, 2010). Briefly, the Fuel Rule is a 2 m stick that is 2.5 cm wide and painted with alternating red and white bands. One side of the stick has bands of 10 cm length, whereas the other side has two scales of 2 and 5 cm lengths starting at opposite ends and each running half its length. Each set of bands was labelled with numbers or letters (see Davies et al., 2008 for detail). In order to take a reading, the stick was placed vertically into a stand of vegetation in the middle of the $60 \text{ cm} \times 60 \text{ cm}$ flux collar. The Fuel Rule was then aligned vertically allowing the vegetation to partially or fully cover at least five bands. Thus, an appropriate scale was chosen for each plot based on the height of the vegetation. Holding the Fuel Rule at arm's length with the obscured bands at eye level, the percentage obscured by the vegetation was estimated. Visual estimation of the ground surface was conducted by looking downward in the collar and recording the

Plot type	Water table (cm) Mean (SD)		Soil temp. – 5 cm (°C) Mean (SD)		Soil temp. – 30 cm (°C) Mean (SD)		Vegetation volume Mean (SD)	
	2008	2009	2008	2009	2008	2009	2009	
Car_aqu	-0.8 (1.8)	6.9 (2.8)	17.8 (1.5)	16.8 (3.2)	15.7 (2.5)	14.0 (2.9)	27.09 (11.24)	
Cal_can	-31.9 (21.0)	-21.1 (14.0)	19.8 (2.3)	17.9 (4.1)	16.8 (2.4)	15.0 (3.5)	11.36 (7.60)	
Equ_arv	-23.1 (10.4)	-18.6 (11.3)	19.6 (2.5)	17.9 (4.2)	16.2 (2.8)	13.6 (5.1)	8.44 (6.44)	
Typ_lat	n.m. ^a	1.3 (8.4)	n.m.	17.6 (4.4)	n.m.	14.0 (3.4)	25.88 (11.91)	
Sci_atr	-32.5 (20.7)	-17.9 (15.4)	17.7 (1.7)	17.7 (3.3)	15.5 (1.9)	13.9 (3.4)	27.09 (12.58)	
Eri_vag	-28.7 (13.9)	-20.4 (12.6)	19.6 (1.8)	16.2 (4.4)	15.7 (2.7)	12.8 (5.2)	17.65 (4.44)	
Р	-54.2 (4.8)	-25.4 (16.3)	18.6 (1.0)	19.7 (4.1)	15.1 (0.3)	14.5 (4.1)	0	
Nhum	-23.0 (22.4)	-29.2 (10.7)	18.2 (2.0)	18.6 (4.9)	15.5 (2.6)	15.8 (4.1)	4.04 (2.77)	
Nhol	-6.8 (6.7)	-6.9 (4.0)	18.7 (2.0)	19.3 (4.8)	16.1 (2.9)	15.8 (4.0)	6.95 (4.47)	
Nshrub	n.m.	-6.7 (4.4)	n.m.	18.9 (5.32)	n.m.	15.7 (4.1)	12.41 (5.24)	

^a n.m. – not measured.

percentage of vascular vegetation and mosses. The Fuel Rule data were analyzed in the computer program *PObscured* to determine volume as described by Davies et al. (2008). All vegetation collars were measured using Fuel Rule every two weeks throughout the field season from May to August 2009.

Mean water table, soil temperature (5 and 30 cm depth), and vegetation volume of study plots in 2008 and 2009.

2.5. Data analysis

Statistical analysis was conducted using Minitab 14.1. Data for CH₄ flux and pore water concentration were found to be not normally distributed; thus the non-parametric Mood's median test was used for analysis of variance between vegetation types. Pearson correlation, linear regression and multiple regressions were used to investigate the relationship between environmental variables and CH₄ flux. In all cases α of 0.05 was used to determine statistical significance.

3. Results

3.1. Plot characteristics

The highest seasonal mean (±standard deviation) vegetation volume was observed for Car_aqu (27.09 ± 11.24) and Sci_atr (27.09 ± 12.58) and lowest in Nhum (4.04 ± 2.77) at the study site (Table 1). The seasonal mean vegetation volume varied from 8.44 ± 6.44 (Equ_arv) to $27.09 \pm 11.24/12.58$ (Car_aqu/Sci_atr) for recolonizing vegetation. Within natural vegetation types mean values were between 4.04 ± 2.77 for Nhum and 12.41 ± 5.24 for Nshrub.

The mean water table varied from -23.04 ± 22.41 cm for Nhum to -6.82 ± 6.69 cm for Nhol in 2008 at the natural site, where negative values indicate water table below the surface. On the cutover site in 2008 the lowest mean water table was measured at the P sites (-54.18 ± 4.83 cm) and the highest water table was measured at Car_aqu (-0.78 ± 1.77 cm). In 2009 lowest mean water table of -25.39 ± 16.26 cm was measured at the P sites and the highest mean of 6.9 ± 2.85 cm at Car_aqu plots on the cutover site. Natural site water table in 2009 was -29.20 ± 10.68 cm, -6.91 ± 3.99 cm and -6.68 ± 4.37 at Nhum, Nhol and Nshrub respectively (Table 1).

The mean soil temperature did not vary much between vegetation types in either year of the study. The highest mean temperature at 5 cm depth was 19.8 ± 2.27 °C at Cal_can and the lowest was 17.7 ± 1.69 °C at Sci_atr and at 30 cm depth temperature ranged from 15.1 ± 0.26 °C at P to 16.8 ± 2.37 °C at Cal_can in 2008. Mean temperatures were slightly cooler in 2009 varying between 19.7 ± 4.06 °C at P and 16.8 ± 3.20 °C at Car_aqu at 5 cm depth; and 15.8 ± 4.00 °C at Nhol and 12.8 ± 5.15 °C at Sci_atr at 30 cm depth.

3.2. CH₄ flux

The CH₄ flux varied between vegetation types in both years of study (Table 2). Seasonal mean (±standard deviation) CH₄ flux ranged from $7.72 \pm 10.31 \,\mu$ mol m⁻² day⁻¹ to $7423.83 \pm 2226 \,\mu$ mol m⁻² day⁻¹ and $6.80 \pm 20.30 \,\mu$ mol m⁻² day⁻¹ to $14,497.40 \pm 6143 \,\mu$ mol m⁻² day⁻¹ in 2008 and 2009, respectively. Among the recolonizing and natural fen communities the median flux was significantly higher at Car_aqu and Eri_vag than all other vegetation types in 2008 (Fig. 2; Mood's median, Chi-square = 33.51; DF = 7; p = 0.00). There was no statistically significant difference among the remaining recolonizing and natural plot types. In 2009 the CH₄ flux for Typ_lat was significantly higher than other species (Fig. 2; Mood's median, Chi-Square = 130.52; DF = 9; p = 0.00). It is important to note that in 2009 the flux of



Fig. 2. Median growing season CH₄ flux in 2009 and 2008. Error bars give interquartile range. Plot types are significantly different from each other if no letters are in common.

Mean, median and standard deviation (SD) for CH ₄ flux in 2008 and 2009 for recolonized, natural vegetation and bare peat plots in μ mol m ⁻² day ⁻¹ .								
Plot type	2008			2009				
	Mean	Median	SD	Mean	Median	SD		
Car_aqu	7423.8	6428.0	2226.9	3507.4	3384.0	874.1		
Cal_can	383.9	303.3	106.3	621.8	551.0	369.6		
Equ_arv	238.0	218.0	120.4	897.0	470.0	752.1		
Typ_lat	n.m.ª	n.m	n.m.	14,497.4	9461.0	6143.6		
Sci_atr	359.2	188.0	194.4	1014.2	659.0	116.0		
Eri_vag	2202.6	2403.0	270.8	2051.9	1786.0	356.4		
Р	7.72	8.58	10.3	6.80	1.11	20.3		
Nhum	132.7	68.7	76.9	203.1	114.9	109.5		
Nhol	478.8	385.0	70.8	978 9	726.0	291 5		

n.m.

Table 2 Mean, median and standard deviation (SD) for CH₄ flux in 2008 and 2009 for recolonized, natural vegetation and bare peat plots in u.mol m⁻² dav

^a n.m. – not measured.

Nshrub

Car_aqu was almost half that of the previous year despite the fact that other species showed a slight rise in flux.

n.m.

n.m.

The temporal variation of CH_4 flux in 2008 shows that the CH_4 flux increases throughout the growing season until July and then declines in August for most of the species except for Equ_arv and Nhum (Fig. 3a and b). Hummocks (Nhum) showed a reverse pattern with a decline in flux during the growing season and increase at the end of the season, while Equ_arv has a continuous decline. Given the relatively small CH_4 fluxes at both these vegetation communities, there was actually little change in flux over the season. In 2009, a similar pattern appears with increases throughout the growing season until July, descending in August (Fig. 3c and d) except for Typ_lat, where fluxes continuously increased.

3.3. Pore water CH₄

Pore water samples were only collected in 2009. The pore water CH₄ concentration at 50 cm varied significantly between plot types

(Fig. 3; Mood's median, Chi-square = 69.0; DF = 8; p = 0.00) with the highest values at P and lowest at Sci_atr. Among the vegetated plots the mean value ranged from $23.85 \pm 23.16 \,\mu$ M for Sci_atr to $569.25 \pm 364.61 \,\mu$ M at Nhol. Natural vegetation communities had higher pore water CH₄ concentrations at 50 cm depth than all recolonizing vegetation types at the cutover site except for Eri_vag which was similar to Nhum (Fig. 4). Other than significantly higher concentration at Eri_vag, all recolonizing vegetation at the cutover site had similar pore water CH₄ concentration. There was no significant correlation between pore water CH₄ concentration at 50 cm depth and CH₄ flux (Pearson correlation -0.265, p = 0.221).

339.5

425.0

Both increasing and decreasing trends were found in depth profiles of pore water CH₄ between 50 and 125 cm below the surface (Fig. 5). The concentration of pore water CH₄ increased with depth for Sci_atr, Typ_lat and Nhum. For P the concentration decreased sharply with depth. Both Cal_can and Nhol had a sharp decrease from 50 to 75 cm, below which there was almost no change with depth.



Fig. 3. Monthly mean CH₄ flux for (a) recolonizing communities in 2008, (b) natural communities in 2008, (c) recolonizing communities in 2009, and (d) natural communities in 2009. Error bars are omitted for clarity, but standard deviation of monthly means is similar to the whole growing season deviations given in Table 2. Note the different scale on plot (c) due to high fluxes at Typ_lat.

318.7



Fig. 4. Median pore water CH_4 concentration at 50 cm depth in 2009. Error bars give interquartile range. Plot types are significantly different from each other if no letters are in common.

Table 3

Pearson correlation between mean monthly water table and CH_4 flux in 2008 and 2009.

Plot type	Water table 08	p-Value	Water table 09	p-Value
Car_aqu	-0.154	0.692	0.269	0.108
Cal_can	0.462	0.053	0.223	0.178
Equ_arv	0.351	0.140	0.247	0.159
Typ_lat	n.m. ^a	n.m.	0.377	0.037
Sci_atr	-0.360	0.187	0.160	0.329
Eri_vag	0.291	0.258	0.079	0.633
Р	n.d. ^b	n.d.	- 0.298	0.040
Nhum	0.143	0.526	-0.201	0.209
Nhol	0.300	0.186	0.313	0.046
Nshrub	n.m.	n.m.	0.247	0.119

Bold type indicates a significant result p < 0.05.

^a n.m. – not measured.

^b n.d. – not determined.

3.4. Potential controls on CH₄ flux

When we included values from all individual flux measurements we found significant correlations (Pearson correlation, p < 0.05) between water table and CH₄ flux at Cal_can in 2008 and Typ_lat, Nhol, and P in 2009 where the latter was negatively correlated (Table 3). Treat et al. (2007) found stronger correlations between CH₄ flux and environmental variables using monthly means, compared to daily flux measurements, so we chose to investigate further correlations using monthly mean values. In our study we found significant correlation between monthly mean water table and CH₄ flux for only Car_aqu (Pearson correlation 0.602, p < 0.05) and Nhol (Pearson Correlation 0.609, p < 0.05) in 2009. The linear regression between monthly mean water table and CH₄ flux also found the water table effect on Car_aqu ($R^2 = 0.362$; p < 0.05), and Nhol ($R^2 = 0.370$; p < 0.05) in 2009 (Table 4). However, we did not find any water table effect for individual vegetation types in 2008. We found a significant relationship between seasonal mean CH₄ flux and water table across the entire site using the mean value of each individual plot in 2008 ($R^2 = 0.322$; p < 0.05) and 2009 ($R^2 = 0.265$; p < 0.05). When we excluded Typ_lat in our 2009 analysis, water table explained slightly more of the variability ($R^2 = 0.344$; p < 0.05) (Fig. 6a).

In 2008, soil temperature was only correlated to CH₄ flux at Eri_vag where all depths from 10 cm to 30 cm had a significant correlation (p < 0.05). In 2009, Typ_lat, Sci_atr, and Eri_vag showed significant correlation (p < 0.05) between soil temperature at every depth (2–30 cm) and CH₄ flux. However, for Car_aqu we found this correlation only from 10 cm to 30 cm depth for 2009. Overall, correlations between soil temperature and CH₄ flux became stronger with depth of temperature measurement. No significant correlations were found between air temperature and CH₄ flux in 2008, but Eri_vag and all natural vegetation (i.e. Nhum, Nhol, and Nshrub) showed significant correlation (p < 0.05) in 2009.

For the whole site we found a strong correlation between CH_4 flux and vegetation volume across at vegetated collars (Pearson correlation 0.706, p < 0.01). This relation is also confirmed by the linear regression of monthly mean vegetation volume and CH_4 flux ($R^2 = 0.498$; p < 0.01). When we tested this for individual vegetation types we found significant regressions between vegetation volume and CH_4 flux for Car_aqu, Typ_lat, Eri_vag, and Nhol (Table 4). We also found significant relationship across the study site using seasonal mean CH_4 flux and vegetation volume ($R^2 = 0.232$; p < 0.05). Vegetation volume explained more of the variability in CH_4 flux between plots ($R^2 = 0.363$; p < 0.01) when we excluded Typ_lat from our analysis (Fig. 6b). No significant relationship was observed between the mean vegetation volume and pore water CH_4 concentration at 50 cm depth.

A significant multiple regression using monthly mean with water table and vegetation volume effects on CH_4 flux was observed for Car_aqu and Typ_lat; however, the main control on CH_4 flux in these cases appears to be vegetation as the inclusion of water table explains little more variability in CH_4 flux than volume alone (Table 4). In contrast, a significant multiple regression was found for Nhol explaining 67.7% of variability in CH_4 flux, while WT and vegetation volume alone explained only 37 and 40.1%, respectively (Table 4). However, when we ran multiple regression using seasonal mean value of CH_4 flux, water table and vegetation volume of individual plot, we found significant multiple regression across



Fig. 5. Depth profile of pore water CH₄ concentration at recolonizing communities, bare peat and natural vegetation in 2009. Error bars are omitted for clarity, but standard deviations are similar to those in Fig. 4.

Table 4
Single and multiple regressions between monthly mean of CH4 flux, water table and vegetation volume in 2009.

Plot type	Water table			Volume			Water table and vegetation		
	R^{2} (%)	F	р	R^{2} (%)	F	р	R^{2} (%)	F	р
Car_aqu	36.2	5.67	0.039	67.4	20.71	0.001	67.8	9.46	0.006
Cal_can	17.1	2.06	0.182	0.00	0.00	0.992	17.1	0.93	0.430
Equ_arv	10.5	1.17	0.305	30.8	4.44	0.061	34.9	2.41	0.145
Typ_lat	6.3	0.67	0.431	48.3	9.33	0.012	48.4	4.23	0.051
Sci_atr	8.5	0.93	0.357	20.9	2.64	0.135	30.7	1.99	0.192
Eri_vag	5.1	0.54	0.479	32.6	4.84	0.052	39.2	2.91	0.106
Nhum	17.0	2.04	0.183	0.1	0.01	0.917	23.9	1.41	0.292
Nhol	37.0	5.88	0.036	40.1	6.68	0.027	67.7	9.41	0.006
Nshrub	13.0	1.49	0.250	0.50	0.05	0.826	16.4	0.89	0.446

Bold type indicates a significant result p < 0.05.



Fig. 6. Regression between seasonal mean CH_4 flux and water table (a) and vegetation volume (b) in 2009 excluding the value of Typ_lat. Regressions remain significant with the inclusion of Typ_lat but amount of variation explained is reduced.

the entire study site ($R^2 = 0.338$; p < 0.01). The effect appeared stronger ($R^2 = 0.517$; p < 0.01) when we excluded Typ_lat from our analysis.

4. Discussion

In peatlands, CH₄ fluxes vary from slight uptake to efflux of more than 65,000 μ mol m⁻² day⁻¹ (Klinger et al., 1994). However, fen vegetation types are generally stronger emitters than bogs because the anaerobic zone is on average closer to the peatland surface (Moore et al., 1990). Methane flux from natural minerotrophic peatlands ranges from 6125 μ mol m⁻² day⁻¹ to

15 562.5 μ mol m⁻² day⁻¹ (Saarnio et al., 2007). The CH₄ fluxes for most of the cutover and natural vegetation communities at the BSF site were substantially lower than the above lowest value except Car_aqu (7423.83 ± 2226.88 μ mol m⁻² day⁻¹) in 2008 and Typ_lat (14,497.40 ± 6143 μ mol m⁻² day⁻¹) in 2009. Data for bare peat CH₄ flux agreed well with that of Waddington and Day (2007) who reported values from bare peat of a cutover site of -87.5 μ mol m⁻² day⁻¹ to 6.25 μ mol m⁻² day⁻¹.

In general, extraction of peatlands decreases CH₄ flux due to drainage, except at ditches where fluxes can remain high (Sundh et al., 2000). This was observed at the BSF peatland with CH₄ from bare cutover peat being lowest of all cover types tested, while also having the deepest water table. In our study CH₄ flux from cutover recolonizing vegetation was higher than cutover bare peat and thus the effect of revegetation was increased CH₄ flux. While shallower water table at some revegetated plots may partially explain the increase in CH₄ flux, results of multiple regression suggest that the increase in biomass also results in higher CH₄ emission. Although one restoration goal is to reduce C and greenhouse gas flux to the atmosphere, our main goal is to return the ecosystem function and thus the system will emit some CH₄ because of its wetland characteristics. On average, measured fluxes were still much lower than the average CH₄ emission rate of minerotrophic peatlands with most vegetation communities on the cutover site having lower efflux than the natural peatland Nhol and Nshrub vegetation types. Similar results were observed in Europe where revegetated cutover peatland CH₄ emissions were lower than adjacent pristine mires (Komulainen et al., 1998; Tuittila et al., 2000a).

In addition to variations in CH_4 flux between vegetation types, there was also noticeable variability between years and over the season. Thus it is apparent that variability in CH₄ flux results from the combined effect of physical (e.g. water table and temperature) and biological factors (e.g. vegetation and microbial communities). As CH₄ is produced only under highly reduced conditions and can be oxidized when oxygen is available, water table position is generally strongly correlated to CH₄ flux in peatlands (Granberg et al., 1997; Bellisario et al., 1999). We found a similar pattern for the overall site in our study (Fig. 6a). However, within a vegetation type water table was only significantly related to CH₄ flux for a limited number of vegetation types (Cal_can, Typ_lat, Nhol). This is likely due to the relatively dry nature of the cutover site and the large difference in water table between vegetation types. When water tables are deep, fluxes tend to be very low (Roulet et al., 1993: Wilson et al., 2008) because most CH₄ produced is oxidized as it diffuses through the unsaturated peat. Thus, at BSF, for vegetation types with deep water tables flux is always low, while at the few wet sites (Car_aqu, Typ_lat, Nhol) CH₄ flux was high and varied temporally due to additional factors such as temperature and vegetation biomass. The high CH₄ flux from Typ_lat relative to its water table and vegetation volume likely indicates the

importance of ebullition. Thus exclusion of this species in the regression analysis increased the amount of variability explained by water table and vegetation volume both of which are more likely to be important when diffusion dominates. More research on the importance of ebullition in cutover and restored peatlands is required to better characterize CH₄ flux from these sites.

A correlation between soil temperature and CH_4 flux has been observed when water table level is at or close to the surface (Tuittila et al., 2000c; Ding et al., 2004). Our findings for Car_aqu, Typ_lat and Nhol are also consistent with this as temperature controls microbial activity and high water table conditions allow for CH_4 production with little oxidation. Soil temperature also played a role for differences in CH_4 flux among vegetation communities at BSF. Sites dominated by vascular, aerenchymatous plants have a stronger positive relationship between CH_4 fluxes and peat temperature at depth than other sites (Saarnio et al., 1998; Shannon and White, 1994). We also found soil temperature– CH_4 flux relationship for aerenchymatous vegetation types, Sci_atr (*S. atrocinctus*) and Eri_vag (*E. vaginatum*) even when the water table was deep. This suggests that deep root systems are venting CH_4 produced below the water table to the atmosphere.

It was observed that presence and productivity of vegetation is important for CH₄ release given the significant relationship between vegetation volume and CH₄ flux found across the site (Fig. 6b). While vegetation appears to play a role in increasing CH₄ emissions across the entire peatland since fluxes from vegetated collars are higher than bare peat, strong correlations were found only at Car_aqu, Typ_lat, Nhol and Eri_vag (Table 4). Several studies have found that vegetation plays a more important role in CH₄ efflux when the water table is close to the surface (Waddington et al., 1996; Strack et al., 2006). Similar results were observed at wet vegetation types Car_aqu, Typ_lat and Nhol, where the shallow water table provides necessary conditions for methanogenesis and vascular vegetation is likely important for provision of fresh substrate. At these sites plant litter deposited at the surface is quickly submerged provided fresh substrate for CH₄ production (Ding et al., 2002). Tuittila et al. (2000b) suggested that substrate availability is an important factor in controlling dynamics of CH₄ fluxes at a cutover peatland. Moreover, when the water table is near the surface, a higher proportion of the rooting zone is anoxic, potentially resulting in greater venting of CH₄ to the atmosphere (Waddington et al., 1996).

Substrate availability is likely also responsible for temporal variation of CH₄ flux during growing season. According to Bergman et al. (2000) the CH₄ produced in peat soils can vary over the growing season due to variations in the supply of available substrate, the activity of the microbial community or changes in temperature. We found that CH₄ flux starts to rise when vegetation volume and temperature was high during the peak season and began to decrease when the plants began senescence and temperature decreased later of the season. So, as has been suggested elsewhere, it is probable that the methanogenic population, in response to substrate supply and temperature, contributed to the observed increase in flux through greater CH₄ production (e.g. Kettunen et al., 1999). The exceptional behaviour of Equ_arv plots in 2008 (continual decline in flux over the season) is mainly controlled by water table position. Though there is substrate available for CH₄ production most would be oxidized due to the deep water tables and lack of plant mediated transport. The continuous rise of CH₄ flux for Typ_lat in 2009 maybe because the water table was always above the surface and thus little oxidation would take place while substrate supplied by the vegetation community by litterfall during senescence would be available at this saturated surface.

High flux from Eri_vag plots clearly illustrates the important role that some vascular species can play in CH₄ transport. Despite

a deep water table, CH₄ flux from Eri_vag is relatively high and significant correlations between both soil temperature and vegetation volume with CH₄ were observed. Frenzel and Karofeld (2000) suggest that E. vaginatum (Eri_vag) is a deep rooting vascular plant species and responsible for venting CH₄ from the anoxic peat layer, particularly in cutover peatlands (e.g. Marinier et al., 2004). Tuittila et al. (2000b) found that increasing primary production and subsequent deposition of substrate to anoxic conditions by this species increased CH₄ flux in a restored cutover site in Europe. A similar result was observed by Waddington and Day (2007) in a Canadian peatland. Plant-mediated transport is likely also important for Car_aqu and Typ_lat as both species have been observed to vent CH₄ to the atmosphere (Joabsson et al., 1999; Ding et al., 2002; Laanbroek, 2009; Lai, 2009). However, as water table is close to the surface at these locations, oxidation in the peat is limited suggesting that the vegetation's role in substrate supply may be more important than transport for maintaining high CH₄ flux at these locations. Sci_atr and Cal_can may also provide plant-mediated transport, however, the low fluxes from these locations suggest that either their ability is limited, or rooting depth is not sufficient to tap anoxic zones where CH₄ is produced.

The pore water CH₄ concentration will be determined mostly by vegetation characteristics, such as biomass production and root system, and as well as environmental factors such as water table, temperature, and atmospheric pressure. The mean pore water CH₄ concentration at BSF site up to 731.22 µM at 50 cm depth is similar to other findings (Clymo and Pearce, 1995; Waddington and Roulet, 1997; Blodau et al., 2007; Strack and Waddington, 2008). At a particular point pore water CH₄ concentration will be controlled by the difference between the rate of CH₄ addition to that point, via production and translocation, and the rate of CH₄ loss via oxidation, translocation or emission (Strack and Waddington, 2008). Given that moderate concentrations of CH₄ were found across the cutover site, it is clear that substrate exists for methanogenesis and that the low fluxes observed likely result from high levels of oxidation due to deep water table. Surprisingly, the highest mean concentration at the study site at 50 cm depth was found at the bare peat (P) plots. We would expect that the deep old peat exposed by extraction would have very little substrate remaining to produce CH₄. As this sampling site is near the margin of the cutover peatland it is possible that some substrate is supplied to this site from the surrounding un-harvested peatland. Moreover, extraction caused the compaction of the peat, possibly limiting the release of CH₄ once it is produced leading to the observed high concentrations. In contrast, fresh litter and root systems at vegetated plots should increase pore size, encouraging CH₄ release at these locations. Among the natural vegetation communities, Nhol had higher concentration than Nhum at 50 cm depth but similar values at 75 cm depth and increasing deeper. This can be explained by the control of water table on pore water CH₄ concentration. CH₄ produced at 50 cm at Nhum is more likely to be oxidized than at Nhol given the deeper water table position at the former.

The pore water concentration of recolonizing vegetation communities at the cutover site is much lower than at the natural fen. The concentration of CH_4 increased with depth for Eri_vag and Sci_atr plots but decreased for Cal_can and Typ_lat although the variation was very small. Popp et al. (1999) suggest that the presence of vascular vegetation may play a role in this small-scale variability as roots provide substrate via root litter and exudates and also transport oxygen below the water table. Eri_vag has a deep root system and it supplies more substrate and oxygen to the deep layer where it is fully saturated. Thus these plots have very high CH_4 flux as well as increased pore water CH_4 concentration with depth. Both Typ_lat and Cal_can have similar pore water CH_4 concentration at 50 cm depth. The water table of Typ.lat was at or above the surface and vegetation volume was high which explained their high surface flux and decreasing trends in pore water concentration with depth. On the other hand Cal_can had deeper water table thus most of the CH₄ produced could become oxidized and the substrate may not reach deeper layers. Thus, we found low surface flux and sharp decrease of pore water concentration from 50 to 75 cm and then no change at all. However, more research is needed to know which combined factors are actually controlling pore water CH₄ concentration with depth.

5. Implications for restoration

It has been observed that vascular vegetation can assist in the establishment of bryophytes on cutover peat by improving microclimatic conditions (Graf and Rochefort, 2010) and thus maintaining these species that have spontaneously recolonized the site may be advantageous. On the other hand, it should be noted that CH₄ flux is only one kind of ecosystem function and that CH₄ accounts for a very limited proportion of total C balance for a species. Before making any decision on inclusion of species in the restored site species pool it is critical to determine other ecosystem functions such as CO₂ dynamics, invasive characteristics, eco-hydrological conditions of their successfully established communities and interaction with bryophyte species. Keeping this in mind, the suitability of the investigated species based on CH₄ flux alone can be considered.

Among the recolonizing vegetation communities, Typ_lat (T. *latifolia*) released the highest CH₄ flux. It grows only in ditches at BSF, a location known to have high CH₄ flux in cutover peatlands due to permanently inundated conditions (Sundh et al., 2000; Waddington and Day, 2007). The presence of T. latifolia likely increases CH₄ flux from the ditches beyond that which would be observed from flooded locations alone due to its ability to provide labile substrate and transport CH₄ from the soil to the atmosphere (Chanton et al., 1992). Moreover, it is highly invasive in nature especially for wetlands (Shih and Finkelstein, 2008). Restoration of peatlands soon after abandonment may help to reduce the abundance of this species. The vegetation type Eri_vag (E. vaginatum) has a deep root system, which vents methane from the anoxic peat layer allowing this vegetation type to emit significantly more CH₄ than other recolonizing species. Additionally this species is known for its proliferous establishment in disturbed peatlands as the dominant vegetation (Malmer, 1986; Lavoie et al., 2005; Tuittila et al., 1999; Frenzel and Karofeld, 2000). When considering CH₄ emission from the fen this species is undesirable, however it has been shown to act as a nurse species for moss establishment (e.g. Tuittila et al., 2000a) and the relative importance of these functions must be considered. The vegetation type Car_aqu (C. aquatilis) also releases significantly greater CH₄ than other species although this is clearly linked to its wet habitat preference. This species has been used in European restoration because of its dispersal-limited characteristics, and therefore limited invasive capabilities (Graf et al., 2008). It is likely that if a restored fen has wet habitats, any sedge species colonizing these areas will have a similar high CH₄ flux. With this in mind, Car_aqu may be a good choice given that it is a dominant species in many natural fens in North America (Graf et al., 2008).

Vegetation types Sci_atr (*Scripus atrocinctus*), Cal_can (*C. canadensis*) and Equ_arv (*E. arvense*) have CH_4 efflux only slightly greater than bare peat and substantially lower than the natural fen. Thus they may be considered for inclusion in restoration protocols. It has been observed that vascular vegetation can assist in the establishment of bryophytes on cutover peat by improving micro-

climatic conditions (Graf and Rochefort, 2010) however, these are not usually found in high densities in undisturbed fens (Graf et al., 2008) and care would need to be taken that they do not overtake more favourable fen communities. More research is required on the ecosystem functions of these species and the role of recolonizing vegetation in peatland restoration plans.

6. Summary

Mean \pm standard deviation 2009 growing season CH₄ emissions were 203.1 ± 109.5 to $978.9 \pm 291.5 \,\mu mol \, m^{-2} \, dav^{-1}$ from vegetation communities of the undisturbed fen and $6.80 \pm 20.3 \,\mu mol \,m^{-2} \,day^{-1}$ from bare peat on the cutover site. Revegetation of the cutover site increased mean CH₄ flux to 621.8 ± 369.6 to $14,497 \pm 6143 \,\mu mol \, m^{-2} \, day^{-1}$, although seasonal efflux varied significantly between vegetation types. The highest fluxes from recolonizing vegetation communities were observed for those dominated by T. latifolia, C. aquatilis and E. *vaginatum*. For the first two community types high rates of CH₄ efflux are likely linked to shallow water table position. In contrast, for the latter, water table was on average greater than 20 cm below the surface and plant-mediated transport of CH₄ was clearly important for maintaining high efflux. In general, the combination of hydrological and ecological controls was important for controlling CH₄ flux across the site. The observation of CH₄ in pore water across all sampling locations suggests that CH₄ is being produced at the cutover peatland and that low measured fluxes likely result from substantial oxidation of CH₄ in the unsaturated zone. Understanding ecosystem functions of spontaneously recolonizing species on cutover fens can help us to make decisions about the inclusion of these communities for future restoration measures. Although CH_4 flux is only one function, we must consider, these results are valuable for restoration planning.

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