

Sedge Succession and Peatland Methane Dynamics: A Potential Feedback to Climate Change

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ABSTRACT

Under the warmer climate, predicted for the future, northern peatlands are expected to become drier. This drying will lower the water table and likely result in reduced emissions of methane (CH₄) from these ecosystems. However, the prediction of declining CH₄ fluxes does not consider the potential effects of ecological succession, particularly the invasion of sedges into currently wet sites (open water pools, low lawns). The goal of this study was to characterize the relationship between the presence of sedges in peatlands and CH₄ efflux under natural conditions and under a climate change simulation (drained peatland). Methane fluxes, gross ecosystem production, and dissolved pore water CH₄ concentrations were measured and a vegetation survey was conducted in a natural and drained peatland near St. Charles-de-Bellechasse, Quebec, Canada, in the summer of 2003. Each peatland also had plots where the sedges had been removed by clipping. Sedges were larger, more dominant, and more productive at the drained peatland site. The natural peatland had

higher CH₄ fluxes than the drained peatland, indicating that drainage was a significant control on CH₄ flux. Methane flux was higher from plots with sedges than from plots where sedges had been removed at the natural peatland site, whereas the opposite case was observed at the drained peatland site. These results suggest that CH₄ flux was enhanced by sedges at the natural peatland site and attenuated by sedges at the drained peatland site. However, the attenuation of CH₄ flux due to sedges at the drained site was reduced in wetter periods. This finding suggests that CH₄ flux could be decreased in the event of climate warming due to the greater depth to the water table, and that sedges colonizing these areas could further attenuate CH₄ fluxes during dry periods. However, during wet periods, the sedges may cause CH₄ fluxes to be higher than is currently predicted for climate change scenarios.

Key words: peatland; ecological succession; vascular plant; methane flux; water table.

INTRODUCTION

Peatlands are global reservoirs of approximately 33% of the world's soil carbon (C). As long-term sinks of atmospheric carbon dioxide (CO₂) (Gorham 1991) and persistent sources of methane (CH₄), they are important components of the global C cycle and represent important biospheric feed-

backs to climate. This feedback is especially important because climate changes are expected to be greatest in northern regions (Mitchell 1989), where most of the world's peatlands are located (Moore 2002). Mitchell (1989) predicted a temperature increase of 3°C and an increase in annual precipitation of 1 mm d⁻¹ for northern Canada in a 2 × CO₂ scenario. Using the Mitchell (1989) scenario and a simple water balance, Roulet and others (1992) predicted that despite the increased precipitation, higher temperatures would lead to

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higher evapotranspiration, and water tables would drop by 14–22 cm in northern Canadian peatlands. The increased depths to the water table would increase the size of the aerobic zone, which would favor CH_4 oxidation. Furthermore, CH_4 production could be reduced because fresh C would not be as available in the deeper anaerobic peat zones as it is in shallower peat depths (Christensen and others 1999). Consequently, many studies have suggested that under drier conditions CH_4 flux from northern peatlands would decrease (Christensen and Cox 1995; Christensen and others 1999; Moore and others 1998). However, a shift in the water table position will have secondary impacts on the peatland ecosystem, such as peat subsidence and ecological succession, which may also affect CH_4 dynamics. Recent research suggests that the overall response of a site to climate change is a function of present-day wetland “wetness.” Strack and others (2004) noted that in “wet” ecotopes (hollows, open water pools) of a poor fen in Québec CH_4 flux was not significantly different from that in previously “wet” ecotopes in an adjacent drained peatland. They hypothesized that lower water tables enabled ecological succession, leading to sedge-dominated zones in previously unvegetated open water ecotopes of the peatland, thereby enhancing CH_4 flux. It has also been determined that the extent to which sedges can enhance CH_4 flux is dependent on the water table position, with flux enhancement being greatest under wetter conditions (Waddington and others 1996). In addition, water table drawdown leads to peat subsidence, altering the peat structure and maintaining water tables close to their original position relative to the surface (Kellner and Halldin 2002; Price and Schlotzhauer 1999; Price 2003), particularly in low-lying areas. This subsidence may in turn affect CH_4 production, oxidation, and transport and the extent of ecological succession at a particular location.

Lawn regions of peatlands are dominated by *Sphagnum* and sedges. Sedges possess aerenchyma, a transport system able to carry oxygen from the atmosphere to the plant roots for root respiration (Chanton and Dacey 1991; Joabsson and others 1999; Lloyd and others 1998). This adaptation enables sedges to grow in waterlogged conditions; however, they thrive in drier conditions that do not require the use of oxygen transport. Moreover, unlike nonvascular *Sphagnum* moss, wetland sedges have roots that penetrate the peat column and often extend below the water table. This characteristic of sedges is important because roots add both labile C, from root litter, and substrates such as carbohydrates, organic acids, amino acids, and

phenolic compounds, from root exudates, which are used by bacteria for methanogenesis in the anaerobic zone (Bellisario and others 1999; Schütz and others 1991; Ström and others 2003). In contrast, *Sphagnum* litter occurs only at the surface, where predominantly aerobic conditions prevent CH_4 production. Therefore, sedges can enhance CH_4 production (by the addition of C and substrates), they can enhance CH_4 oxidation (by the addition of oxygen to the saturated zone), and they can enhance CH_4 transport to the atmosphere. Methane transport by sedges can be an important component of total CH_4 emissions in peatlands because it provides a pathway for CH_4 release that bypasses the oxic zone, thereby limiting CH_4 oxidation (for example, Kelker and Chanton 1997; Schimel 1995). Shifts in the density and composition of above- and belowground biomass in response to a shift in the water table position would alter the relative importance of these processes (CH_4 production, oxidation, and transport).

The concentration of CH_4 dissolved in pore water of clipped and unclipped plots provides information about the cumulative impact of sedges on the subsurface CH_4 pool. Waddington and others (1996) observed greater dissolved CH_4 concentrations in the pore water of unclipped plots than in the pore water of plots where vascular vegetation had been removed and suggested that this effect reflected higher rates of CH_4 production due to a greater supply of labile C. Schimel (1995) clipped *Eriophorum angustifolium* and *Carex aquatilis* at heights of 5 cm above the ground surface and compared the CH_4 fluxes. Kelker and Chanton (1997) clipped *C. aquatilis* and *Carex rostrata* at successive heights (60, 40, 20, 10, and 5 cm above the ground surface). The results of both studies demonstrated that clipping the sedges increased CH_4 flux. Schimel (1995) found that CH_4 fluxes of *E. angustifolium* were significantly higher than those of *C. aquatilis*, indicating that gas transport is not equal in all species. Some researchers have conducted experiments where sedges were clipped and then sealed, either by clipping the plants below the water surface (which acts as a gas seal), or by applying a sealant such as petroleum jelly or paraffin wax to the cut end of the sedge. Shannon and others (1996) found no significant difference between CH_4 fluxes from unclipped and clipped plots of *Scheuchzeria palustris* that were cut below the water surface. Waddington and others (1996) observed a decrease in CH_4 flux from plots of *Eriophorum vaginatum* that were clipped below the water surface. When Kelker and Chanton (1997) sealed *C. aquatilis* and *C. rostrata* plants that were

clipped at 10 cm with petroleum jelly, they observed a decrease in CH₄ flux. The variation in results from these studies implies that gas transport is species specific. This is related to both species-specific differences in C allocation and transport capabilities (Schimel 1995; Ström and others 2003).

Waddington and others (1996) suggest that CH₄ flux enhancement by sedges is most significant under wet conditions, so it is possible that sedges could have a lesser effect in a drier climate change scenario than under current cooler and wetter conditions. However, sedge biomass, leaf area index (LAI), and production will likely be higher under these drier conditions (Strack and others 2004; Waddington and others 1998). The objective of this study was to determine the role of sedges on CH₄ flux under current conditions (natural) and a climate change scenario (drained peatland). We hypothesized that (a) sedge aboveground biomass, LAI, and gross ecosystem production (GEP) would be greater at the drained sites than at the natural sites, (b) CH₄ fluxes at a natural peatland would be greater than at a drained site due to the water table drawdown, and (c) the CH₄ fluxes at the unclipped plots would be greater than the CH₄ fluxes at adjacent clipped plots (at both the natural and drained sites).

METHODS

Study Area

The study was carried out at a poor fen fragment located in the St. Charles-de-Bellechasse peatland (46°40'N, 71°10'W) near Quebec, Canada. The 30-year normals in the region for mean daily temperature are 16.5°C for June and -12.8°C for January. The 30-year normals in the region for mean precipitation are 89.8 mm for January and 114.2 mm for June (Environment Canada 2004). Dominant sedges at the site are *Carex oligosperma*, *Carex limosa*, and *Rhynchospora alba*. Dominant mosses at the site are *Sphagnum papillosum*, *Sphagnum magellanicum*, *Sphagnum cuspidatum*, and *Polytrichum strictum*. The peat is underlain by clay and the depth to this mineral soil varies between 1.0 and 1.5 m throughout the site.

Experimental Design

Two sites at the poor fen fragment were examined: a natural site and a drained site. The water table at the drained site was lowered by approximately 20 cm about 10 years prior to the study. Triplicate metal frame 60 × 60 cm collars were inserted into the peat at a depth of 30 cm at lawns (flat topog-

raphy) of similar moisture conditions (see Strack and others 2004) at both the natural and drained sites. An additional set of triplicate collars were installed at each of the natural and drained sites in plots where the sedges were clipped close to the peat surface using garden shears and sealed with petroleum jelly. To minimize the effects of disturbance, sedge clipping and sealing was always undertaken throughout the study season 1–2 days prior to gas flux measurements. To reduce the amount of productivity during the study season and enable some decomposition of roots prior to the study, the sedges were initially clipped the autumn preceding the study season. However, further root decomposition likely occurred during the study season; thus, while sedge transport was removed, substrate supply could not be completely eliminated at the clipped sites. The study season was from mid-May to September 2003.

Methane Flux

Methane flux was determined by placing an aluminium chamber (60 × 60 × 30 cm) on the water-filled collar. Gas inside the chamber was mixed by a fan and sampled by 10 mL syringe at 5, 15, 25, and 35 min after closure. Samples were analyzed within 48 h of collection on a Varian 3800 gas chromatograph equipped with flame ionization detector at 250°C and Porapak N column at 50°C with helium as the carrier gas and a flow rate of 30 mL min⁻¹. The gas chromatograph was calibrated with standards after each eight samples, and relative standard deviation was less than 3%. A linear concentration increase/decrease ($R^2 > 0.75$) was required for acceptance of the data point.

Gross Ecosystem Photosynthesis

Carbon dioxide fluxes were measured once per week using a dynamic chamber technique whereby a clear plastic chamber was placed into the groove of the collars, and water was poured into the groove to create a gas seal between the interior of the chamber and the surroundings. The temperature inside the chamber was maintained within 5°C of the ambient temperature using a cooling system, consisting of a radiator supplied with cold water. The internal air temperature was monitored with a thermocouple incorporated into the chamber. The amount of photosynthetically active radiation (PAR) was measured using a LI-COR quantum sensor (units of $\mu\text{mol m}^{-2} \text{s}^{-1}$ of light). The sensor was mounted inside the chamber and was read using an external analog meter connected by a wire.

The CO₂ concentration was measured using a PP Systems EGMI infrared gas analyzer. Measurements of temperature, PAR, and CO₂ concentration were recorded at 30 s intervals for 2 min. The chamber was removed from the collar and vented after each measurement set. Three to four measurement sets were conducted for each collar on each measurement date, using shroud shades of varying transparency each time.

The depth to the water table, volumetric water content of the soil, and a soil temperature profile were measured for each collar at the same time that the gas samples were collected for CO₂ concentration analysis. Water table position was measured using 1.3 – 1.9 cm i.d. PVC wells and a manual water level indicator. Gross ecosystem production was calculated by subtracting total respiration (R_{TOT}) from net ecosystem exchange (NEE).

Dissolved Pore Water Methane

Pore water samplers consisting of a 20 cm length PVC pipe, closed at both ends, slotted at the middle 10 cm, and covered in mesh to prevent clogging, were installed at each site. Tygon tubing was inserted at the top, fitted with a three-way valve, and extended above the surface of the peat to enable collection of water with a syringe. Samplers were placed at 25 and 40 cm below the surface. Pore water was collected weekly and CH₄ concentration determined on the Varian 3800 using headspace analysis (Ioffe and Vitenberg 1982) after equilibration with nitrogen.

Sedge Leaf Area Index, Aboveground Biomass, and Rooting Depth

A survey of the plant species present in each unclipped collar was conducted at 2-week intervals. Five quadrats of 7.5 × 7.5 cm were marked in each collar by wooden skewers. The species present in each quadrat were noted, and the leaves of each of the species in the quadrats were counted. Based on the survey of species present in the quadrats, a set of three random plants of each species was selected for leaf size measurements. These measurement plants were located outside of, but close to, the collars at both the natural and drained sites. The length and width of the leaves of these plants were measured once per month. The LAI of the plants of each species at the natural and drained sites was measured by first calculating the area of the leaves of each species for each date of measurement by assuming either an oval or triangular shape. An average area for the leaves of each species was

calculated for each measurement date using the area of each leaf of all three triplicates for that date. The total number of leaves of each species in the quadrats was summed for each collar, and this figure was multiplied by the average leaf area for each plant species. At times, the plant being measured died, so a new plant close in size to the dead plant was chosen to replace it for measurement. This resulted in periodic declines in the measured LAI during the growing season.

The collars were set up in October 2002 at the end of the snow-free period. All aboveground vegetation was clipped within the collars and approximately 75 cm distance around each clipped plot collar. Aboveground biomass (dead and living) was collected from each clipped collar, returned to the lab, dried, and weighed to determine the aboveground biomass. Aboveground sedge biomass was measured during the growing season at the clipped sites by drying the weekly clippings in an oven at 60°C for 24 h. Aboveground biomass was calculated by dividing the dry mass by 2, because the mean C content of peatland vegetation is 50%.

At the conclusion of the study, rooting depth was determined at both the natural and drained sites by hand-cutting 10 × 10 × 60 cm long cores. The cores were divided into 10 cm sections, and all roots were removed from each section. These were dried at 105°C for 24 h and weighed to determine the root mass for each section.

Environmental Data

The research site was equipped with a Campbell Scientific CR10X data logger that continuously measured precipitation using a tipping bucket rain gauge, PAR using a LI-COR quantum sensor, and air temperature using a thermocouple. The depth to the water table was measured manually using a blowpipe at wells located beside each collar. Wells were constructed from 1 in. diameter PVC pipe that was perforated throughout and inserted into the peat until clay was reached (usually 1.0 to 1.5 m). Soil temperature profiles were measured at depth intervals of 5–30 cm depth using a thermocouple probe inserted into the peat and a thermometer.

RESULTS

Site Characteristics

When the water table at all plots was considered, the water table at the drained site was slightly lower than the water table at the natural site (Mann–Whitney, $P = 0.06$). All plots experienced a water table drawdown in July (days of year

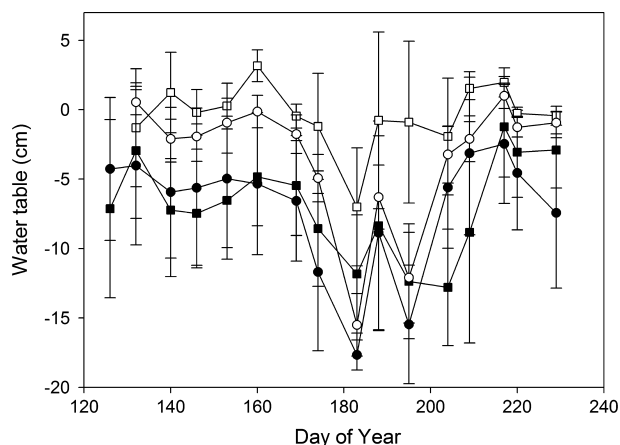


Figure 1. Seasonal water table position (negative is below the surface) at natural (*squares*) and drained (*circles*) sites. *Closed* and *open* symbols represent unclipped and clipped plots, respectively.

183–195) in response to low rainfall, and the water table decline was most pronounced at drained plots (particularly the unclipped plots) (Figure 1). Median water table levels during the study period at the drained site were 6.3 and 1.8 cm below the surface at the unclipped and clipped plots, respectively. At the natural site, the unclipped plots had a median water table depth of 6.4 cm below the surface; whereas at the clipped plots, it was 0.2 cm above the surface. At both sites, the clipped plots were significantly wetter than the unclipped plots (Mann–Whitney, $P < 0.05$), and the natural clipped plots had significantly higher water tables than the drained clipped plots. There was no significant difference between water table position at the natural unclipped and drained unclipped plots.

Median temperatures at 10 cm (below the median water table at all sites) were 17.8 and 18.2°C, at the natural clipped and unclipped plots and 17.7 and 16.5°C, respectively, at the drained clipped and unclipped plots. The drained unclipped plots were significantly cooler than all other plots (Mann–Whitney, $P < 0.05$).

Methane

Methane flux at the natural site unclipped plots increased from 43.2 mg m⁻² d⁻¹ on day 140 (May 20) to 146 mg m⁻² d⁻¹ by day 188 (July 7), whereas at the natural site clipped plots it increased from 2.0 to 29.0 mg m⁻² d⁻¹ for the same period (Figure 2). This trend was also observed for the same dates at the drained site, where CH₄ flux increased from 4.8 to 45.9 mg m⁻² d⁻¹ and from 12.6 to 23.8 mg m⁻² d⁻¹ at unclipped and clipped plots, respectively

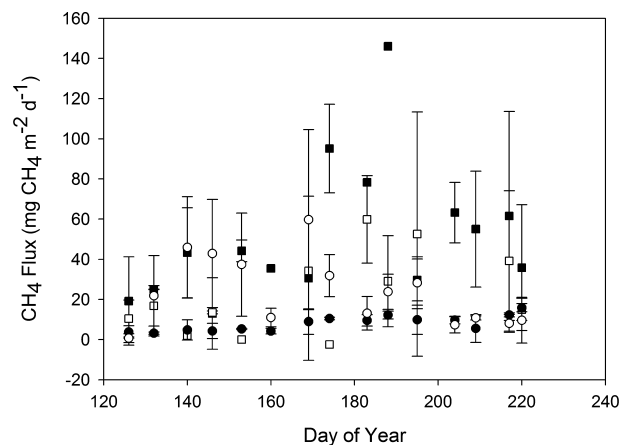


Figure 2. Seasonal methane (CH₄) flux at the natural (*squares*) and drained (*circles*) sites. *Closed* and *open* symbols represent unclipped and clipped plots, respectively.

(Figure 2). The CH₄ flux was significantly greater (Mann–Whitney, $P \leq 0.05$) at the natural site unclipped plots than at the natural site clipped plots (Table 1). However, at the drained site, the CH₄ flux at the unclipped plots was significantly less than that at the adjacent clipped plots. Methane flux was significantly greater at the natural site unclipped plots than at the drained site unclipped plots; however, there was no significant difference between the CH₄ fluxes at the natural site clipped plots (21 mg m⁻² d⁻¹) and the drained site clipped plots (24 mg m⁻² d⁻¹).

Dissolved Pore Water Methane

Dissolved pore water CH₄ concentrations at a depth of 25 cm was significantly (Mann–Whitney, $P \leq 0.05$) greater at the natural site unclipped plots than at the natural site clipped plots (Table 1). However, there was no significant difference between the dissolved CH₄ concentrations of the drained site unclipped plots and the drained site clipped plots. Dissolved pore water CH₄ concentrations at a depth of 40 cm were not significantly different (Mann–Whitney, $P \leq 0.05$) between the natural site unclipped and clipped plots and drained site unclipped and clipped plots. Concentrations were significantly greater (by one order of magnitude) at the natural sites than at the drained sites for both unclipped and clipped plots at both measurement depths.

Sedge Biomass, Leaf Area Index, and Gross Ecosystem Production

Aboveground sedge biomass (living and dead) in October prior to this study was 20.8 ± 6.9 and

Table 1. Median, Minimum, and Maximum Methane (CH₄) Fluxes and Dissolved CH₄ Values for Unclipped and Clipped Plots at the Natural and Drained Sites

Site	Median	Minimum	Maximum
CH ₄ Flux/(mg CH ₄ m ⁻² d ⁻¹)			
Natural, Unclipped	41.0 ^a	0.37	146.0
Natural, Clipped	13.9 ^b	-2.4	95.6
Drained, Unclipped	7.3 ^c	-0.94	18.7
Drained, Clipped	14.5 ^b	-1.1	108.2
Dissolved Pore Water CH ₄ Concentration (mg L ⁻¹) at 25 cm			
Natural, Unclipped	3.6 ^d	0.01	5.3
Natural, Clipped	2.4 ^e	0.04	5.6
Drained, Unclipped	0.12 ^f	0.02	0.45
Drained, Clipped	0.20 ^f	0.02	0.82
Dissolved Pore Water CH ₄ Concentration (mg L ⁻¹) at 40 cm			
Natural, Unclipped	3.4 ^g	0.46	4.4
Natural, Clipped	3.7 ^g	1.4	7.1
Drained, Unclipped	0.13 ^h	0.06	0.23
Drained, Clipped	0.22 ^h	0.01	0.44

Different superscript letters beside the medians values indicate significant differences between sites (Mann–Whitney, $P < 0.05$).

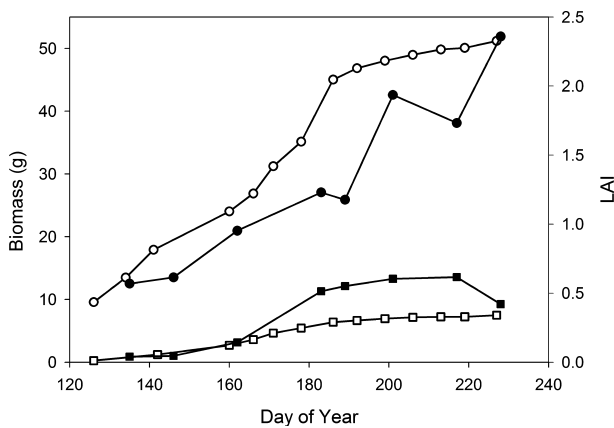


Figure 3. Aboveground biomass (*open*) and seasonal leaf area index (LAI) (*closed*) at the natural (*squares*) and drained (*circles*) sites. Species included in the LAI calculation were the dominant sedges at the sites (*Carex limosa*, *Rhynchospora alba*, and *Eriophorum virginicum* at natural and *Carex oligosperma* at drained).

143.8 ± 47.4 g C m⁻² at the natural and drained sites, respectively. The aboveground sedge biomass was greater at the drained site than at the natural site on the first day of measurement (May 6), (9.6 vs. 0.3 g, respectively), indicating that in early spring (immediately prior to measurement) production was greater at the drained site.

During the study season, cumulative aboveground sedge biomass, determined from the clipped plots, was also consistently greater at the drained site (total = 51.2 g) than the natural site (total = 7.5 g)

(Figure 3). This corresponds to a total production of 10.4 and 71.1 g C m⁻² at the natural and drained sites, respectively. The rate of increase in cumulative biomass appears to increase in the middle of the growing season (approximately day 159 to day 184) at the drained site; this trend is not observed at the natural site (Figure 3).

Higher production at the drained site was also evident in the results of the LAI (Figure 3). At unclipped plots, LAI increased approximately four fold from June to August at the natural site and about two fold at the drained site for the same time period. Leaf area index was consistently higher at the drained site, especially later in the growing season (August 6), (day 218: natural = 0.62, drained = 2.2). Root depth and mass were also greater at the drained site. At the natural site, roots extended to 30 cm; whereas at the drained site, roots were present to a depth of 56 cm. The weight of roots in each 10 cm section was much greater at the drained site for all depths except the 0–10 cm layer (Figure 4).

Gross ecosystem production at the unclipped plots was greater at the drained site than at the natural site for PAR levels above approximately 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 5). Maximum GEP at the unclipped plots was approximately 30 g CO₂ m⁻² d⁻¹ for the drained site, and only about half of that at the natural site (around 15 g CO₂ m⁻² d⁻¹). There was no difference in the GEP–PAR relationship at the natural and drained sites clipped plots. Both clipped plots reached a maximum GEP of only about 10 g CO₂ m⁻² d⁻¹.

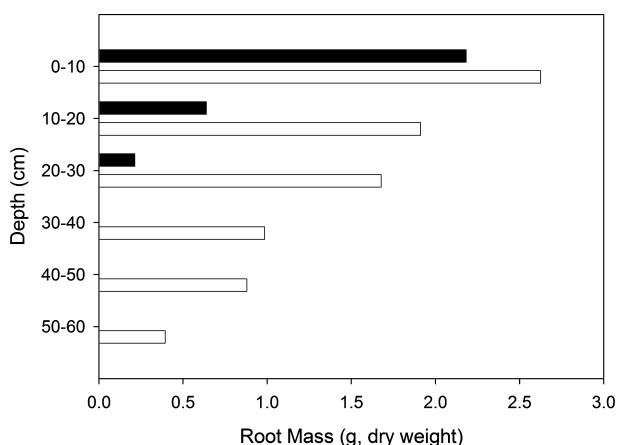


Figure 4. Root distribution at the natural (*black bars*) and drained (*white bars*) sites.

DISCUSSION

Peatland Drainage Ecological Succession

The water table relative to the surface of the drained plots was lower, but not significantly different from the natural plots. In response to the water table drawdown, compression and shrinkage of the peat matrix lowered the surface level at the drained site, enabling the water table to remain close to the surface. However, mean volumetric water content for the upper 60 cm of the peat was greater at the natural site (93%) than at the drained site (86%).

Nonetheless, the drainage has led to measurable ecological succession at the drained site. The drained site had a maximum GEP roughly double that at the natural site. Moreover, prior to the study, there was about seven times more sedge biomass at the drained site than at the natural site. Study season production was also about seven times greater at the drained site. Studies of terrestrialization have determined that hydrosere succession is promoted and enhanced by lower water tables (Campbell and others 1997; Southall and others 2003). Although the current study does not examine terrestrialization, a similar process has occurred because the reduction in water table levels has eliminated open water and seasonally inundated areas and enabled the invasion of *C. oligosperma*. This ecological succession has shifted the conditions at the site, likely causing significantly lower temperatures at the drained unclipped plots due to the shading effect of the sedges. Because peat temperature has been shown to be an important predictor of CH_4 flux (for example, Bellisario and others 1999; Christensen and others 2003; MacDonald and others 1998), this effect may also alter the production and emissions of CH_4 in response to drainage.

The hypothesis that the CH_4 fluxes at the natural site would be greater than those at the drained site was true for the unclipped plots but not for the clipped plots. The difference between the unclipped and clipped plots was the presence of sedges. Unclipped plots have both sedges and mosses, whereas clipped plots have only mosses. Thus, if the drainage-induced ecological succession is ignored, the drainage does not affect CH_4 emissions, likely due to the maintenance of water table positions close to the surface in response to peat subsidence. However, when we compared unclipped plots, we found that the invasion by sedges at the drained site actually appeared to reduce CH_4 emissions from the drained plots.

This conclusion is further supported by the fact that the hypothesis that the CH_4 flux at the unclipped plots would be greater than the CH_4 flux at the clipped plots was true only for the natural site. At the drained site, the CH_4 fluxes from the unclipped plots were significantly lower than those from the clipped plots. This result is opposite to what was expected. The significantly lower temperatures observed at the drained unclipped plots may have limited CH_4 production at this location, resulting in the lower fluxes. The difference in CH_4 flux could also be related to enhanced CH_4 oxidation, caused by aerenchyma transport of oxygen to the saturated zone occurring at the unclipped plots.

Examination of dissolved CH_4 concentration in the pore water provides a further explanation of these processes. At the natural site, the dissolved CH_4 concentration at 25 cm depth was greater at the unclipped plots than at the clipped plots, suggesting that sites at which sedges are present produce more CH_4 than sites with mosses alone. At the sampling depth of 40 cm, there is no significant difference between the dissolved CH_4 concentrations of the unclipped and clipped plots; this could be related to the rooting depth of the sedges (Figure 4). At the drained site, there was no significant difference in dissolved CH_4 concentrations between unclipped and clipped plots at both 25 and 40 cm depths; however, the concentrations at the clipped plots, were consistently lower than those at the unclipped plots. This suggests that CH_4 dissolved in the pore water is being oxidized at a greater rate at the unclipped plots than at the clipped plots, because CH_4 production should be higher at the unclipped sites. Ding and others (2004) observed that CH_4 emissions were correlated to the concentration of CH_4 dissolved in the pore water, which was controlled by rhizospheric oxidation of CH_4 driven by plant photosynthesis. Similar patterns can be observed in this study.

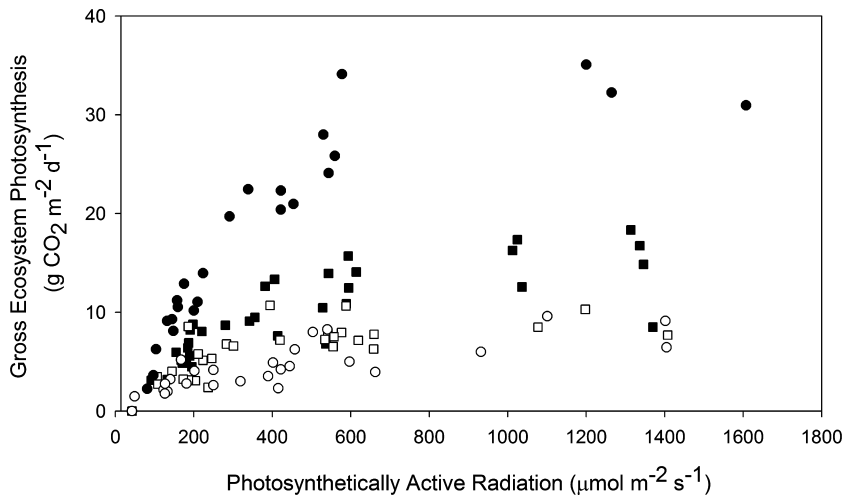


Figure 5. Gross ecosystem production–light response curve (August to early September 2004) for natural (*squares*) and drained (*circles*) sites. *Closed and open symbols* represent unclipped and clipped plots, respectively.

This oxidation of dissolved pore water CH_4 can be explained by a difference in the productivity of the sedges at the natural and drained sites. Figure 5 shows that the sedges at the drained site have a greater GEP than the sedges at the natural site. Sedges at the drained site are larger and/or more numerous than the sedges at the natural site (Figure 3), are more productive (Figure 5), and have a greater root biomass that extends further into the peat column (Figure 4). This increased root density likely leads to an increase in oxygen transport below the water table and increased CH_4 oxidation.

The drainage is almost certainly the cause of the increased productivity and larger size of the sedges at the drained site. Because the water table is not substantially different at the drained site compared to the control site, the ecological succession may result from differences in peat structure, water table oscillation, and nutrient mineralization caused by the drainage. In Figure 1, it is apparent that during dry periods the decline in water table at the drained site is more extensive than at the natural site. This is the result of the peat subsidence that occurred at the site and has led to peat with lower porosity. At the natural site, the peat is more buoyant and has a surface level that oscillates readily with water table changes. The more dynamic water table at the drained site may also affect nutrient mineralization at this location, altering nutrient dynamics and enabling sedge succession. There is a need for further investigation into the effect of drainage on nutrient mineralization in peatlands.

The fact that vascular plants enhanced CH_4 flux only at the wetter natural site suggests that site wetness has a greater control on CH_4 flux than the presence of sedges. If this is the case, then one would expect that there should be a within-season

water table control on CH_4 flux enhancement. A plot of the ratio of unclipped to clipped CH_4 fluxes (Figure 6) reveals that the effect of sedges on CH_4 flux at the drained site is actually related to site wetness. Ratio values above 1 indicate periods when the sedges enhance CH_4 flux, whereas ratio values below 1 indicate periods when the sedges decrease CH_4 flux. A generally increasing trend of the ratio with time is apparent, which is likely related to the growing season of the sedges.

Interestingly, there are apparent peaks in the ratio. Most of these peaks represent instances where the role of the sedges went from decreasing CH_4 flux, to enhancing CH_4 flux, and back to decreasing CH_4 flux. The peaks correspond with the occurrence of either intense precipitation events, or a period of many consecutive precipitation events (Figure 6). As such, vascular plants only enhance CH_4 flux at drained sites later in the growing season, when the site is wet. At the drained site, there is a very high density of roots in the topmost 20 cm of the peat profile. After a large precipitation event, the entire peat column becomes saturated, enabling this high density of roots to come in contact with the anaerobic zone, thereby “tapping” CH_4 production zones. This result is consistent with the findings of Waddington and others (1996); their results indicated that CH_4 flux enhancement was most significant under wet conditions. The fact that these peaks are coincident with precipitation events suggests that factors other than simply site wetness, such as the transport of substrate to the site of methanogenesis, may also have an important effect on the role of sedge in CH_4 transport.

Implications for Climate Change

This study has shown that a persistent lowering of the water table, which is expected under a climate

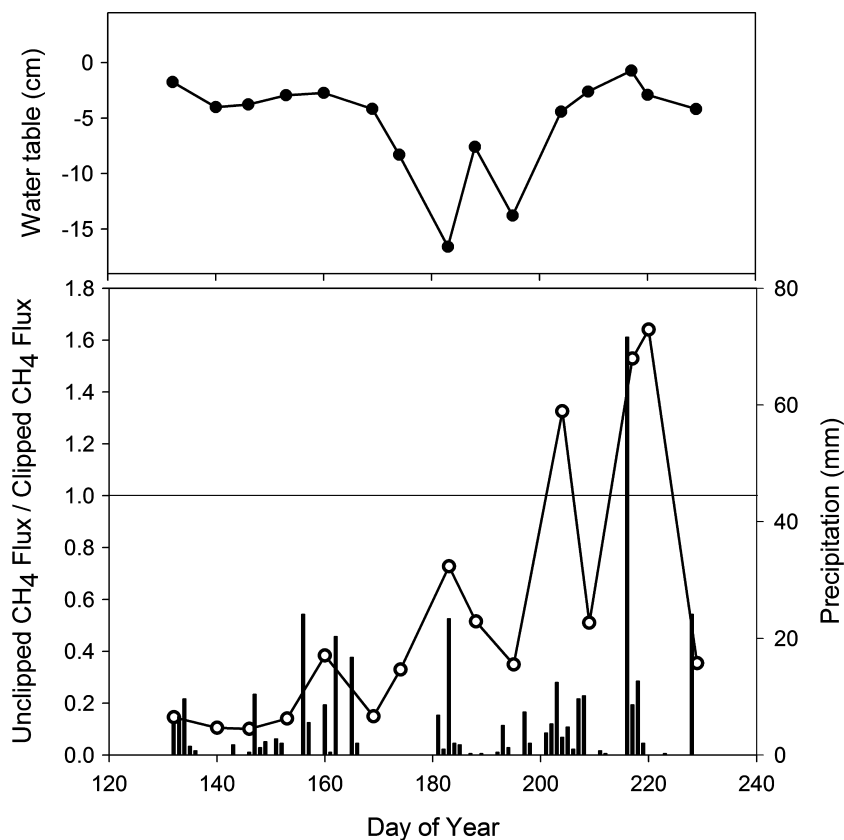


Figure 6. Ratio of unclipped to clipped methane (CH_4) fluxes at the drained site. Values above 1 indicate CH_4 flux enhancement by sedges; values below 1 indicate CH_4 flux decrease by sedges. The vertical bars represent precipitation.

change scenario for northern peatlands (Roulet and others 1992), has had a major impact on plant community and succession at a poor fen. Specifically, present-day lawns and pools were areas that showed the largest increase in sedge colonization.

It is important to understand vegetation succession due to water table drawdown and to incorporate it into peatland C models because sedges attenuate CH_4 flux at the drained peatland during dry conditions but enhance CH_4 flux in the drained peatland during wet conditions. This finding suggests that the common prediction that CH_4 flux would decrease in a climate-warming scenario (Roulet and others 1992) would also hold true for peatlands that are colonized by sedges during dry periods and that the magnitude of the decrease would be larger because of increased rhizosphere oxidation. However, during wet periods, sedges would enhance CH_4 flux and the decrease in predicted CH_4 flux would not be as great. Consequently, it is important not only to know how vegetation succession may respond to water table drawdown, but also to consider the changes in the timing and magnitude of precipitation events. Frequent large precipitation events could lead to substantial CH_4 flux enhancement (particularly later in the growing season), potentially offsetting

the CH_4 flux reduction caused by a lowered water table.

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REFERENCES

- Bellisario LM, Bubier JL, Moore TR, Chanton JP. 1999. Controls on CH_4 emissions from a northern peatland. *Global Biogeochem Cycles*. 13:81–91.
- Campbell DR, Duthie HC, Warner BG. 1997. Post-glacial development of a kettle-hole peatland in southern Ontario. *Eco-science*. 4:404–18.
- Chanton JP, Dacey JWH. 1991. Effects of vegetation on methane flux, reservoirs, and carbon isotopic composition. In: Sharkley

- TD, Holland EA, Mooney HA, Eds. Trace gas emissions by plants. Toronto: Academic Press. p 64–92.
- Christensen TR, Cox P. 1995. Response of methane emission from arctic tundra to climate change: results from a model simulation. *Tellus* 47B:301–309.
- Christensen TR, Jonasson S, Callaghan TV, Havström M. 1999. On the potential CO₂ release from tundra soils in a changing climate. *Appl Soil Ecol* 11:127–134.
- Christensen TR, Ekberg A, Ström L, Mastepanov M, Panikov N, Öquist M, Svensson BH, and others. 2003. Factors controlling large scale variations in methane emissions from wetlands. *Geophys Res Lett.* 30:1414. DOI: 10.1029/2002GL016848.
- Ding W, Cai Z, Tsuruta H. 2004. Diel variation in methane emission from the stands of *Carex lasiocarpa* and *Deyeuxia angustifolia* in a cool temperate freshwater marsh. *Atmospheric Environment.* 38:181–188.
- Environment Canada. 2004. Canadian climate normals 1971–2000. [Online]. URL: http://climate.weatheroffice.ec.gc.ca/climate_normals/results_e.html (2004, Mar. 29).
- Gorham E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol Appl* 1(2):182–195.
- Ioffe BV, Vitenberg AG. 1982. Head-space analysis and related methods in gas chromatography. New York: Wiley-Interscience.
- Joabsson A, Christensen TR, Wallén B. 1999. Vascular plant naturals on methane emissions from northern peatforming wetlands. *Trends Ecol Evol* 14(10):385–388.
- Kelker D, Chanton J. 1997. The effect of clipping on methane emissions from *Carex*. *Biogeochemistry* 39:37–44.
- Kellner E, Halldin S. 2002. Water budget and surface-layer water storage in a Sphagnum bog in central Sweden. *Hydrol Process* 16:87–103.
- Lloyd D, Thomas KL, Benstead J, Davies KL, Lloyd SH, Arah JRM, Stephens KD. 1998. Methanogenesis and CO₂ exchange in an ombrotrophic peat bog. *Atmos Environ* 32(19):3229–38.
- MacDonald JA, Fowler D, Hargreaves KJ, Skiba U, Leith ID, Murray MB. 1998. Methane emission rates from a northern wetland: response to temperature, water table and transport. *Atmospheric Environment.* 32:3219–27.
- Mitchell JFB. 1989. The “greenhouse” effect and climate change. *Rev Geophys* 27(1):115–39.
- Moore PD. 2002. The future of cool temperate bogs. *Environ Conserv* 29(1):3–20.
- Moore TR, Roulet NT, Waddington JM. 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Clim Change* 40:229–45.
- Popp TJ, Chanton JP, Whiting GJ, Grant N. 2000. Evaluation of methane oxidation in the rhizosphere of a *Carex* dominated fen in north central Alberta, Canada. *Biogeochemistry* 51:259–281.
- Price JS. 2003. Role and character of seasonal peat soil deformation on the hydrology of undisturbed and cutover peatlands. *Water Resour Res* 39:1241. DOI: 10.1029/2002WR001302.
- Price JS, Schlotzhauer SM. 1999. Importance of shrinkage and compression in determining water storage changes in peat: the case of a mined peatland. *Hydrol Process* 13:2591–601.
- Roulet N, Moore T, Bubier J, Laffleur P. 1992. Northern fens: methane flux and climatic change. *Tellus* 44B:100–5.
- Schimel JP. 1995. Plant transport and methane production as naturals on methane flux from arctic wet meadow tundra. *Biogeochemistry* 28:183–200.
- Schütz H, Schröder P, Rennenberg H. 1991. Role of plants in regulating the methane flux to the atmosphere. In: Sharkley TD, Holland EA, Mooney HA, Eds. Trace Gas Emissions by Plants. Toronto: Academic Press. p 29–63.
- Shannon RD, White JR, Lawson JE, Gilmour BS. 1996. Methane efflux from emergent vegetation in peatlands. *J Ecol* 84:239–246.
- Southall EJ, Dale MP, Kent M. 2003. Spatial and temporal analysis of vegetation mosaics for conservation: Poor fen communities in a Cornish valley mire. *J Biogeogr* 30:1427–1443.
- Strack M, Waddington JM, Tuittila E-S. 2004. The effect of water table drawdown on northern peatland methane dynamics: implications for climate change. *Global Biogeochem Cycles* 18:GB4003. DOI: 10.1029/2003GB002209.
- Waddington JM, Roulet NT, Swanson RV. 1996. Water table natural of CH₄ emission enhancement by vascular plants in boreal peatlands. *J Geophys Res* 101(D17):22775–85.
- Waddington JM, Griffis TJ, Rouse WR. 1998. Northern Canadian wetlands: net ecosystem CO₂ exchange and climatic change. *Clim Change* 40:267–75.