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The disappearance of relict permafrost in boreal north America: Effects on peatland carbon storage and fluxes

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Abstract

Boreal peatlands in Canada have harbored relict permafrost since the Little Ice Age due to the strong insulating properties of peat. Ongoing climate change has triggered widespread degradation of localized permafrost in peatlands across continental Canada. Here, we explore the influence of differing permafrost regimes (bogs with no surface permafrost, localized permafrost features with surface permafrost, and internal lawns representing areas of permafrost degradation) on rates of peat accumulation at the southernmost limit of permafrost in continental Canada. Net organic matter accumulation generally was greater in unfrozen bogs and internal lawns than in the permafrost landforms, suggesting that surface permafrost inhibits peat accumulation and that degradation of surface permafrost stimulates net carbon storage in peatlands. To determine whether differences in substrate quality across permafrost regimes control trace gas emissions to the atmosphere, we used a reciprocal transplant study to experimentally evaluate environmental versus substrate controls on carbon emissions from bog, internal lawn, and permafrost peat. Emissions of CO_2 were highest from peat incubated in the localized permafrost feature, suggesting that slow organic matter accumulation rates are due, at least in part, to rapid decomposition in surface permafrost peat. Emissions of CH_4 were greatest from peat incubated in the internal lawn, regardless of peat type. Localized permafrost features in peatlands represent relict surface permafrost in disequilibrium with the current climate of boreal North America, and therefore are extremely sensitive to ongoing and future climate change. Our results suggest that the loss of surface permafrost in peatlands increases net carbon storage as peat, though in terms of radiative forcing, increased CH_4 emissions to the atmosphere will partially or even completely offset this enhanced peatland carbon sink for at least 70 years following permafrost degradation.

Keywords: boreal, carbon, CH_4, climate change, CO_2, degradation, litter quality, peat, peatlands, permafrost

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Introduction

The boreal forest region occupies 12–14 million km^2, equal to about 10% of the vegetated surface of the globe (Dixon *et al*., 1994; McGuire *et al*., 1995). Peatland ecosystems occur mainly in boreal regions, covering 25–30% of the boreal forest region globally (Gorham, 1991; Wieder *et al*., 2006). Throughout the Holocene, boreal peatlands have served as an important reservoir for atmospheric carbon (C) (Harden *et al*., 1992; Vasander & Kettunen, 2006). Estimates of the total northern peatland C pool have ranged from 42 to 489 Pg (reviewed by Vasander & Kettunen, 2006), though Turunen *et al*. (2002) suggest that boreal peatlands globally store between 270 and 370 Pg, a substantial proportion of the estimated total boreal forest C stock of 471 Pg [Intergovernmental Panel on Climate Change (IPCC), 2000]. Given that the boreal forest region dominates terrestrial interactions with the Earth's climate north of 50°N (Chapin *et al*., 2000; McGuire *et al*., 2006) and that global warming generally is predicted to

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be most pronounced in the high latitudes of the northern hemisphere (Raisanen, 1997; Cubasch *et al*., 2001), C exchange between boreal peatlands and the atmosphere is particularly relevant to the climate system (Roulet, 2000).

Permafrost [i.e. earth materials remaining at or below 0 °C for 2 or more years (van Everdingen, 2005)] is an important control on the structure and function of many northern ecosystems. In the discontinuous permafrost zone, permafrost is found in locally cold settings such as north-facing slopes and low-lying and/or poorly drained areas. Boreal and subarctic peatlands often are underlain by permafrost, reflecting the thermal insulating qualities of peat (Zoltai & Tarnocai, 1975; Beilman, 2001). Vegetation and soils within peatlands promote the aggradation and maintenance of permafrost due to their strong control on surface energy balances (Beilman, 2001). In western continental Canada, about 30% of peatlands are underlain by permafrost, which can occur as palsas (mounds with a perennially frozen core of alternating layers of segregation ice and organic or mineral material) (Zoltai, 1971; Seppälä, 1988; Harris, 1998; van Everdingen, 2005), or as peat plateaus (features with low relief that contain segregated ice that may or may not extend downward into the underlying mineral soil strata) (Zoltai, 1971; Brown, 1980; Harris, 1998; van Everdingen, 2005). Additionally, at its southernmost occurrence, permafrost is restricted exclusively to peatlands, creating densely treed, elevated landforms situated in largely unfrozen peatlands. These localized permafrost features represent relict permafrost from the Little Ice Age that have been preserved by the insulative nature of dry surface peat (Vitt *et al*., 1994; Halsey *et al*., 1995; Beilman *et al*., 2001). In total, boreal peatlands underlain by permafrost store about 13 Pg of soil C in western Canada, representing 30% of the region's total peatland C stocks (Vitt *et al*., 2000a).

Long-term monitoring records show increases in near-surface permafrost temperatures over the past several decades in response to changing air temperatures and snow cover across boreal North America (Osterkamp *et al*., 2000; Jorgenson *et al*., 2001; Osterkamp, 2005; Taylor *et al*., 2006). Consequential changes in surface energy balance and permafrost temperatures have triggered widespread permafrost degradation across many northern landscapes (Thie, 1974; Brown, 1980; Vitt *et al*., 1994; Camill & Clark, 1998; Osterkamp *et al*., 2000; Beilman *et al*., 2001; Jorgenson *et al*., 2001; Osterkamp, 2005). In particular, localized permafrost features in peatlands are in disequilibrium with the current climate of boreal North America, and are degrading across continental Canada where current mean annual temperatures are above 0 °C (Halsey *et al*., 1995), suggesting a link between regional climate warming and permafrost degradation. Permafrost in Canadian peatlands continues to degrade at its southernmost limit, with no evidence of regeneration (Vitt *et al*., 1994, 2000b; Halsey *et al*., 1995; Beilman & Robinson, 2003).

Permafrost degradation in northern ecosystems can enhance internal drainage or can result in increased saturation of soil layers depending on slope position, soil texture, and hydrology (Jorgenson & Osterkamp, 2005). Permafrost degradation in peatlands generally results in thermokarst and increased saturation of surface peat, as peat surfaces collapse to levels at or below the water table during thaw. While degradation of permafrost in many arctic ecosystems generally is expected to increase the emissions of greenhouse gases, particularly methane (cf. Walter *et al*., 2006), the influence of surface permafrost degradation on carbon balance in peatlands is not clear. For example, while several studies have documented increased methane emissions following thaw in palsas or peat plateaus (Liblik *et al*., 1997; Christensen *et al*., 2004) and localized permafrost features (Turetsky *et al*., 2002), other studies have shown that surface permafrost degradation in boreal peatlands leads to enhanced carbon storage as peat (Robinson & Moore, 2000; Turetsky *et al*., 2000; Camill *et al*., 2001). Thus, permafrost degradation in peatlands can serve either as a positive or a negative feedback to net radiative forcing depending on permafrost conditions and differential effects of thaw on net primary productivity (NPP) and heterotrophic respiration. Here, our goals are (1) to determine the influence of differing permafrost regimes (unfrozen bogs without surface permafrost, localized permafrost features with intact surface permafrost, internal lawns representing permafrost degradation) on peat accumulation rates and soil organic matter quality at the southernmost limit of permafrost across boreal, continental Canada, and (2) to experimentally evaluate environmental vs. substrate controls on CO_2 and CH_4 fluxes from unfrozen bog, internal lawn, and localized permafrost peat at a single site in Saskatchewan.

Materials and methods

Study sites

We studied three peatland complexes situated near the southern edge of permafrost occurrence in western Canada, specifically in the vicinity of Anzac Alberta (AB), Patuanak Saskatchewan (SK), and Moose Lake Manitoba (MB) (Table 1). These sites are situated in the isolated patches permafrost region where permafrost is restricted to wooded localized permafrost features

Table 1 Location and climate data for three study sites across western Canada

	Study site		
	Anzac, AB	Patuanak, SK	Moose Lake, MB
Latitude; longitude	56°39′N; 111°13′W	54°07′N; 108°31′W	53°58′N; 101°06′W
Elevation (m)	369	480	270
Mean annual temperature (°C)	0.7	0.8	0.1
Coldest month (Jan) temperature (°C)	−18.8	−18.1	−20.6
Warmest month (Jul) temperature (°C)	16.8	16.6	17.7
Days with maximum temperature >20 °C	82.2	89.2	76.7
Days with maximum temperature ≤0 °C	116.9	115.2	133.3
Mean annual rainfall (mm)	342.2	314.2	323.8
Mean annual snowfall (mm)	155.8	121.3	154.9

Climate data 1971–2000 means are taken from the nearest weather station (Fort McMurray in Alberta, Meadow Lake in Saskatchewan, The Pas in Manitoba; http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html).

(Vitt *et al.*, 1994). Each site is characterized by continental climatic conditions. The Moose Lake MB site has somewhat colder winter and warmer summer temperatures than the other sites (Table 1). With mean annual precipitation <500 mm, our sites are at the dry end of the spectrum of precipitation regimes in which boreal peatlands are found (Gignac & Vitt, 1994; Wieder *et al.*, 2006).

We used aerial photography to identify three ombrotrophic unfrozen bogs, three localized permafrost features, and three internal lawns within each of our three sites. All features within a site are situated within a 2–3 km^2 area. Ombrotrophic continental bogs are the most extensive peatland feature within each site. These bogs are characterized by open canopies of black spruce (*Picea mariana*), abundant ericaceous shrubs (*Ledum groenlandicum* and *Chamaedaphne calyculata*), and nearly continuous cover of *Sphagnum* mosses (mostly *Sphagnum fuscum*, *S. magellanicum*, and *S. angustifolium*). Situated within the unfrozen bog matrix at each site are localized permafrost features with seasonal active layers of about 50 cm. Localized permafrost features in western Canada are characterized by stands of *P. mariana* that are denser and taller than in unfrozen bogs, ericaceous shrubs (mostly *L. groenlandicum*), and a nearly continuous cover of the true mosses, *Pleurozium schreberi* and *Hylocomium splendens*, along with the lichens *Cladina mitis* and *C. rangiferina*. While surface peat in permafrost peatlands can be relatively warm, the permafrost buffers deeper soil temperatures from fluctuations in air temperatures (Fig. 1). Adjacent to each of our selected localized permafrost features was an internal lawn (i.e., an area of recent permafrost thaw that resulted in the formation of a wet depression) dominated by *Sphagnum* species (*S. riparium*, *S. angustifolium*) and sedges (*Carex* spp.) typical of wet environments (Beilman, 2001). Black spruce trees pitch and eventually die when their root systems become submerged during permafrost degradation (Fig. 1). Thus, internal lawns lack live trees and direct incoming radiation leads to warmer surface peat temperatures (Fig. 1). A change in peat type is always visible in internal lawns marking the transition from sylvic/feather moss-dominated peat layer indicative of the original surface of the localized permafrost feature to *Sphagnum*-derived peat that accumulated vertically following permafrost degradation (Vitt *et al.*, 1994).

Peat accumulation rates

Peat cores were collected from the unfrozen bogs, localized permafrost features, and internal lawns at each site using 10 cm diameter, 1 m long sections of polyvinyl chloride (PVC) pipe with sharpened bottom edges. After making a 10 cm diameter incision into the fibrous surface peat using a bread knife, the PVC pipe was inserted into the peat and driven to a depth of 1 m with a sledge hammer. Only cores with <5 cm of compaction were retrieved. Cores were excavated and returned to the laboratory where they were frozen and sectioned on a band saw into 3 cm depth intervals. Each depth section was dried and weighed for bulk density measurements before grinding with a Tecator Cyclotec sample mill. To assign a date to the bottom of each 3 cm depth interval, cores were ^{210}Pb-dated by acid digestion of a subsample from each core section (adding a known amount of ^{209}Po as a chemical yield tracer) and α spectrometry followed by the application of the constant rate of supply model (Appleby & Oldfield, 1978; Wieder *et al.*, 1994; Brenner *et al.*, 2004; Turetsky *et al.*, 2004). Overall efficiencies of the digestion and counting procedure (recovery of the ^{209}Po chemical yield tracer) averaged 3.6 + 0.1% (mean±1 standard error; $n = 558$). Total unsupported ^{210}Pb inventories (23.2 ± 2.0 pCi

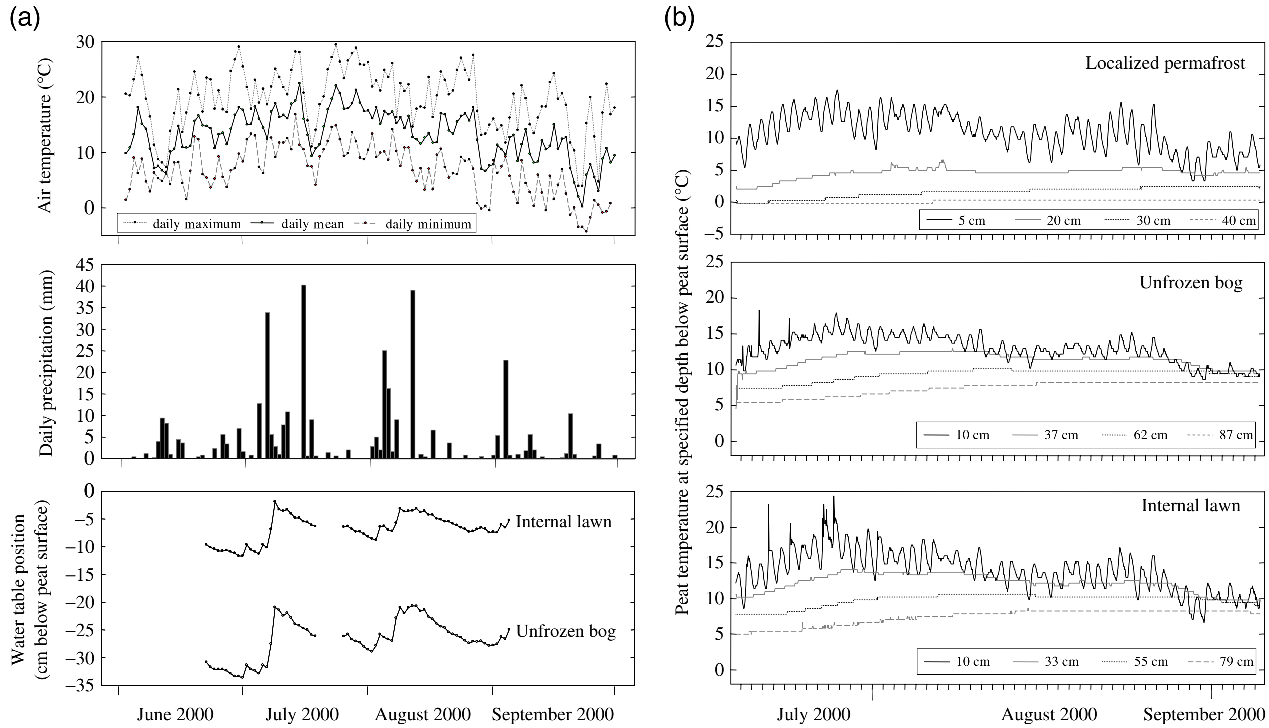

Fig. 1 (a) Air temperature and daily precipitation trends for the growing season of 2000 from the nearest weather station (Meadow Lake, Saskatchewan) to the Patuanak, Saskatchewan site (top two panels). Continuous records of water table position (Remote Data Systems Inc., Whiteville, NC) were logged at this site in the internal lawn and unfrozen bog (bottom panel). Manual probing of depth to permafrost showed that active layer thickness in the localized permafrost features was approximately 40 cm. (b) Continuous peat temperature measurements (HOBO probes, Onset Computer Corp., Pocasset, MA) showed a general trend of decreasing temperatures and dampening temperature fluctuations with depth in the peat profile, particularly in the permafrost peatland.

cm^{-2}; $n = 41$) and corresponding atmospheric ^{210}Pb deposition rates (0.73 ± 0.06 pCi $cm^{-2} yr^{-1}$; $n = 41$) were comparable to published values (Appleby & Oldfield, 1978). Two of the cores (internal lawn cores from the Patuanak AB site) had total residual unsupported ^{210}Pb contents and corresponding estimated ^{210}Pb fluxes from the atmosphere to the peat surface that were much lower than published values (e.g. Appleby & Oldfield, 1978) and, therefore, were considered not dateable. Net vertical accumulation ($cm\,m^{-2}$) and cumulative net organic matter accumulation (kg organic matter m^{-2}) were calculated over the past 25-, 50-, and 100-year intervals, and were analyzed using two-way analysis of variance models with site (Anzac, AB; Patuanak, SK; and Moose Lake, MB), peatland feature (unfrozen bog, localized permafrost feature, internal lawn), and interactions between site × feature as fixed effects.

Organic matter quality

We used a sequential extraction procedure (Wieder & Starr, 1998) to characterize the peat from each depth interval of each core into five proximate fractions: soluble non-polars (fats, oils, waxes), hot-water-soluble carbohydrates, water-soluble phenolics, holocellulose, and acid insoluble material. Fractions are expressed on an ash-free dry mass basis following measurement of organic matter concentrations (via loss on ignition at 450 °C) of each proximate residue. We also quantified total nitrogen and total phosphorus (Kjeldahl digestion) concentrations of peat in each depth interval.

Pyrolysis-mass spectrometry (Evans & Milne, 1987; Magrini *et al*., 2002) was used to characterize the biomolecular structure of bog, internal lawn, and localized permafrost peat from the Patuanak, SK site only. Subsamples of homogenized peat from each depth interval of cores were rapidly heated in an inert, helium atmosphere at 500 °C at ambient pressure in a quartz reactor, which was connected to the inlet of a molecular beam mass spectrometer (Evans & Milne, 1987). The generated pyrolysis products were sampled directly in real time by expanding through a sampling orifice with subsequent formation of the molecular beam, which provides rapid sample quenching and inhibits sample condensation. The mass spectrometer provides universal detection of all sampled products and the molecular beam sampling ensures that representative products from the original molecules are detected. Mass spectral data from 15–200 amu were acquired using 22 eV electron impact ionization. Repetitive scans (typically one 200 amu scan) were recorded during the evolution of a pyrolysis wave from each subsample. To use the resultant pyrolysis mass spectra to characterize the composition of each peat type (bog, internal lawn, frost mound peat), we processed data by (1) averaging the 20–30 spectra that accumulated during each subsample pyrolysis, (2) normalizing the average spectra to 100% total ion intensity, which corrects for differences in sample size and organic matter content of the samples, and (3) scaling the matrix of normalized data to ensure that each mass has an equal variance by dividing each mass variable intensity by the standard deviation for that mass variable for all samples. Factor analysis, using the Interactive Self-Modeling Multivariate Analysis (ISMA) program (Windig *et al*., 1987), was performed on the correlation around the origin matrix in ISMA, which allows for the resolution of components from complex mixtures where standards and calibration references are not available.

Controls on CO_2 and CH_4 emissions across permafrost regimes

While CO_2 and CH_4 emissions across multiple unfrozen bogs, localized permafrost features and internal lawns at the Patuanak SK site are described in Turetsky *et al*. (2002), here we describe a reciprocal peat core transplant experiment that quantifies site vs. substrate quality controls on gaseous C emissions. We collected 15 10 cm diameter, 50 cm peat cores each from a localized permafrost feature, an adjacent internal lawn, and a surrounding unfrozen bog (Fig. 1) using sections of PVC with sharpened bottom edges. After extraction, each core was wrapped with nylon window screening. Of the 15 cores extracted from each feature, five were transplanted back into the holes from their original feature and 5 cores were transplanted into each of the other two features, representing a full reciprocal transplant. Core transplantation was in an alternating, regular pattern, along a 3×5 grid at 2 m spacings. After transplanting, a PVC connection collar was inserted into the peat around the upper section of each core to serve as a collar for a static gas sampling chamber.

Static gas sampling chambers consisted of 20 cm tall sections of black PVC, capped at the top with a rubber septum to allow headspace gas sampling using a syringe. During a sampling event, 15 mL of headspace gas were collected in a gas-tight syringe fitted with a three-way Luer-lock stopcock at 0, 15, and 30 min. Syringes were transported to the University of Alberta and concentrations of headspace CO_2 and CH_4 were analyzed within 24 h using a Hewlett-Packard (Montreal, QC, Canada) 5890 Series II gas chromatograph using a Chromosorb 102 column, purified He as a carrier gas, and thermal conductivity and flame ionization detectors, respectively. Flux rates were determined as the slope of linear relationships between headspace gas concentrations and time. Gas sampling across our full factorial design occurred on seven dates: September 4, 1999, October 23, 1999, June 18, 2000, July 19, 2000, September 5, 2000, October 21, 2000, and July 1, 2001.

Gas flux data were analyzed using a repeated measures analysis of variance with site of origin (feature from which a core was collected), incubation site (feature into which a core was transplanted), the site of origin $\times$ incubation site interaction as the between-subjects fixed effects, and sampling date as the within-subjects (repeated) effect. This model was conducted in SAS using a repeated measures model (Proc Mixed).

Results

Peat accumulation

Age-depth relationships determined by ^{210}Pb dating (Fig. 2a) allow for the calculation of vertical peat accumulation rates over different time horizons. Net vertical peat accumulation over the most recent 25-year period varied by feature (unfrozen bogs, internal lawns, localized permafrost features) ($P < 0.0001$; $F_{2,32} = 29.16$), with no site (Anzac, AB; Patuanak, SK; Moose Lake, MB) ($P = 0.6978$; $F_{2,32} = 0.36$) or site $\times$ feature interaction ($P = 0.3394$; $F_{4,32} = 0.34$) (Fig. 3a). Net vertical accumulation was slower in the permafrost features than in unfrozen bogs or internal lawns across our sites, averaging 8 ± 1, 16 ± 1, and 18 ± 1 cm over the most recent 25-year horizon in localized permafrost features, unfrozen bogs, and internal lawns, respectively (data are means ± 1 standard error). Although net vertical peat accumulation over both the most recent 50-year and a 100-year time interval varied by a feature $\times$ site interaction (50-year: $P = 0.0129$, $F_{4,32} = 3.76$; 100-year: $P < 0.0011$, $F_{4,31} = 5.95$), generally, vertical accumulation of peat over these longer time intervals was slower for permafrost features than for either unfrozen bogs or internal lawns (Fig. 3a).

We used depth–age relationships (Fig. 2a) and profiles of bulk density and organic matter concentrations to quantify rates of net organic matter accumulation (kg organic matter m^{-2}) over time (Fig. 2b). From these relationships, we calculated net organic matter storage over the most recent 25, 50, and 100 years horizons, and

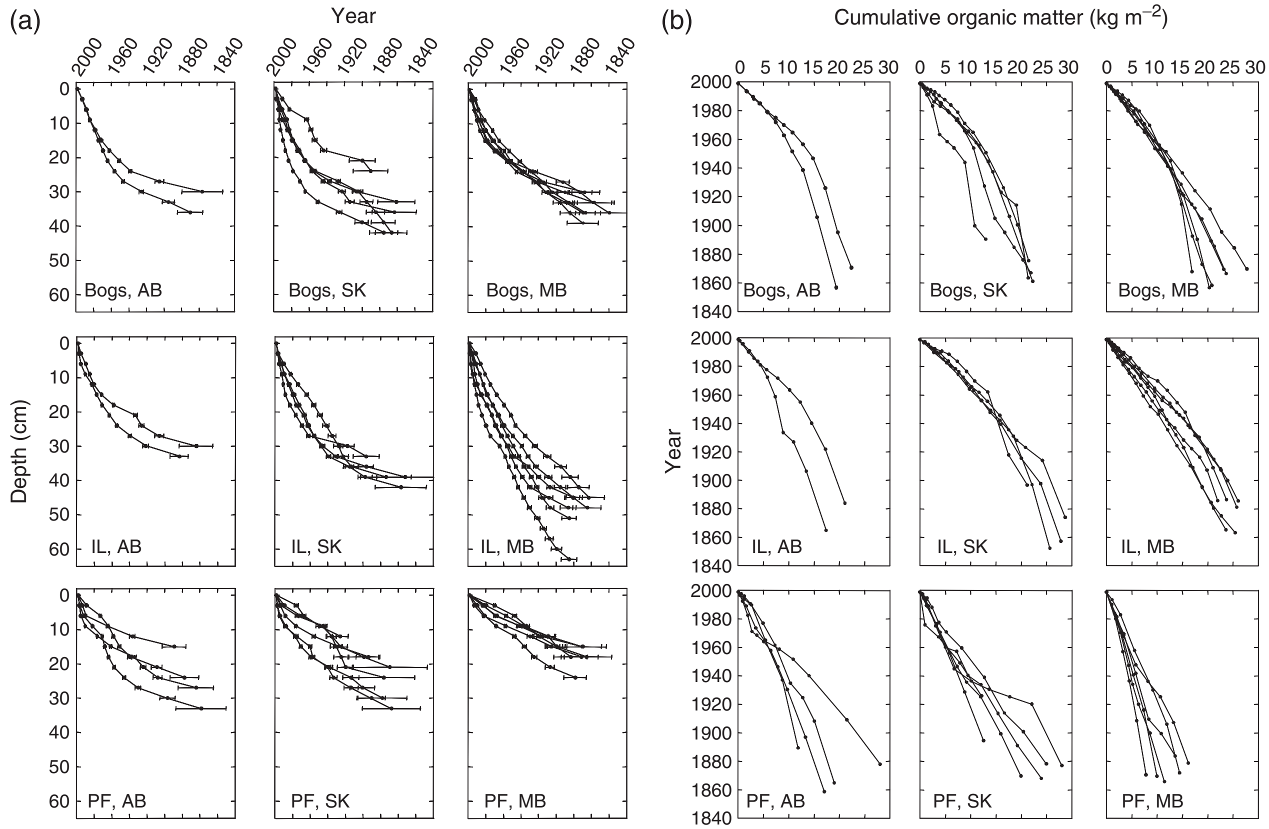

Fig. 2 (a) Depth-age relationships and (b) Cumulative net organic matter accumulation (kg organic matter m^{-2}) determined by ^{210}Pb-dating of peat cores collected in unfrozen bogs, internal lawns (IL) and localized permafrost features (PF) located near Anzac, AB; Patuanak, SK; and Moose Lake, MB.

found patterns that were similar to those for net vertical peat accumulation (Fig. 3b). Over the most recent 25-year time interval, organic matter accumulation varied by feature ($P = 0.0001$; $F_{2,32} = 49.40$), but not by site ($P = 0.3138$; $F_{2,32} = 1.20$), with no site × feature interaction ($P = 0.1657$; $F_{2,32} = 1.74$; Fig. 3). Net organic matter accumulation was consistently lower for localized permafrost features than for either unfrozen bogs or internal lawns. Over this 25-year horizon, unfrozen bogs accumulated on average 270 ± 41 g organic matter $m^{-2} yr^{-1}$, permafrost features accumulated 134 ± 30 g organic matter $m^{-2} yr^{-1}$, and internal lawns accumulated 279 ± 40 g organic matter $m^{-2} yr^{-1}$, respectively (means ± 1 standard error, Figs 2 and 3).

Net organic matter storage over the most recent 50 and 100 years varied by site × feature interactions (50 years: $P = 0.0277$; $F_{4,32} = 45.33$; 100 years: $P = 0.0525$; $F_{4,31} = 2.61$). The pattern of localized permafrost features accumulating less organic matter than in either unfrozen bogs or internal lawns diminishes as the time horizon is extended further into the past.

Organic matter quality

Peat in permafrost features had larger bulk densities, and higher concentrations of acid insoluble material, ash, nitrogen, and phosphorus than peat from internal lawns or unfrozen bogs (Table 2). Peat from internal lawns and unfrozen bogs had greater concentrations of holocellulose than localized permafrost peat, while concentrations of soluble fractions (hot water-soluble carbohydrates, hot water-soluble phenolics) were greater in unfrozen bogs and permafrost features than in internal lawn peat.

Factor analysis of pyrolysis mass spectra clearly distinguished the localized permafrost, internal lawn, and unfrozen bog peat from the Patuanak, SK site (Fig. 4). Factor score 1 separated permafrost peat from unfrozen bog and internal lawn peat with a greater amount of phenolic markers in permafrost peat and a greater amount of cellulosic and hemicellulosic markers in bog and internal lawn peat. Factor score 2 mainly separated unfrozen bog from internal lawn peat, with large influence of cellulosic markers in bog peat, and

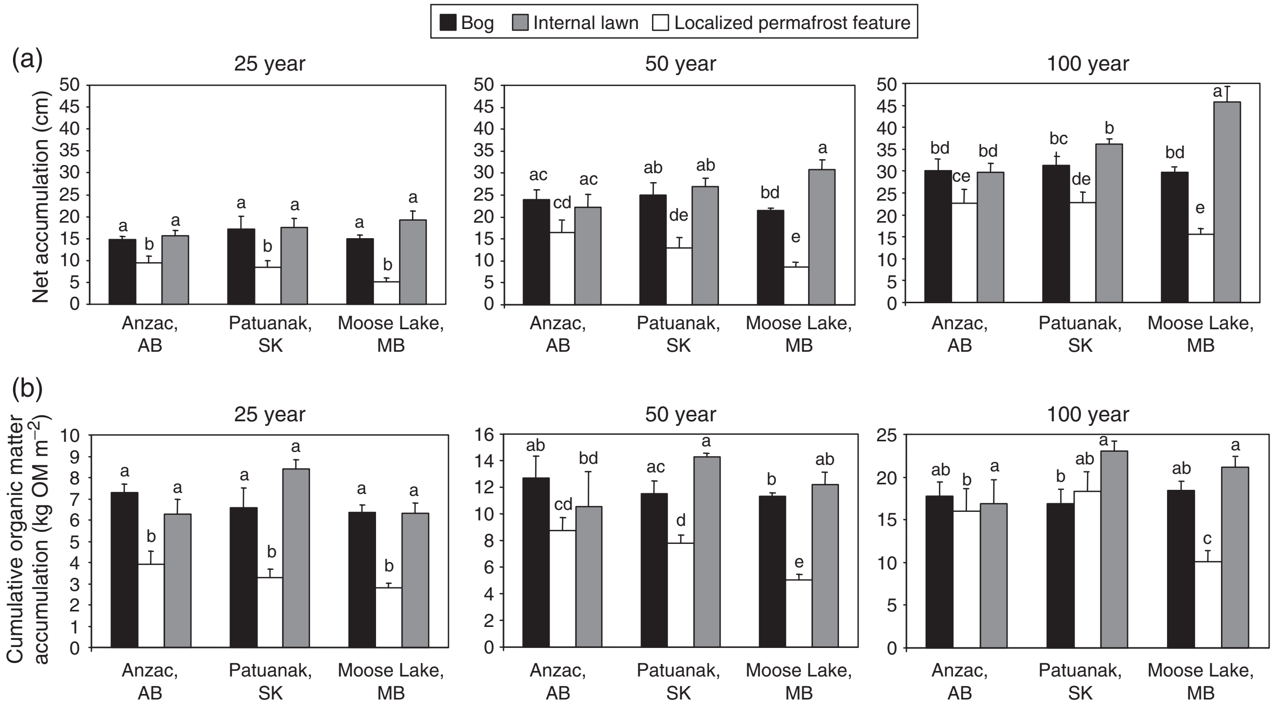

Fig. 3 (a) Net vertical accumulation (cm) and (b) Cumulative net organic matter accumulation (kg organic matter m^{-2}) over the past 25-, 50-, and 100-year intervals in unfrozen bogs, internal lawns, and localized permafrost features. Nonsignificant differences are shown by same letter superscripts as determined by post hoc comparison of means.

Table 2 Chemical characteristics of the surface 30 cm of peat; values are means ± standard errors

	Bog	Internal Lawn	Frost Mound
Acid insoluble material (mg g^{-1})	380.2 ± 8.8^b	492.7 ± 22.7^a	536.2 ± 15.7^a
Holocellulose (mg g^{-1})	477.3 ± 7.5^b	573.4 ± 8.1^a	303.2 ± 8.5^c
Soluble nonpolars (mg g^{-1})	43.3 ± 1.8^b	43.5 ± 1.9^b	61.2 ± 2.0^a
Hot water soluble carbohydrates (mg g^{-1})	48.7 ± 1.7^a	28.0 ± 1.6^b	47.6 ± 1.6^a
Hot water soluble phenolics (mg g^{-1})	5.2 ± 0.1^b	3.7 ± 0.2^c	6.1 ± 0.2^a
Ash (%)	2.3 ± 0.1^b	2.0 ± 0.1^b	3.2 ± 0.2^a
Bulk density (g cm^{-3})	0.056 ± 0.002^b	0.047 ± 0.002^c	0.087 ± 0.004^a
N (mg g^{-1})	4.86 ± 0.15^b	5.15 ± 0.19^b	8.08 ± 0.27^a
P (mg g^{-1})	0.32 ± 0.01^b	0.30 ± 0.01^b	0.57 ± 0.02^a

All variables varied by a feature effect (unfrozen bogs, internal lawns, frost mounds; one way ANOVA model, $P<0.01$). All organic matter fractions are expressed on an ash-free dry mass basis (except ash concentrations, which are on a dry mass basis). For each variable, means with the same letter superscript do not differ significantly (*a posteriori* Bonferroni-corrected least significant difference tests).

a large influence of aromatic products, such as vinyl phenol and phenol markers, in internal lawn peat.

Controls on peatland CO_2 and CH_4 emissions across permafrost regimes

Carbon dioxide emissions across our reciprocal core transplant experiment exhibited a peat origin (unfrozen bog, localized permafrost features, or internal lawn peat) by destination site (transplantation into the unfrozen bog, permafrost feature, or internal lawn) interaction (Table 3, Fig. 5). Peat from localized permafrost features had higher CO_2 emissions when placed in its native site than when placed in either the bog or internal lawn. When transplanted into the localized permafrost feature, CO_2 emission differed between all three peat types, with permafrost peat having the highest and internal lawn peat having the lowest average emissions. When transplanted into either the unfrozen bog or the internal lawn, the three peat types did not

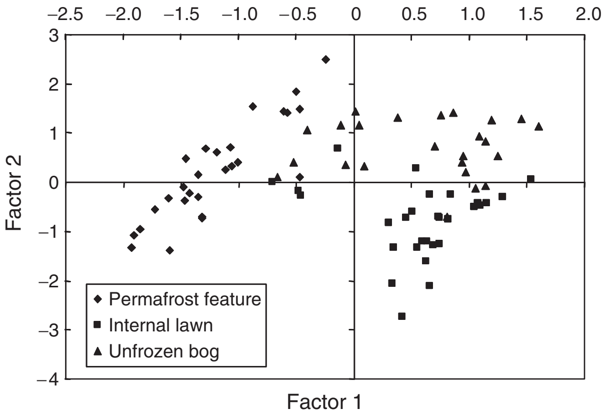

Fig. 4 Results of a factor analysis characterizing the pyrolysis mass spectra of the surface 30 cm of bog, internal lawn, and localized permafrost peat from the Patuanak SK site. Factor score 1 was positively correlated with large influences of cellulosic and hemicellulosic markers (e.g., masses 114, 60, 47, 73, 43, 31) and was negatively correlated with large influences of phenolic markers (e.g., masses 138, 137, 151). Factor score 2 was positively associated with large influences of cellulosic markers (e.g., masses 60 and 70) and was negatively correlated with large influences of aromatic (mass 91), vinyl phenol (mass 120) and phenol (mass 94) markers.

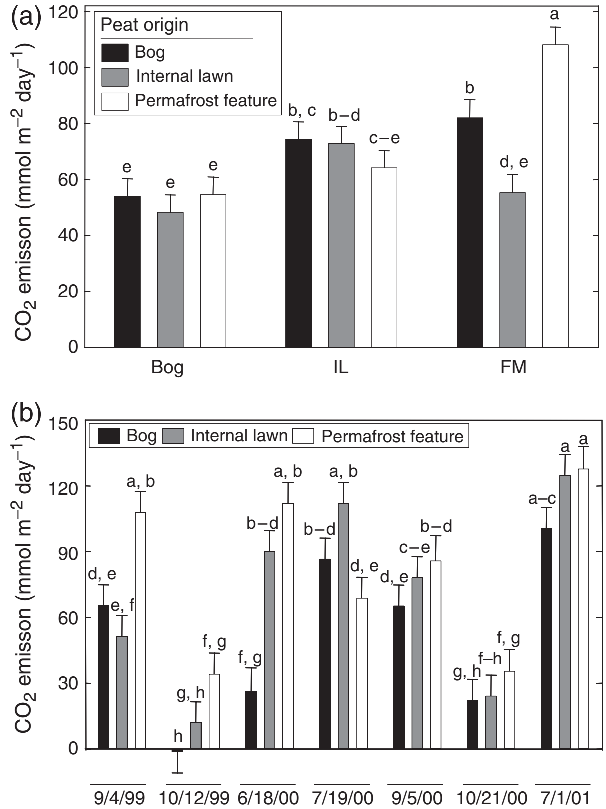

Fig. 5 Results for CO_2 emissions across the reciprocal core transplantation experiment (Table 3). (a) Mean CO_2 emissions across site of origin and incubation sites. (b) Mean CO_2 emissions across incubation site and sampling date.

differ with respect to CO_2 emission (Fig. 5a). Carbon dioxide emission also exhibited a sampling date by destination site interaction (Table 3). Averaged across the three peat types, differences in CO_2 fluxes between destinations were obtained for the first four sampling dates, but not beyond (Fig. 5b).

Methane emission varied by destination site, with no effects of sampling date, peat origin, or interactions among these main effects (Table 3). Rates of CH_4 emissions were greater from peat placed into the internal lawn than from peat placed into either the unfrozen bog or permafrost feature (Fig. 6). Mean CH_4 emissions did not differ from zero in the bog or localized permafrost feature.

Discussion

At the southernmost limit of permafrost in western Canada, unfrozen bogs and internal lawns had net organic matter accumulation rates two-times faster than rates of accumulation in localized permafrost features over the most recent 25-year horizon. It is important to note that our values for net organic matter accumulation do not represent estimates of net ecosystem production (NEP) as they do not include organic matter losses in peat beneath our 25-year time horizon. Nonetheless, the dense but shallow layers of surface sylvic peat that accumulate in localized permafrost features appear to store less organic matter, and thus less C, than the *Sphagnum*-dominated peat that accumulates in unfrozen bogs and internal lawns. *Sphagnum* is a minor component of the moss layer in localized permafrost features; peat in these permafrost landforms is derived mainly from feathermosses and *P. mariana* fine roots. At all of our sites, the conversion of localized permafrost features to internal lawns following permafrost degradation results in an increase in net organic matter storage (Fig. 3). This agrees with patterns of peat accumulation reported in other Canadian studies (Robinson & Moore, 2000; Turetsky *et al.*, 2000; Camill *et al.*, 2001) and suggests that permafrost degradation within peatland environments, likely triggered by climate change, could serve as a negative feedback to net radiative forcing via enhanced carbon accumulation as peat.

The transition from sylvic peat formed in localized permafrost features to *Sphagnum*-dominated internal lawn peat is easily observed within peat profiles, thus the timing of permafrost degradation can be determined via dating techniques such as ^{210}Pb-dating

Table 3 Results from repeated-measures analysis of variance for CH_4 and CO_2 emission (units of mmol m^{-2} day^{-1}), conducted using PROC MIXED in SAS (denominator df is 242 for all ANOVA terms)

	CH_4 emission			CO_2 emission		
	Numerator df	Type III F	$P>F$	Numerator df	Type III F	$P>F$
Origin	2	1.14	0.3230	2	5.54	0.0045
Destination	2	4.32	0.0144	2	16.43	<0.0001
Origin × destination	4	1.42	0.2294	4	6.43	<0.0001
Date	6	0.87	0.5199	6	41.39	<0.0001
Date × origin	12	0.82	0.6264	12	0.43	0.9513
Date × destination	12	0.65	0.7984	12	4.37	<0.0001
Date × origin × destination	24	0.73	0.8233	24	1.46	0.0832

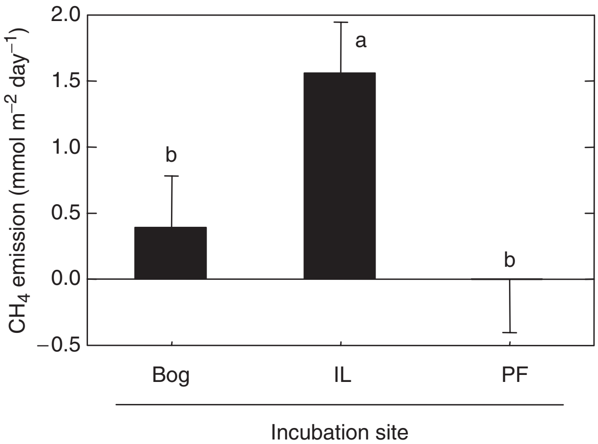

Fig. 6 Results for CH_4 emissions across the reciprocal core transplantation experiment (Table 3).

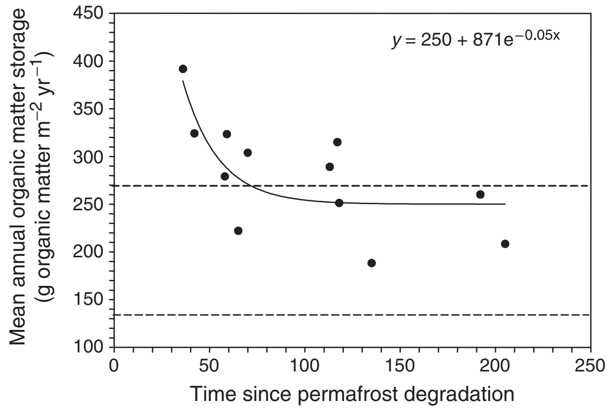

Fig. 7 Results of an exponential decay model of the effect of time as permafrost degradation on mean annual organic matter accumulation over the past 25 year-horizon in internal lawns located in western Canada (Proc Model, SAS; root mean square error = 45.82, model df = 3, error df = 9; model $R^2 = 0.53$). The asymptote (250 ± 19) was significant ($t = 12.87$, $P < 0.01$) while the y intercept (871 ± 1216) and slope (0.05 ± 0.03) terms in the model were not significant ($P > 0.2$). The dashed lines represent mean annual organic matter accumulation over the past 25 year-horizon in unfrozen bogs (270 ± 41 g organic matter m^{-2} yr^{-1}) and localized permafrost features (134 ± 30 g organic matter m^{-2} yr^{-1}). Data represent means ± 1 standard error.

(Turetsky *et al*., 2004). Examination of recent (past 25 year horizon) net organic matter accumulation as a function of time since permafrost degradation (Fig. 7) reveals that the enhancement of organic matter accumulation following permafrost degradation declines progressively over time, approaching a constant rate of organic matter accumulation (~240 g organic matter m^{-2} yr^{-1}) between 60 and 100 years post-thaw. This pattern of organic matter accumulation is related to successional development in internal lawns, which progressively leads to the gradual replacement of mesotrophic *Sphagnum* and *Carex* species with typical ombrotrophic bog vegetation (Beilman, 2001). Within 70 years following permafrost degradation, rates of organic matter accumulation in internal lawns are similar to those in unfrozen bogs. However, internal lawns continue to accumulate more organic matter than localized permafrost features (Fig. 7).

Differences in organic matter accumulation as peat between localized permafrost landforms, internal lawns, and bogs can result from differences in net primary productivity and/or heterotrophic respiration rates. Permafrost degradation in peatlands leads to a rapid reduction in the cover of woody species (*P. mariana*) and a shift in bryophyte community structure toward more aquatic *Sphagnum* species (Beilman, 2001; Camill *et al*., 2001). Despite these dramatic shifts in vegetation composition, Camill *et al*. (2001) reported similar rates of aboveground-NPP between peatlands underlain by permafrost and those that had experienced surface permafrost degradation in Manitoba, though there were pronounced shifts in functional group contributions to productivity (mainly black spruce in permafrost vs. *Sphagnum* in thaw sites). Surface permafrost degradation in peatlands also can influence decomposition rates either through changes in soil climate conditions that influence decomposer activity and/or by altering organic matter quality of accumulating peat. Generally, rates of C mineralization, as well as soil CH_4 emissions, are greater in areas of recent permafrost thaw than in peatlands with intact surface permafrost (Liblik *et al.*, 1997; Turetsky *et al.*, 2002; Turetsky, 2004; Wickland *et al.*, 2006; Yavitt *et al.*, 2006).

We used sequential chemical digestions (proximate analysis) and compound specific, pyrolysis mass spectrometry to explore the influence of permafrost regimes in peatlands on surface organic matter quality (Table 2, Fig. 4). We hypothesized that unfrozen bog and internal lawn peat would have more labile chemical signatures than peat in localized permafrost features given the sylvic (woody) nature of permafrost peat. Indeed, peat in localized permafrost features had greater concentrations of ash and acid insoluble material (Table 2) and greater influence of phenolic compounds in the mass spectra data (Fig. 4) than unfrozen bog or internal lawn peat, likely due to greater amounts of woody material inputs in localized permafrost features. However, the mass spectra data also indicated differences in the type of phenolic compounds present in surface peat among these peatland types. Ratios of phenol to methoxy-phenol averaged 1.0 ± 0.0, 1.8 ± 0.1, and 1.5 ± 0.1 in permafrost features, unfrozen bog, and internal lawn peat, respectively (means $\pm$ 1 standard error). Given that softwood lignin typically is based solely on methoxy-phenols, it is likely that the low phenol:methoxy-phenol ratios in permafrost features, and to a lesser extent in unfrozen bogs, is due to black spruce contributions to soil organic matter. While the peat accumulating in permafrost features clearly is more phenolic-rich than *Sphagnum*-dominated peat, permafrost peat had large concentrations of total nitrogen and phosphorus as well as soluble fractions (soluble fats, oils and waxes, hot water-soluble carbohydrates and phenolics; Table 2) that typically are associated with more labile organic matter.

To determine whether substrate quality differences between these peatland types are important controls on soil C fluxes, we reciprocally transplanted bog, localized permafrost, and internal lawn peat cores into their native site and into the other two peatland types. Our results (Table 3, Fig. 5) suggest that the relatively low organic matter accumulation in permafrost features may be due, at least in part, to relatively fast decomposition rates, which could be linked to the relatively dry conditions that characterize the surface peat layers of many permafrost landforms. Moreover, the relatively high organic matter accumulation that we observed in internal lawns appears not to be related to depressed decomposition, and so must be a result of enhanced net primary production.

We found no effect of peat type (permafrost feature, internal lawn, bog) on CH_4 emission (Table 3). Continental peatlands of western Canada tend to have low CH_4 emissions to the atmosphere (Basiliko & Yavitt, 2001; Turetsky *et al.*, 2002) likely due to thick acrotelms (peat layers above the water table) that promote CH_4 oxidation. Indeed, we report mean CH_4 emissions that are not different from zero from peat transplanted into the unfrozen bog or permafrost feature (Fig. 6). However, the water-saturated conditions of the internal lawn created by surface permafrost degradation stimulated CH_4 emission, either by increasing methane production or by decreasing CH_4 oxidation.

Methane is 23 times more effective in absorbing long-wave radiation than CO_2 per molecule on a 100-year time scale (62 times more effective over a 20-year period; Ramaswamy *et al.*, 2001). Given that the degradation of surface permafrost in localized permafrost features appears to increase net organic matter accumulation (Figs 2 and 3) and increase CH_4 emissions to the atmosphere, the net effect of surface permafrost degradation in peatlands on atmospheric radiative forcing is not clear because CO_2 and CH_4 fluxes are affected in opposite directions and because of the stronger warming potential of CH_4. However, given that internal lawns succeed relatively quickly (within 70 years) to more bog-like conditions (Fig. 7) and that bogs in continental Canada are associated with low CH_4 emissions (Fig. 6), the degradation of localized permafrost in peatlands is likely over the long-term to serve as a negative feedback to radiative forcing.

Permafrost underlies approximately 24% of the northern hemisphere land surface (Brown *et al.*, 1997). About 1/3 of the peatlands across western continental Canada are underlain by permafrost (Vitt *et al.*, 2000a). In this region, permafrost in peatlands reached its maximum extent in the late-Holocene, well after the initiation of peat accumulation (Zoltai, 1995). Thus, permafrost controls on carbon storage processes likely have not served as an important mechanism for C stabilization in these peatland soils. Recent studies have shown that the degradation of permafrost in arctic regions, particularly areas containing C-rich yedoma soils in Siberia, can lead to large C emissions via the mineralization of old C substrates (Walter *et al.*, 2006). At our peatland sites, the degradation of surface permafrost appears to stimulate plant productivity more so than soil C mineralization, which can be at least partially attributed to the relatively young age of permafrost in these peatlands as well as the saturated soil drainage conditions immediately following permafrost thaw. Given that localized permafrost landforms are in disequilibrium with the current climate of boreal North America, it is likely that the isolated patches region of the discontinuous permafrost zone, where permafrost largely is constrained to peatlands, soon will become completely free of surface permafrost in North America.

Conclusions

Our results indicate that surface permafrost degradation in Canadian peatlands will enhance organic matter accumulation and hence net carbon storage, particularly in the first 60–100 years post-thaw, likely as a result of high rates of net primary production by the wet-loving *Sphagnum* mosses and other plant species that are early colonizers of internal lawns. In terms of radiative forcing, increased CH_4 emissions to the atmosphere following permafrost degradation in peatlands will partially or even completely offset the enhanced peatland carbon sink for at least 70 years following permafrost degradation, after which C fluxes in internal lawns are likely to resemble those of unfrozen bogs. Over longer time scales, given that unfrozen bogs accumulate soil C at rates faster than localized permafrost features and are associated with small CH_4 emissions, the degradation of permafrost in Canadian peatlands is likely to represent a small net C sink. We suggest that the ongoing degradation of localized permafrost features in boreal peatlands, and resultant changes in carbon cycling, should be considered an early and sensitive indicator of climate change effects on boreal landscapes. Changes in organic matter accumulation and carbon cycling in peatlands may have implications for local and regional carbon budgets and for broader radiative forcing, with most of the changes in greenhouse gas emissions occurring within a century following permafrost degradation.

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