



Boreal peatland C fluxes under varying permafrost regimes

Merritt R. Turetsky^{a,*}, R. Kelman Wieder^b, Dale H. Vitt^c

^aDepartment of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada

^bDepartment of Biology, Villanova University, Villanova, PA 19085, USA

^cDepartment of Plant Biology, Southern Illinois University, Carbondale, IL 62901, USA

Received 15 May 2001; received in revised form 19 December 2001; accepted 9 January 2002

Abstract

Discontinuous permafrost in peatlands has recently been melting across western Canada, creating wet *Sphagnum-Carex* lawns (internal lawns) interspersed within drier ombrotrophic bog. Permafrost degradation alters peat hydrology, thermal regimes and plant species assemblages, all of which could affect gaseous C emissions in peatlands. We quantified CO₂ and CH₄ fluxes across the peat-atmosphere boundary using dark static chambers in adjacent internal lawns, continental bogs and frost mounds in an area of localized permafrost in north-central Saskatchewan. Carbon dioxide and CH₄ fluxes ranged from 0.2 to 14.6 mmol CO₂ m⁻² d⁻¹ and from -24 to 344 μmol CH₄, respectively, and differed significantly among peatland types and sampling dates. Our estimates of CH₄ flux are low compared to previous estimates from boreal wetlands, with net consumption of CH₄ typically in frost mounds. Permafrost melt in our study area is associated with 1.6- and 30-fold increases in CO₂ and CH₄ emissions, respectively. More widespread thaw across the discontinuous permafrost region will be an important consideration to boreal C budgets with future climatic changes. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Carbon dioxide; Methane; Peatlands; Permafrost; Permafrost melt

1. Introduction

Peatlands cover over 365 000 km² in Alberta, Saskatchewan, and Manitoba and store about 48 Pg of C as peat and living biomass (Vitt et al., 2000a). Within this region, about 28% of peatlands are underlain by permafrost that, in total, store 13 Pg of C (Vitt et al., 2000a). However, permafrost distribution ranges from continuous coverage in the northern continuous permafrost zone to discontinuous ice lenses in the localized permafrost zone (LPZ; Zoltai, 1995; Beilman et al., 2001). Near its southern limit in the LPZ, permafrost is restricted to ombrotrophic peatlands where black spruce (*Picea mariana*) stands and the underlying peat promote ice aggradation or persistence (Zoltai, 1995; Halsey et al., 1995; Vitt et al., 2000b).

The maximum extent of permafrost in western Canada occurred during the Little Ice Age (Halsey et al., 1995). Over the past 150–200 yr, temperatures across the boreal forest have increased by about 1 °C (Campbell and McAndrews, 1993), resulting in widespread permafrost degradation (Halsey et al., 1995; Vitt et al., 2000b). Peat-

land surface topography collapses with ice melt, increasing water availability, and increasing insolation by inundation of *P. mariana* roots resulting in tree death (Vitt et al., 1994, 2000b). Internal lawns are open, relatively wet *Sphagnum-Carex* lawns that represent localized permafrost degradation (Vitt et al., 1994).

Peatlands globally are believed to function as a net sink for atmospheric CO₂ and as a net source of CH₄ (Roulet et al., 1992; Bartlett and Harriss, 1993; Cao et al., 1998; Whalen and Reeburgh, 2000). Detailed C balance studies, however, often reveal that individual peatlands may switch from net C sinks to sources on an annual basis (Alm et al., 1997; Rivers et al., 1998; Waddington and Roulet, 2000). The presence or absence of permafrost may have important consequences for C cycling in peatlands, and for our understanding of the future responses of boreal systems to climatic change. However, there are few data comparing C emissions between peatlands with differing permafrost patterns (Bubier et al., 1995; Liblik et al., 1997).

Our research goal was to investigate differences in CO₂ and CH₄ fluxes across the peatland-atmosphere boundary between peatlands with differing permafrost regimes on a local spatial scale in the LPZ. Here, we quantify CO₂ and CH₄ fluxes in internal lawns, and compare these to C fluxes from surrounding peatlands, including frost mounds (with intact permafrost) and continental bogs (i.e. with no

* Corresponding author. Tel.: +1-403-780-492-1298; fax: +1-403-780-492-9234.

E-mail addresses: turetsky@ualberta.ca, mturesk@nrcan.gc.ca (M.R. Turetsky).

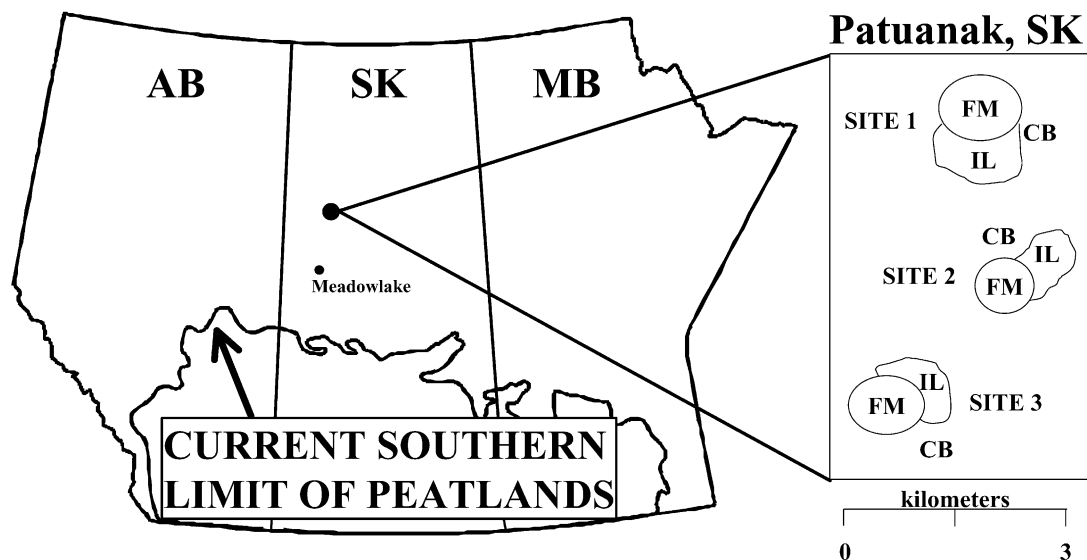


Fig. 1. Map of western, continental Canada [Alberta (AB), Saskatchewan (SK), Manitoba (MB)] showing the location of our study area in central Saskatchewan, and a schematic outlining our sampling design. We measured gaseous C emissions in three sites, each of which contained a bog underlain with intact permafrost (FM), an internal lawn (IL) and continental bog (CB).

evidence of permafrost; Vitt et al., 1994). We did not aim to capture the full extent of variability in emission rates over a growing season. Instead, we sampled in adjacent peatland features (internal lawn, frost mound, and bog) simultaneously to determine the influence of permafrost and permafrost melt on C emissions.

2. Materials and methods

2.1. Field sites

Our study area is a peatland complex near Patuanak, Saskatchewan ($55^{\circ}51' \text{ N}$, $107^{\circ}41' \text{ W}$) situated in the LPZ (Fig. 1). Ombrotrophic bog, dominated by *P. mariana*, *Ledum groenlandicum*, and *Sphagnum fuscum*, is the most common wetland feature in the area. Isolated frost mounds are also present as well as internal lawns; the latter of which represent recent past or ongoing permafrost melt. Bogs underlain by permafrost have closed canopies of *P. mariana*; moss cover typically consists of *Pleurozium schreberi* and *Hylocomium splendens*. Internal lawns of western Canada are characterized by *S. riparium*, *S. angustifolium*, and *Carex* sp.

We established three study sites, each consisting of a frost mound, an adjacent internal lawn, and a nearby expanse of continental bog (Fig. 1). The internal lawns formed with the collapse of permafrost more than 100 yr ago (Turetsky, unpub data). Sites were sampled three times throughout the growing season of 1998 (referred to as 8/98, 9/98, 10/98). In the spring of 1999, a wildfire burned through Site 1, causing considerable melting of the local permafrost lens and extensive damage through the creation of a fire break (Turetsky and Wieder, 2001). We did not sample this site in

1999, but continued to quantify C emissions on four sampling dates (referred to as 7/99, 8/99, 9/99, 10/99) in the two unburned sites.

2.2. Sampling for CO_2 and CH_4 flux

Fluxes of CO_2 and CH_4 were quantified in each site using opaque closed chambers (2.5 l , 0.2 m^2 area) fitted with rubber septa for headspace sampling. On each sampling date, the three peatland features (frost mound, internal lawn, and continental bog) within a site were sampled simultaneously at midday. Five replicate chambers with sharp plastic edges were placed randomly on each peatland surface and inserted into the peat to a depth of about 5–8 cm. We attempted to minimise installation disturbance by cutting into the peat surface 15–30 min prior to final chamber placement and using temporary boardwalks during sampling in wet areas. Both vascular shrub and non-vascular communities were well represented within chambers, although our chamber volume necessitated the exclusion of larger shrubs and trees. We used syringes equipped with 3-way Luer-lock stopcocks to mix headspace gas within the chamber prior to collecting 15 ml of headspace gas at 0, 15, 30 and 45 min following the start of the measurement period. At each chamber during the measurement period, we recorded air temperatures near the peat surface and peat temperature at 5 cm depth. Afterwards, water table position relative to the peat surface was measured at several locations throughout the area of chamber placement.

Syringes were transported back to the University of Alberta and processed within 48 h. Gas samples were analyzed on a Hewlett Packard 5890 Series II chromatograph using a Chromosorb 102 column and purified He as

Table 1

Analysis of variance results conducted on ranks of the data, with site as a blocked effect, feature as a fixed effect and date as a random effect. The error mean square term is equivalent to variation among chambers for each site \times feature \times date combination. The feature \times date mean square term is used to calculate the F statistic for the fixed feature effect; error mean square terms are used to calculate other F statistics (cf. Underwood, 1997)

	df	Type III sum of squares	F	P
CO ₂ model effects				
Site	2	2188	0.71	0.4950
Feature	2	17437	3.84 ^a	0.0513
Date	6	99961	10.76	< 0.0001
Feature \times Date	12	27233	1.47	0.1475
Error	146	226081		
CH ₄ model effects				
Site	2	10267	3.69	0.0271
Feature	2	93781	12.04 ^a	0.0014
Date	6	47630	5.71	< 0.0001
Feature \times Date	12	46721	2.80	0.0017
Error	155	215402		

^a Feature \times Date mean square used to calculate F statistic.

a carrier gas. Flame ionization and thermal conductivity detectors were used to quantify CH₄ and CO₂ concentrations, respectively. We used external standards of both CH₄ and CO₂ (Scott Gases, Plumsteadville, PA) for calibration, with standard error of multiple injections <5%. Flux rates were calculated from the slopes of headspace gas concentration regressed with time. Nonlinear regressions with R^2 values <0.95 (approximately 10% of chamber flux rates) due to disturbance or ebullition were rejected; data for these chambers are not included in our analysis.

2.3. Statistical design

Our design corresponds to a randomized complete block design with site (site 1,2,3) as the block effect, peatland feature (bog, frost mound, internal lawn) as a fixed effect, and date as a random effect (Fig. 1). Variation among individual chambers, placed randomly on each peatland feature within each site during each sampling date, represent the residual or error term in the ANOVA (cf. Underwood, 1997). The feature by \times date mean square term was used

to calculate the F statistic for the fixed feature effect; error mean square terms were used to calculate other F statistics (cf. Underwood, 1997). Residuals obtained subsequent to running the ANOVA were not normally distributed, for both CO₂ (Shapiro–Wilk, $W = 0.3373$; $P < 0.0001$) and CH₄ (Shapiro–Wilk, $W = 0.8076$; $P < 0.0001$). Therefore, we report results from an ANOVA run on rank-transformed data. Subsequent to obtaining a significant effect, a posteriori comparisons of rank means were accomplished using Tukey's Honestly Significant Difference tests (SAS, 1998).

Stepwise multiple regressions were used to determine the influence of peat temperature, air temperature, and water level height on both CO₂ and CH₄ respiration. We used a Spearman's correlation test to determine whether CO₂ and CH₄ fluxes were correlated, and Pearson's Correlation tests to investigate correlation between soil temperatures, air temperatures and water table height (SAS, 1998).

3. Results

3.1. CO₂ fluxes

CO₂ fluxes varied by feature and sampling date, with no significant interaction between these main effects (Table 1). Internal lawns had higher CO₂ fluxes (mean \pm s.e.: 2.59 ± 0.34) than either frost mounds (1.62 ± 0.29) or bogs (1.94 ± 0.31 mmol CO₂ m⁻² d⁻¹; Table 2). Across peatland types, C fluxes generally were higher during the 1998 sampling events compared to those in 1999 (Table 2; means \pm s.e. for 1998 and 1999 of 2.44 ± 0.27 and 0.80 ± 0.14 mmol CO₂ m⁻² d⁻¹, respectively).

3.2. CH₄ fluxes

CH₄ fluxes varied by a feature \times sampling date interaction (Table 1). In 1998, fluxes were greater from internal lawns than from frost mounds; fluxes from bogs were intermediate and not different from fluxes from either internal lawns or frost mounds (Table 2). In contrast, in 1999 fluxes from internal lawns were lower than in 1998, such that there were no statistically significant differences between features.

Table 2

Mean (s.e.) CO₂ and CH₄ fluxes from adjacent bogs, internal lawns (melted permafrost), and frost mounds (intact permafrost) in north-eastern Saskatchewan on seven sampling dates. For CO₂, different superscript letters or numbers denote significant a posteriori differences between dates or features, respectively (Tukey's HSD). For CH₄, different letter superscripts denote significant a posteriori differences between feature \times date means

Date	CO ₂ flux (mmol m ⁻² d ⁻¹)			CH ₄ flux (μ mol CH ₄ m ⁻² d ⁻¹)		
	Bogs ²	Internal lawns ¹	Frost mounds ²	Bogs	Internal lawns	Frost mounds
8/98	3.40 (0.35) ^a	4.44 (0.54) ^a	2.25 (0.41) ^a	6.26 (2.20) ^{a-c}	26.18 (5.76) ^a	0.26 (0.71) ^{de}
9/98	2.89 (1.16) ^b	1.38 (0.25) ^b	1.66 (0.55) ^b	3.64 (2.10) ^{b-c}	9.18 (2.63) ^{a-c}	0.28 (0.99) ^{de}
10/98	2.01 (0.94) ^b	3.39 (1.12) ^b	2.49 (1.30) ^b	2.64 (0.55) ^{a-c}	38.27 (28.03) ^{ab}	-1.20 (0.69) ^c
7/99	0.78 (0.27) ^{bc}	2.00 (0.43) ^{bc}	0.29 (0.08) ^{bc}	-0.11 (0.32) ^{de}	0.56 (0.75) ^{de}	0.04 (0.35) ^{de}
8/99	0.82 (0.27) ^{bc}	3.17 (2.19) ^{bc}	0.72 (0.23) ^{bc}	-0.40 (0.44) ^{de}	1.50 (1.72) ^{b-c}	-0.68 (0.83) ^c
9/99	0.86 (0.18) ^{bc}	1.55 (0.67) ^{bc}	1.45 (0.52) ^{bc}	3.76 (1.23) ^{a-d}	3.94 (2.80) ^{b-c}	0.71 (8.16) ^{c-c}
10/99	0.38 (0.07) ^c	0.42 (0.15) ^c	0.59 (0.11) ^c	0.69 (0.15) ^{c-c}	3.48 (1.26) ^{a-c}	0.002 (0.19) ^{de}

Table 3

Mean surface peat temperatures, air temperatures, and water table position (\pm s.e.; $n = 15$ and 10 in 1998 and 1999, respectively) in continental bogs, internal lawns, and frost mounds during the 1998 and 1999 sampling events. In frost mounds, we measured depth to the permafrost table or active layer (i.e. seasonally melting ice lying above the permafrost table). Water tables at 0 cm would be flush with the moss surface

	Bogs	Internal lawns	Frost mounds
Air temperature ($^{\circ}$ C)			
8/98	40.0 \pm 0.5	30.5 \pm 0.3	28.7 \pm 0.3
9/98	14.0 \pm 0.7	14.0 \pm 0.7	12.0 \pm 0.5
10/98	12.0 \pm 0.4	12.0 \pm 0.4	9.7 \pm 0.5
7/99	25.5 \pm 0.5	23.5 \pm 0.5	22.0 \pm 0.01
8/99	18.5 \pm 0.8	20.0 \pm 1.3	19.0 \pm 0.01
9/99	21.0 \pm 0.3	17.0 \pm 0.3	16.0 \pm 1.3
10/99	9.5 \pm 1.8	9.0 \pm 1.7	8.5 \pm 1.5
Peat temperature ($^{\circ}$ C)			
8/98	21.1 \pm 0.8	15.6 \pm 0.8	21.9 \pm 0.5
9/98	11.9 \pm 0.5	10.0 \pm 0.4	13.6 \pm 0.5
10/98	9.1 \pm 0.4	7.6 \pm 0.5	8.7 \pm 0.2
7/99	19.1 \pm 0.8	21.5 \pm 0.2	21.1 \pm 0.3
8/99	15.4 \pm 1.2	16.1 \pm 1.4	14.4 \pm 0.8
9/99	13.6 \pm 1.8	9.9 \pm 0.5	9.4 \pm 0.4
10/99	7.2 \pm 1.07	5.2 \pm 0.5	7.1 \pm 1.0
Water table height (cm)			
8/98	36.6 \pm 2.3	18.0 \pm 1.4	65.0 \pm 7.2
9/98	44.8 \pm 2.9	19.8 \pm 0.6	54.4 \pm 1.1
10/98	70.7 \pm 6.4	20.4 \pm 1.9	57.8 \pm 2.5
7/99	31.2 \pm 0.6	18.8 \pm 1.2	39.5 \pm 1.8
8/99	36.5 \pm 1.5	10.3 \pm 0.5	30.4 \pm 0.8
9/99	26.0 \pm 0.5	14.8 \pm 1.5	40.2 \pm 3.7
10/99	30.7 \pm 2.1	12.2 \pm 3.1	40.0 \pm 1.2

3.3. Interrelationships

Fluxes of CO_2 and CH_4 were significantly and positively correlated (Spearman's correlation coefficient = 0.47, $P = 0.0001$). Stepwise multiple regressions showed that both air and surface peat temperatures, but not water table position (Table 3), were significant predictors of CO_2 emission (model $R^2 = 0.27$; air temperature, $P < 0.0001$; peat temperature, $P = 0.0026$). Water table level and peat temperature, but not air temperature, were significant, but surprisingly weak predictors of CH_4 flux (model $R^2 = 0.18$; water level, $P < 0.0001$; peat temperature, $P = 0.0084$).

Peat temperature and air temperature were positively correlated throughout the two year sampling period (Pearson's correlation coefficient, $r = 0.81$, $P = 0.0001$). While water table levels and peat temperatures showed no correlation ($r = 0.09$, $P = 0.1381$), water table levels were negatively correlated with air temperatures ($r = -0.12$, $P = 0.0580$).

4. Discussion

CO_2 flux measurements using dark static chambers include respiration from living aboveground and below-

ground plant parts (mosses, sedges, short-statured shrubs) as well as aerobic and anaerobic microbial activity within the peat column. Generally, our values for CO_2 flux (mean \pm s.e. = 2.05 ± 0.18 $\text{mmol m}^{-2} \text{d}^{-1}$ across 170 chambers) agree with other studies using static chambers to quantify CO_2 flux from peatlands. CO_2 emissions averaged 1.20 and 3.95 $\text{mmol m}^{-2} \text{d}^{-1}$ for a bog and poor fen in Alberta, respectively (Vitt et al., 1990). Moore and Knowles (1987) reported rates of CO_2 evolution from subarctic fens in Quebec ranging from 2.00 to 29.00 $\text{mmol CO}_2 \text{m}^{-2} \text{d}^{-1}$, while fluxes measured in drained swamp peatlands in southern Quebec ranged from 0 to 0.36 $\text{mmol CO}_2 \text{m}^{-2} \text{d}^{-1}$ (Shannon et al., 1993).

Both field and laboratory approaches have identified soil temperatures and water table position as important environmental controls on C mineralization to CO_2 in organic soils (cf. Scanlon and Moore, 2000; Chapman and Thurlow, 1998; Yavitt et al., 1987, 1997; Alm et al., 1997; Laine et al., 1996; Silvola et al., 1996). In this study, peat and air temperatures during chamber incubation (Table 3) together explained only about 25% of the variation in CO_2 flux, and showed significant collinearity. Additionally, height of water levels (bogs and internal lawns) or permafrost tables (frost mounds; Table 3) were not important controls on CO_2 flux in these boreal peatlands.

Methane fluxes from peatlands typically show large variation, both temporally and spatially (cf. Waddington and Roulet, 1996; Van den Pol-Van Dasselaar, 1999; Kettunen et al., 2000). Methane flux from our peatland sites ranged from -24.2 to 344.4 $\mu\text{mol CH}_4 \text{m}^{-2} \text{d}^{-1}$, and averaged 6.4 ± 2.1 $\mu\text{mol CH}_4 \text{m}^{-2} \text{d}^{-1}$ (across 178 chamber measurements). These flux estimates are low compared to other published values. We note, however, that few studies have investigated CH_4 flux from western continental peatlands where conditions tend to be dry with low water tables (but see Suyker et al., 1996). Vitt et al. (1990) also used static chambers to quantify CH_4 emissions from peatlands in northern Alberta, and measured negligible CH_4 emissions from a bog, and mean rates of 56.3 $\mu\text{mol CH}_4 \text{m}^{-2} \text{d}^{-1}$ from a poor fen. Episodic rain events may play important roles in controlling pulses of CH_4 emissions from these moisture deficient peatlands (cf. Kettunen et al., 2000). This process is difficult to characterize in a remote field setting, but points to the need for more temporally intensive measurements of CH_4 emissions in peatlands affected by permafrost melt.

Ombrotrophic peatlands in continental Canada typically have water tables lower than 40–50 cm below the moss surface. Low water tables probably contribute to minimal CH_4 flux to the atmosphere as CH_4 produced at depth is oxidized as it diffuses upward through the aerobic surface peat layers. Although water tables in our sites were slightly higher in 1999 than in 1988, particularly within frost mounds (Table 3), they were not high enough to significantly enhance CH_4 emission relative to 1998. Water level measurements in our sites were correlated

with air temperatures, yet neither were important predictors of CH₄ flux.

Peat accumulation represents the balance between net primary production (NPP) and gaseous C losses from heterotrophic respiration plus dissolved C losses. Previous work has shown that internal lawns accumulate near-surface peat at rates faster than in bogs or frost mounds (Turetsky et al., 2000; Camill et al., 2001; Turetsky, unpub data). Here, we show that conversion of frost mounds to internal lawns is associated with 1.6- and 30-fold increases in CO₂ and CH₄ emissions, respectively. This suggests that internal lawn NPP also must be high compared to NPP in frost mounds, from which internal lawns are derived.

While frost mounds may act to remove CH₄ from the atmosphere through oxidation pathways, internal lawns showed elevated net CH₄ flux to the atmosphere in our sampling over two frost-free seasons. As CH₄ shows greater greenhouse warming potential relative to CO₂ (Schimel et al., 1996), continued permafrost melt on a regional scale in the LPZ of boreal western Canada may represent a positive feedback on climate change. Although internal lawns will undergo succession, eventually to continental bogs (Camill, 1999; Turetsky et al., 2000), the temporal trajectory of this development is poorly known. The internal lawns studied here formed from permafrost collapse more than a century ago (Turetsky, unpub data), suggesting that permafrost melt may yield elevated emissions of CH₄ over prolonged periods, particularly in the LPZ where temperatures may be too warm to support permafrost re-aggradation (Halsey et al., 1995). Different permafrost regimes appear to influence CH₄ and CO₂ fluxes across the peatland-atmosphere boundary, and therefore the patchy spatial distribution of peatland features (bogs without permafrost, frost mounds, and internal lawns representing recent thaw) should be considered when scaling-up from site-specific studies to estimate boreal peatland C budgets to regional scales.

Acknowledgements

Research funding was provided by the National Science Foundation to R.K. Wieder and J.B. Yavitt, the Collaborative Natural Sciences and Engineering Research Council to D.H. Vitt, the Canadian Circumpolar Institute at the University of Alberta to M.R. Turetsky and D.H. Vitt, and the Society of Wetland Scientists to M.R. Turetsky. We thank Jen Bachand, Susan Crow, Linda Halsey, Shelley Manchur, John Navaratnam, Lauren Snook, and Chris Williams for assistance in the laboratory or field.

References

Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykanen, H., Martikainen, P.J., 1997. Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia* 110, 423–431.

Bartlett, K.B., Harriss, R.C., 1993. Review and assessment of methane emissions from wetlands. *Chemosphere* 26, 261–320.

Beilman, D.W., Vitt, D.H., Halsey, L.A., 2001. Localized permafrost peatlands in western Canada: definitions, distributions and degradation. *Arctic, Antarctic, and Alpine Research* 33, 70–77.

Bubier, J.L., Moore, T.R., Bellisario, L., Comer, N.T., Crill, P.M., 1995. Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. *Global Biogeochemical Cycles* 9, 455–470.

Camill, P., 1999. Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany* 77, 721–733.

Camill, P., Lynch, J.A., Clark, J.S., Adams, J.B., Jordan, B., 2001. Changes in biomass, aboveground net primary production and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecosystems* 4, 461–478.

Campbell, I.D., McAndrews, J.H., 1993. Forest disequilibrium caused by Little Ice Age cooling. *Nature* 366, 336–338.

Cao, M., Gregson, K., Marshall, S., 1998. Global methane emission from wetlands and its sensitivity to climate change. *Atmospheric Environment* 32, 3293–3299.

Chapman, S.J., Thurlow, M., 1998. Peat respiration at low temperatures. *Soil Biology and Biochemistry* 30, 1013–1021.

Halsey, L.A., Vitt, D.H., Zoltai, S.C., 1995. Disequilibrium response of permafrost in boreal continental western Canada to climate change. *Climatic Change* 30, 57–73.

Kettunen, A., Kaitala, V., Alm, J., Silvola, J., Nykanen, H., Martikainen, P.J., 2000. Predicting variations in methane emissions from boreal peatlands through regression models. *Boreal Environment Research* 5, 115–131.

Laine, J., Silvola, J., Tolonen, K., Alm, J., Nykanen, H., Vasander, H., Sallantausta, T., Savolainen, L., Sinisalo, J., Martikainen, P.J., 1996. Effect of water-level drawdown on global climatic warming: Northern peatlands. *Ambio* 25, 179–184.

Liblik, L.K., Moore, T.R., Bubier, J.L., Robinson, S.D., 1997. Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, Northwest Territories, Canada. *Global Biogeochemical Cycles* 11, 485–494.

Moore, T.R., Knowles, R., 1987. Methane and carbon dioxide evolution from subarctic fens. *Canadian Journal of Soil Science* 67, 77–81.

Rivers, J.S., Siegel, D.I., Chasar, L.S., Chanton, J.P., Glaser, P.H., Roulet, N.T., McKenzie, J.M., 1998. A stochastic appraisal of the annual carbon budget of a large circumboreal peatland, Rapid River Watershed, Northern Minnesota. *Global Biogeochemical Cycles* 12, 715–727.

Roulet, N.T., Ash, R., Moore, T.R., 1992. Low boreal wetlands as a source of atmospheric methane. *Journal of Geophysical Research* 97, 3739–3749.

SAS 1998. SAS/SYSTAT operating system, Version 4.10. SAS Institute, Cary, North Carolina.

Scanlon, D., Moore, T., 2000. Carbon dioxide production from peatland soil profiles: the influence of temperature, oxic-anoxic conditions and substrate. *Soil Science* 165, 153–160.

Schimel, D., Alves, D., Enting, I., Heimann, M., Joos, F., Raynaud, D., Wigley, T., 1996. Radiative forcing of climate change. CO₂ and the carbon cycle. In: Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A., Maskell, K., et al. (Eds.), *Climate Change 1995. The Science of Climate Change*, Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, pp. 65–131.

Shannon, G., Heyes, A., Moore, T., 1993. Carbon dioxide and methane fluxes from drained peat soils, southern Quebec. *Global Biogeochemical Cycles* 7, 247–257.

Silvola, J., Alm, J., Ahlholm, U., Nykanen, H., Martikainen, P.J., 1996. CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. *Journal of Ecology* 84, 219–228.

Suyker, A.E., Verma, S.B., Clement, R.J., Billesbach, D.P., 1996. Methane flux in a boreal fen: season-long measurement by eddy correlation. *Journal of Geophysical Research-Atmospheres* 101, 28637–28647.

- Turetsky, M.R., Wieder, R.K., Williams, C.J., Vitt, D.H., 2000. Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. *Écoscience* 7, 379–392.
- Turetsky, M.R., Wieder, R.K., 2001. A direct approach to quantifying organic matter lost as a result of peatland wildfire. *Canadian Journal of Forest Research* 31, 363–366.
- Underwood, A.J., 1997. *Experiments in Ecology*. University Press, Cambridge.
- Van den Pol-Van Dasselaar, A., Van Beusichem, M.L., Oenema, O., 1999. Determinants of spatial variability of methane emissions from wet grasslands on peat soil. *Biogeochemistry* 44, 221–237.
- Vitt, D., Bayley, S., Jin, T., Halsey, L., Parker, B., Craik, R., 1990. Methane and carbon dioxide production from wetlands in boreal Alberta. Report on Contract No. 90-0270 to Alberta Environment, 9820-106 St. Edmonton Alberta.
- Vitt, D., Halsey, L.A., Zoltai, S.C., 1994. The bog landforms of continental western Canada in relation to climate and permafrost patterns. *Arctic and Alpine Research* 26, 1–13.
- Vitt, D.H., Halsey, L.A., Bauer, I.E., Campbell, C., 2000a. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences* 37, 683–693.
- Vitt, D.H., Halsey, L.A., Zoltai, S.C., 2000b. The changing landscape of Canada's western boreal forest: the current dynamics of permafrost. *Canadian Journal of Forest Research* 30, 283–287.
- Waddington, J.M., Roulet, N.T., 1996. Atmosphere-wetland carbon exchanges: scale dependency of CO₂ and CH₄ exchange on the developmental topography of a peatland. *Global Biogeochemical Cycles* 10, 233–245.
- Waddington, J.M., Roulet, N.T., 2000. Carbon balance of a boreal patterned peatland. *Global Change Biology* 6, 87–97.
- Whalen, S.C., Reeburgh, W.S., 2000. Methane oxidation, production, and emission at contrasting sites in a boreal bog. *Geomicrobiology Journal* 17, 237–251.
- Yavitt, J.B., Lang, G.E., Wieder, R.K., 1987. Control of carbon mineralization to CH₄ and CO₂ in anaerobic, *Sphagnum*-derived peat from Big Run Bog, West Virginia. *Biogeochemistry* 4, 141–157.
- Yavitt, J.B., Williams, C.J., Wieder, R.K., 1997. Production of methane and carbon dioxide in peatland ecosystems across North America: effects of temperature, aeration, and organic chemistry of peat. *Geomicrobiology Journal* 14, 299–316.
- Zoltai, S.C., 1995. Permafrost distribution in peatlands of west-central Canada during the Holocene warm period 6000 years BP. *Géographie Physique et Quaternaire* 49, 45–54.