

# Decomposition and Organic Matter Quality in Continental Peatlands: The Ghost of Permafrost Past

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## ABSTRACT

Permafrost patterning in boreal peatlands contributes to landscape heterogeneity, as peat plateaus, palsas, and localized permafrost mounds are interspersed among unfrozen bogs and fens. The degradation of localized permafrost in peatlands alters local topography, hydrology, thermal regimes, and plant communities, and creates unique peatland features called “internal lawns.” I used laboratory incubations to quantify carbon dioxide (CO<sub>2</sub>) production in peat formed under different permafrost regimes (with permafrost, without permafrost, melted permafrost), and explored the relationships among proximate organic matter fractions, nutrient concentrations, and decomposition. Peat within each feature (internal lawn, bog, permafrost mound) is more chemically similar than peat collected within the same province (Alberta, Saskatchewan) or within depth intervals (surface,

deep). Internal lawn peat produces more CO<sub>2</sub> than the other peatland types. Across peatland features, acid-insoluble material (AIM) and AIM/nitrogen are significant predictors of decomposition. However, within each peatland feature, soluble proximate fractions are better predictors of CO<sub>2</sub> production. Permafrost stability in peatlands influences plant and soil environments, which control litter inputs, organic matter quality, and decomposition rates. Spatial patterns of permafrost, as well as ecosystem processes within various permafrost features, should be considered when assessing the fate of soil carbon in northern ecosystems.

**Key words:** carbon; peat; peatlands; boreal forest; permafrost; climate warming; decomposition; organic matter quality; moss; bryophytes

## INTRODUCTION

Boreal regions represent about 10% of the Earth's land area, covering roughly 14.3 million km<sup>2</sup>, and store up to 40% of the world's terrestrial carbon (C) (Apps and other 1993). In North America, most of this soil C is found in deep peat deposits extending across about 14% of the boreal ecoregion (National Wetlands Working Group 1998; Bhatti and others

2002). Peat is partially decomposed plant material that accumulates where plant production exceeds organic matter losses through heterotrophic respiration, leaching or dissolved export, fire combustion and/or other disturbance-related losses. Peatland C stocks in boreal and subarctic regions have accumulated slowly since the last deglaciation and represent a long-term sink for atmospheric carbon dioxide (CO<sub>2</sub>).

Soil temperatures, particularly in thick layers of insulating organic soil, can be buffered from variation in atmospheric temperatures. Ecosystem processes in surface peatland soils may show lags in response to modern climatic flux, while C stored in

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deep peat may be protected to some extent from future climate change (see Camill and Clark 2000). Currently, distributions of discontinuous permafrost in continental North America are not in equilibrium with regional climate. Insulative properties of organic matter, as well as the high albedo of mosses and lichens, enable soil ice to persist where climate would not otherwise support permafrost (Koster 1995; Halsey and others 1995; Beilman and others 2001). As a result, permafrost at its southern limit exists in boreal peatlands where mean annual air temperatures exceed 0°C.

Global models predict that climate warming will be most severe at high latitudes (Raisanen 1997). Soil processes in peatlands with localized permafrost may serve as indicators of future soil–climate interactions. After the Little Ice Age, average temperatures across Canada's boreal forest have increased by about 1°C. This warming triggered widespread thaw of localized permafrost in peatlands near the southern limit of discontinuous permafrost (Thie 1974; Zoltai 1993; Vitt and others 1994, Vitt and others 2000). Permafrost continues to degrade in peatlands across much of the boreal forest ecoregion, in response to either recent warming and/or increased fire frequency. Thaw of localized permafrost in peatlands creates unique peatland ecosystems in continental boreal regions called "internal lawns." Initially colonized by semi-aquatic *Sphagnum* mosses and *Carex* species (Vitt and others 1994), internal lawns are wet fens surrounded by unfrozen peatland. Further north, permafrost collapse within larger peat plateaus or palsas also occurs with fire, local disturbance, or permafrost maturity. Vegetation in internal lawns remains distinct from the surrounding landscape for hundreds of years (Beilman 2001) and can be detected through aerial photography and satellite imagery. Over time, peat accumulation above the water table leads to drier soil conditions in internal lawns, with subsequent succession to bog communities (Beilman 2001; Camill and others 2001).

Permafrost stability contributes to spatial heterogeneity in boreal regions, controlling surface hydrology, thermal regimes, and species communities in peatlands. Such changes to plant and soil environments may influence rates of litter inputs, litter turnover rates, and organic matter quality in peatlands, with implications for regional peatland C emissions and storage. My objectives in this study were (a) to determine whether permafrost regimes (that is, sites with permafrost, without permafrost, and with melted permafrost) in peatlands influence organic matter quality and laboratory rates of soil CO<sub>2</sub> production and (b) to explore controls of or-

ganic matter quality, nutrients, and/or moisture availability on peat CO<sub>2</sub> production. Several approaches currently are used to characterize litter or soil quality, including elemental, isotopic, and compound-specific techniques. I relied on proximate analysis to sequentially quantify organic matter fractions, including (a) water-soluble carbohydrates (simple carbohydrates such as glucose, sucrose, and fructose), (b) soluble nonpolar (fats, oils, and waxes), (c) water-soluble phenolics, (d) holocellulose (structural glucose polymer), and (e) acid-insoluble material (AIM; tannins, cutins, and lignin) (Preston and others 1997). Proximate analysis condenses the complexity of organic matter characterization into several fractions and thus may be useful for large spatial analysis or modeling. However, such an approach requires a better understanding of correlations between substrate pools and ecosystem processes in boreal peatlands, and spatial variations in the nature and size of substrate pools in heterogeneous boreal landscapes.

## STUDY REGION

Samples were collected from a peatland complex about 10 km south of Patuanak, Saskatchewan (55°51'N, 107°41'W) in the localized permafrost zone of Canada. Mean annual temperatures and precipitation in this area averaged -1.0°C and 444 mm, respectively, from 1951 to 1980 (Environment Canada 1998). Most peatland in the area is ombrotrophic bog, dominated by understories of *Ledum groenlandicum*, and *Sphagnum fuscum* and sparse canopies of *Picea mariana*. Also present on the landscape are isolated permafrost mounds, with intact permafrost tables usually 60–80 cm beneath the vegetation surface. Permafrost mounds have dense canopies of *P. mariana*, with groundcover of feather mosses (usually *Pleurozium schreberi* and *Hylocomium splendens*) and lichen species (Beilman 2001). Internal lawns, representing recent and/or ongoing permafrost melt, commonly are associated with localized permafrost in North America (Beilman and others 2001). Internal lawns are open fens characterized by *Sphagnum riparium*, *Sphagnum angustifolium*, and *Eriophorum vaginatum*.

## METHODS

Three study sites were established using aerial photography to locate internal lawns. Each site consisted of an adjacent permafrost mound, internal lawn, and continental bog (Beilman 2001; see also Turetsky and others 2002). Sites were sampled three times during the growing season of 1998 and

four times throughout 1999. In the spring of 1999, a wildfire burned through one of the sites. I did not sample this site in 1999, but continued to sample within the two unburned sites.

On each sampling date, three replicate peat cores were randomly collected at each site within the three peatland features (internal lawns, bogs, permafrost mounds), for a total of nine cores in each site per sampling date, using PVC cylinders 1 m in height, 10 cm in diameter. Cores were extruded in the field, and peat was harvested from two depth intervals: (a) surface peat located 5–10 cm beneath the living moss surface, and (b) deep peat located 65–75 cm from the moss surface. Both deep and surface peat from the bog features tended to be dominated by *S. fuscum* remains. Peat from the permafrost mounds was always located above the permafrost table in the active layer and was comprised of feather moss, lichen, and root material. Internal lawn stratigraphies always contain a transition at depth from dense sylvic peat of the former permafrost bog to less dense *S. riparium/Carex* peat (representing peat accumulation post-thaw) near the surface. This physical–botanical transition marks the locality of permafrost collapse within peat profiles. I sampled immediately above the collapse transition to avoid sampling peat from the former permafrost mound at depth. Samples were not mixed and were stored at field moisture levels in Ziploc bags. Headspace was removed from each bag, and samples were transported on ice to the University of Alberta for analysis within 48–72 h.

## Carbon Dioxide Production Rates

I incubated peat samples under both aerobic and anaerobic conditions at 18–20°C. Ten-gram subsamples of peat at field moisture conditions were placed in 125-ml Mason jars with rubber septa inserted through lids. Aerobic subsamples were incubated in room air headspace. For anaerobic subsamples, I removed air within Mason jars using a vacuum pump and replaced the headspace with O<sub>2</sub>-free N<sub>2</sub>, repeating this procedure five times. Stopcock grease was used around lids and septa to prevent headspace leakage. Jars were gently shaken periodically to enhance mixing of the headspace gas with peat. I removed 15 ml of headspace gas with plastic syringes equipped with three-way Luer-lock stopcocks at 0, 4, 12, 24, and 48 h after the Mason jars were sealed. Gas samples were replaced with equal volumes of room air and N<sub>2</sub> in the aerobic and anaerobic incubations, respectively. After the incubation, headspace volume within each jar was estimated from the weight of water

required to fill each jar to capacity. Samples were dried at 60°C to a constant mass for dry-mass determinations.

Gas samples were analyzed on a Hewlett Packard 5890 Series II chromatograph using a Chromosorb 102 column and purified helium as a carrier gas. Thermal conductivity and flame ionization detectors were used to quantify CO<sub>2</sub> and CH<sub>4</sub> concentrations, respectively. I used external standards of CO<sub>2</sub> (500, 1,000, and 10,000 μmol mol<sup>-1</sup> in helium) and CH<sub>4</sub> (0.5, 1, and 5 μmol mol<sup>-1</sup>) (Scott Gases, Plumsteadville, PA, USA) for calibration, with SE of multiple injections less than 5%. Production rates were calculated from the slopes of headspace (within the Mason jar) gas concentration regressed with time. Corrections were made for the N<sub>2</sub> or room air dilutions during laboratory incubations. Nonlinear slopes ( $P < 0.05$ ), due to possible disturbance effects, headspace leaking, or headspace saturation, were rejected (about 10% of total slopes). Most samples neither produced nor consumed CH<sub>4</sub> (slopes were not significantly different from 0;  $P > 0.05$ ), these data are not reported here.

I used a randomized complete block design in which CO<sub>2</sub> production rates were analyzed using a four-way mixed model analysis of variance. Site was included as the block effect, peatland feature (internal lawns, bogs, and permafrost mounds), and aeration status (aerobic versus anaerobic incubations) were included as fixed effects; date (seven sampling dates) and depth (surface versus deep peat) were included as random effects. Variation among replicate incubation jars represents the residual or error term in the analysis of variance (ANOVA). The feature × date × aeration status × depth mean square term was used to calculate the  $F$  statistic for the fixed effects; the error mean square terms were used to calculate other  $F$  statistics (Underwood 1997). A *posteriori* comparisons of means were accomplished using Tukey's Honestly Significant Difference tests (SAS Institute, Cary, NC, USA). All production rates are shown as means ± one SE and are expressed as μmol g dry mass<sup>-1</sup> d<sup>-1</sup>.

## Organic Matter Quality

A suite of organic fractions was quantified on subsamples from the 1998 collections. Sequential extractions were used to separate the following proximate organic fractions: soluble nonpolar, hot water-soluble carbohydrates, hot water-soluble phenolics, holocellulose, and AIM following Wieder and Starr (1998). All organic chemistry data are

**Table 1.** Results of a Four-way, Mixed Model Analysis of Variance for Carbon Dioxide Production Rates, with Site as a Blocked Effect, Date and Depth as Random Effects, and Feature and Aerobic Status as Fixed Effects

| Model Effects               | df  | Type III       |        |        |
|-----------------------------|-----|----------------|--------|--------|
|                             |     | Sum of Squares | F      | P      |
| Site                        | 2   | 817.55         | 1.31   | 0.2705 |
| Feature                     | 2   | 78,24.93*      | 22.26  | 0.0002 |
| Date                        | 6   | 10,485.97      | 5.61   | 0.0001 |
| Depth                       | 1   | 60,283.46      | 193.44 | 0.0001 |
| Aeration Status             | 1   | 2,895.48*      | 16.47  | 0.0023 |
| Feature*Date                | 12  | 3,687.73       | 0.99   | 0.4612 |
| Feature*Depth               | 2   | 887.95         | 1.42   | 0.2418 |
| Feature*Aeration            | 2   | 204.39         | 0.33   | 0.7206 |
| Date*Depth                  | 6   | 7,444.26       | 3.98   | 0.0007 |
| Date*Aeration               | 6   | 830.52         | 0.44   | 0.8491 |
| Depth*Aeration              | 1   | 495.26         | 1.59   | 0.2081 |
| Feature*Date*Depth          | 11  | 1,815.97       | 0.53   | 0.8832 |
| Feature*Date*Aeration       | 12  | 1,953.85       | 0.52   | 0.9004 |
| Feature*Depth*Aeration      | 2   | 62.16          | 0.10   | 0.9051 |
| Date*Depth*Aeration         | 6   | 1,807.60       | 0.97   | 0.4474 |
| Feature*Date*Depth*Aeration | 10  | 1,757.54       | 0.56   | 0.8433 |
| Error                       | 416 | 129,639.27     |        |        |

\*Feature  $\times$  date  $\times$  depth  $\times$  aerobic mean square used to calculate F statistic

The error mean square term is equivalent to variation among replicate incubation jars for each site  $\times$  feature  $\times$  date  $\times$  depth  $\times$  aerobic combination. The feature  $\times$  date  $\times$  depth  $\times$  aerobic mean square term is used to calculate the F statistic for the fixed feature effects; error mean square terms are used to calculate other F statistics.

expressed on an ash-free, dry-mass basis. Subsamples also were analysed for nitrogen (N) and phosphorous (P) by Kjeldahl digestions and colorimetric determination on a Technicon Autoanalyzer II. Stepwise multiple regressions were used to investigate the influence of proximate organic fractions, nutrients, and gravimetric moisture content on rates of CO<sub>2</sub> production from the 1998 sampling events (SAS Institute, Cary, NC, USA). Following Turetsky and others (2000), I performed a canonical discriminant analysis using organic matter fractions and nutrient concentrations from internal lawns, permafrost mounds, and bogs located in Saskatchewan (this study) and Alberta (Turetsky and others 2000).

## RESULTS

Rates of CO<sub>2</sub> production vary by (a) aeration status, (b) peatland feature, and (c) depth  $\times$  sampling date, with no other interactions among main effects (Table 1). Across all peat samples, aerobic incubations produced more CO<sub>2</sub> than did anaerobic incubations, averaging  $28.1 \pm 1.6$   $\mu\text{mol CO}_2$  g dry wt<sup>-1</sup> d<sup>-1</sup> and  $22.9 \pm 1.4$   $\mu\text{mol CO}_2$  g dry wt<sup>-1</sup> d<sup>-1</sup>, respectively ( $n = 150$ ). Internal lawn peat respire

more CO<sub>2</sub> than the other peat types, with production rates almost twice as high as permafrost mound peat (Figure 1). Surface peat generally produces more CO<sub>2</sub> than deep peat across the 1998 and 1999 sampling events (Figure 2). Production rates average  $37.3 \pm 2.2$  and  $43.2 \pm 2.1$   $\mu\text{mol CO}_2$  g dry wt<sup>-1</sup> d<sup>-1</sup> for the 1998 and 1999 seasons, respectively.

Organic matter fractions, nutrients, and moisture content generally each vary by a depth  $\times$  feature interaction (Table 2). Permafrost mound peat has greater concentrations of ash and greater gravimetric moisture content than the other peatland types, whereas surface permafrost peat has large concentrations of hot water-soluble phenolics and carbohydrates (Table 2). Concentrations of AIM, N, and P are large in permafrost peat at depth, although AIM concentrations are also large in deeper bog peat. Internal lawn peat has greater concentrations of holocellulose than the other peatland types.

Multivariate analysis was used to explore changes in soil properties across peatland features (internal lawns, permafrost mounds, bogs), across province (Alberta versus Saskatchewan), and with depth (surface, deep) (Figure 3). Bog peat samples cluster relatively tightly, whereas samples from the

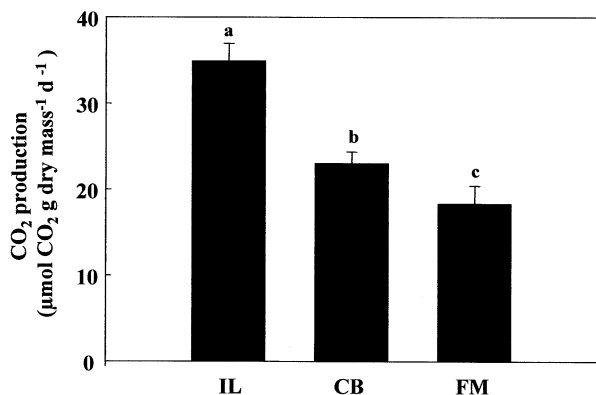


Figure 1. Carbon dioxide (CO<sub>2</sub>) production rates across sampling dates and depths for peat collected within internal lawns (IL), continental bogs (CB), and permafrost mounds (FM). Data are means ± one SE. Means with same letter superscripts do not differ from one another (Table 1; 204 incubations per mean).

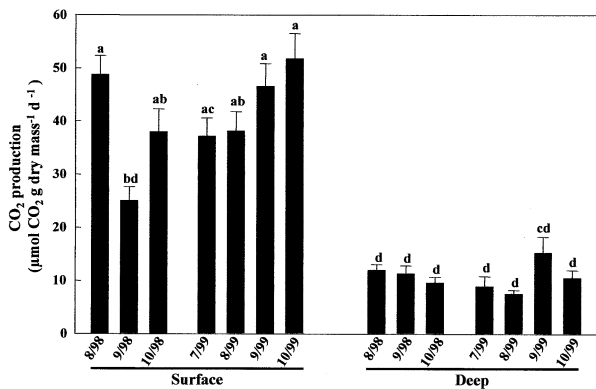


Figure 2. Carbon dioxide (CO<sub>2</sub>) production rates for surface and deep peat across sampling dates in 1998 and 1999. Data are means ± one SE. Means with same letter superscripts do not differ from one another (Table 1;  $n = 54$  incubations for 1998 sampling dates and 36 incubations for 1999 postfire sampling dates).

permafrost mound form a broader band across both axes. Internal lawn peat is more variable in soil properties than the other peatland features. The first axis largely separates permafrost peat from the other peatland features, with greater concentrations of nutrients, ash, soluble proximate fractions, and AIM. For the Saskatchewan data (Alberta data are for surface peat only), samples collected at depth within each feature are more positively correlated with axis one than the surface peat. This suggests that concentrations of nutrients, ash, and certain proximate fractions increase with depth.

I used a series of regression models to explore relationships between organic matter quality and

rates of CO<sub>2</sub> production (Table 3). Acid-insoluble material (AIM), AIM/N ratios, and soil moisture are significant predictors across peat types; together they explain about 29% of the variation in both aerobic and anaerobic CO<sub>2</sub> production rates. Separate regression models for each peatland feature suggest that bogs, internal lawns, and permafrost mounds have different soil controls on CO<sub>2</sub> production. Hot water-soluble fractions (water-soluble phenolics or carbohydrates) are significant predictors within all peatland features. The statistical models generally are stronger for the bog and internal lawn peat (explaining 45% and 43% of variation in CO<sub>2</sub> production, respectively) than for the permafrost peat (explaining 18% of variation in CO<sub>2</sub> production) (Table 3).

Regression models specific to depth intervals explain 7% and 55% of CO<sub>2</sub> production rates in surface and deep peat, respectively. Moisture content is the only significant predictor of CO<sub>2</sub> production in surface peat, whereas soluble fractions (water-soluble phenolics and carbohydrates) are important predictors of CO<sub>2</sub> production in deeper peat samples (Table 3).

## DISCUSSION

Rates of gaseous C production quantified through laboratory incubations of soil or peat represent heterotrophic respiration from a given mass or volume of peat. Over short time frames, autotrophic respiration from severed roots in near-surface samples also may contribute to CO<sub>2</sub> production. Longer-term laboratory incubations (weeks to months) are useful for evaluating shifting substrate and microbial pools during organic matter decomposition. Longer incubations also allow more time for samples to equilibrate following sampling and transport disturbances, which may have resulted in greater anaerobic production rates in this study. However, short-term incubations (days), combined with consistent headspace mixing and rigorous data assessment (that is, rejection of nonlinear gas production), are useful for assessing spatial and temporal heterogeneity in CO<sub>2</sub> production allowing for greater sample sizes.

Although any methodology for estimating soil decomposition involves some level of disturbance, results from laboratory incubations must be interpreted as potential rates of C mineralization in light of sample manipulation and controlled incubation environments. In this study, I expected CO<sub>2</sub> production rates largely to reflect microbial utilization of the most labile and abundant substrates.

**Table 2.** Soil Properties for Boreal Peat Collected at Two Depths: Surface (5–10 cm from vegetation surface) and Deep (65–80 cm from vegetation surface)

|  | Frost mounds              |                           | Internal Lawns             |                             | Bogs                      |                             |
|--|---------------------------|---------------------------|----------------------------|-----------------------------|---------------------------|-----------------------------|
|  | Surface                   | Deep                      | Surface                    | Deep                        | Surface                   | Deep                        |
| <b>Organic fractions</b>                   |                           |                           |                            |                             |                           |                             |
| Soluble nonpolars                          | 8.6 ± 2.8 <sup>c</sup>    | 21.8 ± 4.3 <sup>b</sup>   | 6.2 ± 2.0 <sup>e</sup>     | 6.9 ± 2.2 <sup>e</sup>      | 7.7 ± 2.5 <sup>d</sup>    | 33.5 ± 4.6 <sup>a</sup>     |
| Hot H <sub>2</sub> O-soluble carbohydrates | 63.7 ± 1.7 <sup>a</sup>   | 17.0 ± 0.5 <sup>e</sup>   | 27.9 ± 1.0 <sup>c</sup>    | 18.5 ± 0.7 <sup>e</sup>     | 47.1 ± 1.5 <sup>b</sup>   | 20.9 ± 0.9 <sup>d</sup>     |
| Hot H <sub>2</sub> O-soluble phenolics     | 8.0 ± 0.1 <sup>a</sup>    | 2.4 ± 0.1 <sup>e</sup>    | 4.8 ± 0.1 <sup>c</sup>     | 3.0 ± 0.1 <sup>d</sup>      | 5.4 ± 0.1 <sup>b</sup>    | 2.5 ± 0.1 <sup>e</sup>      |
| Holocellulose                              | 233.7 ± 3.5 <sup>e</sup>  | 239.5 ± 4.5 <sup>e</sup>  | 572.8 ± 4.8 <sup>a</sup>   | 548.9 ± 6.8 <sup>b</sup>    | 485.3 ± 4.8 <sup>c</sup>  | 384.5 ± 10.2 <sup>d</sup>   |
| Acid insoluble material (AIM)              | 565.0 ± 10.2 <sup>b</sup> | 710.1 ± 16.2 <sup>a</sup> | 285.7 ± 7.2 <sup>e</sup>   | 347.2 ± 12.1 <sup>d</sup>   | 403.3 ± 12.6 <sup>c</sup> | 700.8 ± 26.5 <sup>a</sup>   |
| <b>Nutrients</b>                           |                           |                           |                            |                             |                           |                             |
| Phosphorus (P)                             | 0.9 ± 0.03 <sup>c</sup>   | 2.4 ± 0.6 <sup>a</sup>    | 0.6 ± 0.01 <sup>d</sup>    | 0.7 ± 0.2 <sup>d</sup>      | 0.4 ± 0.01 <sup>e</sup>   | 1.9 ± 0.3 <sup>b</sup>      |
| Nitrogen (N)                               | 9.4 ± 0.2 <sup>b</sup>    | 16.8 ± 0.6 <sup>a</sup>   | 6.5 ± 0.2 <sup>e</sup>     | 8.3 ± 0.3 <sup>c</sup>      | 3.9 ± 0.1 <sup>f</sup>    | 7.3 ± 0.3 <sup>d</sup>      |
| AIM/N                                      | 63.1 ± 1.2                | 106.3 ± 25.7              | 45.6 ± 1.0                 | 53.2 ± 8.8                  | 108.3 ± 4.9               | 104.4 ± 6.0                 |
| <b>Edaphic Properties</b>                  |                           |                           |                            |                             |                           |                             |
| Ash  | 4.5 ± 0.1 <sup>a</sup>    | 3.8 ± 0.1 <sup>b</sup>    | 2.9 ± 0.2 <sup>e</sup>     | 3.4 ± 0.2 <sup>c</sup>      | 3.1 ± 0.1 <sup>d</sup>    | 2.9 ± 0.1 <sup>e</sup>      |
| Moisture                                   | 107.2 ± 11.9 <sup>e</sup> | 543.3 ± 27.0 <sup>d</sup> | 1697.0 ± 93.7 <sup>a</sup> | 1,677.0 ± 82.1 <sup>a</sup> | 893.2 ± 24.4 <sup>c</sup> | 1,177.0 ± 52.2 <sup>b</sup> |

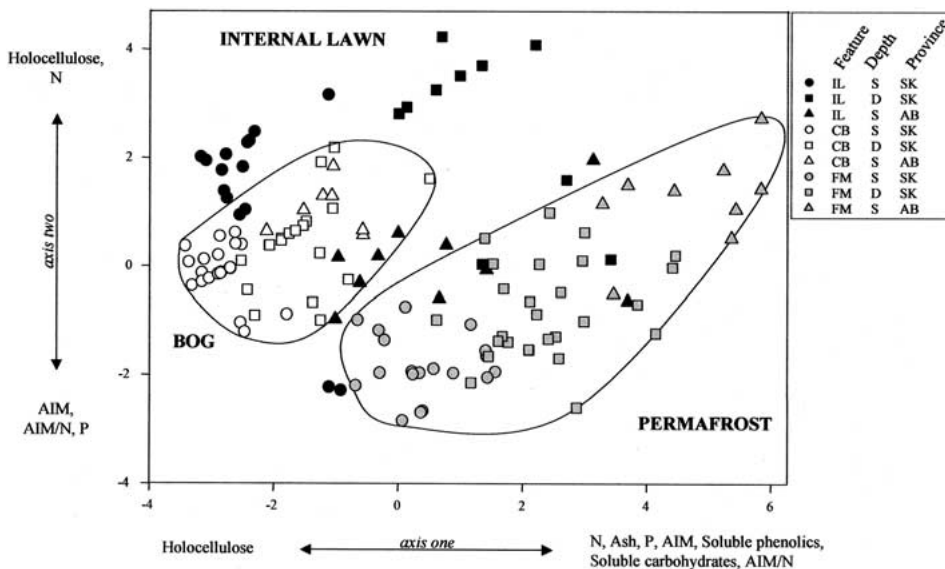
Data are means ± one SE.

Concentrations of organic fractions and nutrients are shown in mg g<sup>-1</sup> ash-free dry mass; ash and moisture content are shown in % dry mass.

All variables except AIM/N varied by a depth × feature interaction.

Means with the same letter superscripts do not differ significantly ( $P < 0.05$ ;  $n = 27$  incubations).

AIM/N varied by feature ( $P = 0.0001$ ; 2 df;  $F = 11.85$ ;  $n = 54$  incubations), with the highest ratio in bogs ( $106.55 \pm 3.82^a$ ), followed by permafrost mounds ( $84.24 \pm 12.68^b$ ) and internal lawns ( $49.29 \pm 4.33^c$ ).



**Figure 3.** Results of a canonical discriminant analysis of eight soil properties, which significantly distinguished data within each feature × depth province combination (Wilks' lambda  $F = 10.14$ ;  $P < 0.0001$ ). Each plotted point represents a peat sample collected from internal lawns (IL), bogs (CB), or permafrost mounds (FM) in a peatland complex in Alberta (data from Turetsky and others 2000) or Saskatchewan (this study). Peat was collected either near the vegetation surface (S; 2–10 cm) or from deeper peat layers (D; 65–75 cm). Because peat from the Alberta sites was collected in 40-cm length cores, only surface data are shown for the Alberta features. The first and second canonical axis explained 67% and 17% of the total variation in soil chemistry, respectively. Significant positive or negative Pearson correlations ( $P < 0.05$ ) between the axes and soil parameters are indicated beneath and to the left of the graph in ranked order. Lines drawn around the permafrost and bog data are for illustrative purposes only.

**Table 3.** Results of Stepwise Multiple Regression Models Assessing the Influence of All Measured Soil Parameters on Rates of Carbon Dioxide Production for the 1998 Sampling Events

| Soil Properties             | Partial $R^2$ | Slope $\pm$ SE    | $F$   | $P$    |
|-----------------------------|---------------|-------------------|-------|--------|
| All Peat                    |               |                   |       |        |
| Acid insoluble material     | 0.2208        | $-0.02 \pm 0.01$  | 19.66 | 0.0001 |
| Moisture                    | 0.0563        | $0.01 \pm 0.002$  | 2.15  | 0.0001 |
| AIM/N                       | 0.0134        | $0.24 \pm 0.17$   | 2.12  | 0.0475 |
| Model $R^2$                 | 0.2905        |                   |       |        |
| Within Features             |               |                   |       |        |
| Bogs                        |               |                   |       |        |
| Soluble phenolics           | 0.3511        | $4.81 \pm 0.02$   | 48.70 | 0.0001 |
| Soluble carbohydrates       | 0.0748        | $.28 \pm 0.16$    | 6.79  | 0.0107 |
| Holocellulose               | 0.0219        | $0.05 \pm 0.03$   | 3.45  | 0.0467 |
| Model $R^2$                 | 0.4478        |                   |       |        |
| Permafrost mounds           |               |                   |       |        |
| Soluble carbohydrates       | 0.1739        | $0.46 \pm 0.23$   | 20.54 | 0.0001 |
| Acid insoluble material     | 0.0087        | $0.02 \pm 0.02$   | 1.09  | 0.0402 |
| Model $R^2$                 | 0.1826        |                   |       |        |
| Internal lawns              |               |                   |       |        |
| Soluble phenolics           | 0.3284        | $5.07 \pm 2.16$   | 4.42  | 0.0185 |
| Holocellulose               | 0.0457        | $-0.24 \pm 0.07$  | 5.22  | 0.0249 |
| Moisture                    | 0.0297        | $-0.71 \pm 0.37$  | 3.50  | 0.0451 |
| Acid insoluble material     | 0.0289        | $-0.08 \pm 0.04$  | 2.26  | 0.0468 |
| Model $R^2$                 | 0.4327        |                   |       |        |
| Within Depths               |               |                   |       |        |
| Surface peat                |               |                   |       |        |
| Moisture                    | 0.0747        | $0.007 \pm 0.004$ | 9.88  | 0.0020 |
| Model $R^2$                 | 0.0747        |                   |       |        |
| Deep peat                   |               |                   |       |        |
| Water-soluble phenolics     | 0.3141        | $6.16 \pm 2.40$   | 10.07 | 0.0044 |
| Water-soluble carbohydrates | 0.1206        | $0.17 \pm 0.06$   | 5.28  | 0.0325 |
| Acid insoluble material     | 0.0536        | $-0.01 \pm 0.003$ | 2.53  | 0.0485 |
| Holocellulose               | 0.0638        | $0.01 \pm 0.01$   | 3.39  | 0.0522 |
| Model $R^2$                 | 0.5521        |                   |       |        |

Statistical models linking peat quality to  $\text{CO}_2$  production enable an initial assessment of the substrates correlated to  $\text{CO}_2$  production.

Direct comparison between incubation studies can be difficult due to differing laboratory conditions during incubation trials. As with other soil types, rates of  $\text{CO}_2$  production in peat vary with the degree and duration of decomposition, temperature, and water content (Scanlon and Moore 2000). However, rates of  $\text{CO}_2$  production measured here generally agree well with published values. For example, mean estimates of  $\text{CO}_2$  production from boreal peat range from 0.1 to 113.0  $\mu\text{mol CO}_2 \text{ g dry wt}^{-1} \text{ d}^{-1}$  (compare Moore and Dalva 1997; Scanlon and Moore 2000; Waddington and others 2001), whereas production rates in this study range from 0 to 162.0  $\mu\text{mol CO}_2 \text{ g dry wt}^{-1} \text{ d}^{-1}$ . From a variety of northern peat types,

Moore and Dalva (1997) measured average  $\text{CO}_2$  production rates of 22.7 and 11.4  $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ d}^{-1}$  under aerobic and anaerobic conditions, respectively. Although rates of aerobic mineralization in this study (averaging 28.1  $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ d}^{-1}$ ) agree well with their data, my estimates of anaerobic production (averaging 22.9  $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ d}^{-1}$ ) are higher than reported estimates. Molar ratios of aerobic:anaerobic  $\text{CO}_2$  production have averaged between 7:1 and 2.5:1 (Moore and Dalva 1997; Bergman and others 1999; Scanlon and Moore 2000). Here aerobic:anaerobic ratios for  $\text{CO}_2$  production in bogs, internal lawns, and permafrost mounds each averaged 1.2:1, reflecting high anaerobic production rates across peat types. In this study, longer laboratory incubations may have yielded greater differences between aerobic and anaerobic  $\text{CO}_2$  production.

## Permafrost Conditions

Peat collected from internal lawns produces more CO<sub>2</sub> than bogs or permafrost mounds (Figure 1). Increased moisture availability under dry continental climates or more labile substrate chemistry after permafrost thaw likely leads to greater decomposition. Saturated conditions in internal lawns can persist for decades to centuries, although eventually peat accumulation above the water table will allow for the colonization of drier moss and lichen species (Beilman 2000; Camill and others 2001).

Internal lawns and other collapse features in peatlands have faster rates of peat accumulation than bogs or permafrost mounds (Robinson and Moore 2000; Turetsky and others 2000; Camill and others 2001). Carbon dioxide production rates quantified in this study, along with field measurements of ecosystem respiration (Turetsky and others 2002) and litterbag mass losses (Turetsky 2002) suggest that heterotrophic respiration is greater in internal lawns than other peatland types. Thus, faster rates of soil C storage post-thaw in these sites likely are driven by increased net primary production rather than decreased decomposition (see Camill and others 2001 for processes in collapse scars).

Canonical discriminant analysis is a dimension-reduction multivariate procedure related to principal component analysis and canonical correlation. Here I build on a canonical discriminant analysis from Turetsky and others (2000) to explore variation in soil chemistry: (a) within peatland features with depth, (b) between peatland features differing in permafrost regime, and (c) between peatland complexes in two provinces (Alberta data from Turetsky and others 2000, Saskatchewan data from this study). Bog peat clusters more tightly than the other peat types and thus is chemically more similar across depths and provinces (Figure 3). Peat from the other peatland features, particularly internal lawn samples, is more variable with wider separation of points across both axes. Such trends in organic matter quality likely reflect differences in botanical composition (that is, *Sphagnum fuscum* in the bogs, wetter *Sphagnum* species in the internal lawns, feather mosses and black spruce in the permafrost mounds) and/or the history of decomposition and substrate utilization in each peatland feature. Permafrost mounds are associated with low rates of vertical peat accumulation (cm/y) (Turetsky and others 2000); therefore, deeper permafrost peat is likely to be older than all other peat samples.

Generally, soil samples within each peatland feature cluster more tightly than soil within each province or depth. Differences in soil chemistry between peatland features, then, are greater than regional differences occurring between provinces or within-site differences occurring with depth. This suggests that botanical controls are more important to peat chemistry than climatic or diagenic controls. Permafrost stability and its influence on peatland vegetation, temperature, and soil moisture regimes is important for understanding patterns of organic matter quality across boreal landscapes.

## Substrate Controls on Carbon Dioxide Production

Regression models were used to provide information on substrate (organic matter fractions and nutrients) and moisture controls on CO<sub>2</sub> production (Table 3). This approach suggests that three soil properties (AIM, moisture content, and AIM/N) are important to CO<sub>2</sub> production across the peatland features. AIM is the most important predictor of CO<sub>2</sub> production rates. This agrees with upland decomposition models, in which AIM or AIM/N often are strong predictors of decomposition (see Melillo and others 1989; Preston and others 2000; Trofymow and others 2002). In this study, concentrations of AIM explained only about 22% of variation in CO<sub>2</sub> production rates, representing a significant but somewhat weak predictor.

Mosses tend to decompose more slowly than vascular species (Aerts and others 1999; Hobbie and others 2000), and common litter quality indices have not adequately characterized nonvascular plant decomposition (Hobbie and others 2000). Nonvascular species have unique physiological and structural characteristics that may influence organic matter decay (see Turetsky 2003). For example, bryophytes lack true lignin structures, although *Sphagnum* and other moss species are known to possess lignin-like polymers comprised of monomers linked by simple ether/ester bonds (see Williams and others 1998). Additionally, the production of antimicrobial agents (Verhoeven and Toth 1995; Verhoeven and Liefveld 1997) and low nitrogen requirements (Press and Lee 1982) may influence correlations between substrate quality and decomposition rates in bryophyte-derived litter and soils.

I constructed a separate regression model for each peatland feature to determine whether controls on CO<sub>2</sub> production vary between *Sphagnum*-dominated (internal lawns and bogs) and feather-

moss/*P. mariana*-dominated (permafrost) peatlands (Table 3). Within each peatland feature, soluble fractions such as hot water-soluble phenolics or carbohydrates are the most important predictors for CO<sub>2</sub> production. AIM is insignificant or explains little variation in CO<sub>2</sub> production within each peatland feature. This suggests that CO<sub>2</sub> production within a single boreal peat type is correlated to the size of relatively small, labile C pools (see Updegraff and others 1995). However, across broader spatial scales or a more complex boreal landscape, decomposition in peatlands is better predicted by more recalcitrant AIM (see Trofymow and others 2002). Scale-dependent correlations between ecosystem processes and substrate pools or other soil properties may have important consequences for ecosystem modeling at large scales.

Surprisingly, soil chemistry is a better predictor of CO<sub>2</sub> production in *Sphagnum*-derived bog and internal lawn peat, explaining 45% and 43% of CO<sub>2</sub> variation, respectively, than in permafrost peat. Soil chemistry, dominated by the proximate fractions, explained only 18% of variation in CO<sub>2</sub> production in peat from the feather moss/*P. mariana* permafrost mounds (Table 3). In this study area, Navaratnam (2003) measured greater concentrations of ergosterol (indicative of fungal biomass) in a permafrost mound than in adjacent peatland features. Estimates of microbial diversity using Jaccard's coefficients also are dissimilar across peat from a bog, permafrost mound, and internal lawn (Navaratnam 2003). Distinct microbial communities may preferentially utilize different substrates (see Fisk and others 2003), which might explain differences in correlations among substrate pools and CO<sub>2</sub> production in these peatland features. However, relatively poor model fits within each peatland feature, particularly in the permafrost mound (Table 3), also suggest that traditional organic matter characterization is not sufficient for predicting peat decomposition.

### Within-Site Variability

Laboratory incubations of peat collected at various field depths enable an assessment of where CO<sub>2</sub> can be produced throughout a peat profile. Not surprisingly, peat just beneath the vegetation surface produces more CO<sub>2</sub> than older samples collected from deeper peat layers (Figure 2). These surface samples also have greater concentrations of hot water-soluble carbohydrates, hot water-soluble phenolics, and holocellulose than deeper peat layers (Table 2). Hot water-soluble carbohydrates and phenolics in litter and surface soils can be

leached or degraded through microbial activity. Over time, C in recalcitrant soil structures may be chemically protected from microbial decay, particularly in peatlands where C also can be physically protected through burial or transfer to anaerobic settings.

Moisture content is the only significant predictor of CO<sub>2</sub> production in surface peat, but it explains only 7% of observed variation (Table 3). Generally, moisture availability and water table position are important controls on C mineralization in peatlands (see Svensson and Rosswall 1984; Moore and Knowles 1989; Shurpali and others 1995; Silvola and others 1996). However, here moisture content is positively correlated to CO<sub>2</sub> production (that is, with a positive slope). Thus, low moisture availability may limit decomposition near the surface of these continental peatlands. This is reasonable particularly in the bogs and permafrost mounds where water/permafrost tables can be more than a meter beneath the vegetation surface.

Previous work shows that concentrations of hot water-soluble carbohydrates explain about 80% of variation in moss litter turnover in continental peatlands (M. R. Turetsky unpublished). In this study, however, soluble fractions are not significant predictors of surface peat CO<sub>2</sub> production (Table 3). Surface peat (likely 5–15 years of age) is older than bryophyte litter, and labile compounds may already have undergone diagenesis. Surprisingly, however, soluble proximate fractions are the strongest predictors of CO<sub>2</sub> production in deeper peat samples (Table 3). Mean concentrations of water-soluble phenolics and carbohydrates are 57% and 59% smaller, respectively, at depth than at the surface (Table 2). Yet low concentrations of soluble fractions remain important to CO<sub>2</sub> production in older organic material (Table 3). Labile soluble compounds likely degrade quickly in surface peat layers over time. Generally, however, soluble compounds also are transported downward from surface material with leaching and are used by microbes (see Charman and others 1999; Chasar and others 2000). Microbial biomass and/or microbial metabolic products also may influence soluble material in deeper peat.

Correlations between substrate pools and decomposition likely are influenced by the increased chemical complexity of bulk surface peat relative to moss litter. Although peat in continental boreal regions tends to be bryophyte-dominated (Turetsky 2003), organic soils generally represent a mixture of vascular and nonvascular litter, as well as products from fire and microbial activity. Proximate analysis represents a fairly simplistic approach for

characterizing organic matter (that is, several fractions) and is useful for understanding controls on litter turnover at the species level (M. R. Turetsky unpublished). A more detailed characterization of soil quality and microbial communities, or a chemical marker sensitive to diagenesis, is required to accurately predict decomposition in peat samples.

## CONCLUSION

Widespread degradation of permafrost in North American boreal peatlands has occurred with climate warming since the Little Ice Age (see Thie 1974; Halsey and others 1995; Zoltai 1995; Vitt and others 2000). Localized permafrost collapse creates unique peatland ecosystems called "internal lawns". Initially after permafrost collapse, internal lawns are wet *Sphagnum* fens that accumulate peat more quickly than other peatland types (Robinson and Moore 2000; Turetsky and others 2000; Camill and others 2001). Multivariate analysis suggests that soils within each peatland feature are more chemically similar than soils within each province (Saskatchewan, Alberta) or within depth intervals (Figure 3). Peat from internal lawns produced about twice as much CO<sub>2</sub> during laboratory incubations than permafrost peat (Figure 1), suggesting that hydrological, thermal, and/or botanical changes with permafrost collapse stimulate decomposition in peat. AIM is the single most important predictor of CO<sub>2</sub> production across *Sphagnum* and woody peat types (Table 3), but it explains only about 30% of variation in CO<sub>2</sub> production. Soluble proximate fractions are more important predictors of CO<sub>2</sub> production within each peatland type, suggesting that spatial scale or landscape complexity influences correlations between substrate pools and ecosystem processes such as decomposition. Together, these results suggest that permafrost patterning (including the thaw of permafrost decades or centuries in the past) has important influences on soil chemistry, with feedbacks to ecosystem processes such as decomposition.

Soil organic matter represents a heterogeneous mixture of compounds decomposing at individual rates. The poor fit of regression models in this study suggests that traditional fractionation techniques are not adequate for predicting the decomposition of northern peat. To better characterize the quality and turnover of soil organic matter, future studies and modeling work in northern ecosystems should consider (a) the unique chemical structures of *Sphagnum* species and other bryophytes that may

influence ecosystem processes, (b) the importance of small labile C pools that can be decomposed in litter and surface soils or transported to deeper soil layers, (c) chemical C stabilization through the production of recalcitrant organic matter as well as physical protection of soil C in anaerobic peat layers, and (d) landscape complexity in plant communities and soil environments occurring with permafrost patterning.

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