Decomposition of peat from upland boreal forest: Temperature dependence and sources of respired carbon

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[1] The response of large stores of carbon in boreal forest soils to global warming is a major uncertainty in predicting the future carbon budget. We measured the temperature dependence of decomposition for upland boreal peat under black spruce forest with sphagnum and feather moss understory using incubation experiments. CO_2 efflux rates clearly responded to temperature, which ranged from $-10°$ to $+8°C$ by $\sim 2°C$ increments. At temperatures below $0°C$, significant decomposition was observed in feather moss peat but not in wetter sphagnum peat. Above $0°C$, decomposition was exponentially related to temperature, corresponding to a Q(10) (the ratio of the rate of CO_2 evolution at one temperature divided by that at a temperature $10°C$ cooler) of 4.4 for feather moss and 3.1 for sphagnum peat. The greatest change in CO_2 evolution rate with temperature occurred between $-2°$ and $0 °C$, which coincided with the phase transition of soil water. We saw no large change in the rate of CO_2 evolution between incubation experiments separated by a 6 month storage period for feather moss peat. Stable C isotope measurements of evolved CO_2 and the rate of change of CO_2 evolution with time suggest different substrates are used to sustain heterotrophic respiration above and below freezing. Radiocarbon signatures of CO_2 respired from both types of peat reflected significant contributions from C fixed in the last 35 years ("bomb" ^{14}C) as well as C fixed prior to 1950. We observed no change in the $\Delta^{14}C$ of respired CO_2 with temperature. Isotopic signatures of peat components showed that a combination of substrates must contribute to the CO_2 evolved in our incubations. Decomposition of fine roots (which made up less than 7% of the total peat C) accounted for $\sim 50\%$ of respired CO_2 in feather moss peat and for $\sim 30\%$ of respired CO_2 in sphagnum peat. Fine-grained (<1 mm), more humified material that makes up $60-70\%$ of the bulk peat organic carbon contributed significantly to heterotrophic respiration ($\sim 30\%$ in feather moss and $\sim 50\%$ in sphagnum moss peat), despite slow decomposition rates. Increased temperatures caused enhanced decomposition from all pools without changing their relative contributions. Because the contribution of peat decomposition is a small portion of total soil respiration at the study site, increased respiration rates would be difficult to measure as increased fluxes in the field. Nonetheless, sustained warming could lead to significant loss of C from these peat layers. *INDEX TERMS:* 1615 Global Change: Biogeochemical processes (4805); 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 0330 Atmospheric Composition and Structure: Geochemical cycles; 1040 Geochemistry: Isotopic composition/chemistry; *KEYWORDS:* decomposition, peat, soil carbon, radiocarbon, temperature response, boreal forest

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1. Introduction

[2] Nearly half of the carbon stored in forested ecosystems is in boreal forests, and 84% of it is stored in soil organic matter [*Dixon et al.*, 1994]. The amount of carbon stored in boreal peatlands alone is 190–550 Pg C [*Gorham*, 1991]. This carbon has accumulated over the time since retreat of the last major ice sheets [*Harden et al.*, 1992] and is preserved in part because cold temperatures and poor

drainage limit decomposition rates. At present, boreal forests are thought to be a sink of CO_2 throughout the first part of the growing season and a source of CO_2 during late summer, fall and winter, when respiration exceeds photosynthesis and soil temperatures are warmer than air temperatures [*Goulden et al.*, 1998]. The annual net carbon balance of individual boreal forest stands depends on factors such as stand age, drainage, and weather variability [*Frolking*, 1997; *Goulden et al.*, 1998; *Rapalee et al.*, 1998; *Harden et al.*, 2000; *Litvak et al.*, 2002].

[3] Boreal and northern continental regions have warmed faster than other parts of the globe in recent decades [*Chapman and Walsh*, 1993]. While warming is expected to stimulate both plant production and organic matter decomposition [*Kirschbaum*, 1995; *Keyser et al.*, 2000], related changes in precipitation and inundation may cause other responses [*Chapin et al.*, 1995]. Of major concern is whether higher carbon storage expected in boreal forest biomass will offset the loss of carbon from soils by enhanced decomposition. Recently, some have argued that increased temperature might stimulate decomposition for only a limited time: until the reserves of easily decomposable carbon are depleted [*Giardina and Ryan*, 2000; *Grace and Rayment*, 2000]. To resolve this issue, we need both reliable quantitative relationships between rates of organic matter decomposition and temperature, and information about the substrates that support heterotrophic decomposition.

[4] Increased organic matter decomposition with temperature has been reported for boreal soils in heating and incubation experiments. Heating the forest floor at a black spruce site in Alaskan taiga approximately 9°C above the ambient soil temperature increased microbial activity and caused a decline of 20% in forest floor biomass over the 3-year period [*Van Cleve and Yarie*, 1986]. *Flanagan* [1986] reported that surface litter layers in birch and black spruce stands increased their respiration rates 2.7 and 2.8 times respectively in response to a temperature increase from 10° to 20°C. However, a warming experiment conducted in northern Sweden showed that after five years of warming the increase in CO_2 efflux from the forest floor in warmed plots was only 10% higher than that from nonwarmed plots [*Jarvis and Linder*, 2000].

[5] Incubation studies [*Nadelhoffer et al.*, 1991; *Clein and Schimel*, 1995] have demonstrated increased temperature dependence of peat decomposition at the freeze-thaw transition. In incubations of taiga and tundra soils from Alaska, *Clein and Schimel* [1995] derived Q(10) values from 1 to 9.8 for the temperature interval from −5 to −2°C, and 5.2 to 23.4 for the interval from −2 to +5°C. While air temperatures in boreal forest vary from −40° to 30°C, peat temperatures in the active layer vary less, from a few degrees below zero in winter to a few degrees above zero°C C in summer. Nonetheless, these relatively small temperature changes could be of major importance if decomposition rates are strongly affected by the freeze-thaw transition.

[6] Organic matter in boreal peat is comprised of at least two major carbon pools that differ in their morphology, chemistry and turnover time [*Trumbore and Harden*, 1997]. Surface detrital carbon represents a smaller part of total organic carbon, and accumulates between disturbances such as fire. It has turnover times ranging from years to decades, depending on factors like substrate and soil drainage. The bulk of organic carbon is stored in deep humic and mineral horizons. It has slower decomposition rates, with turnover times ranging from several hundred years to millennia [*Trumbore and Harden*, 1997]. Although it decomposes slowly, there are sufficient stocks of deep carbon to contribute 9–22% of total heterotrophic respiration in a mature black spruce forest stand [*Trumbore and Harden*, 1997].

[7] *Goulden et al.* [1998] suggested that warming might significantly increase the contribution of this deep carbon pool to soil respiration. Eddy covariance, isotopes in respired CO_2, chamber and laboratory observations at their study site near Thompson, Manitoba, showed increased contribution of decomposition of deep carbon to CO_2 emissions in late summer [*Goulden et al.*, 1998] and in winter [*Winston et al.*, 1997]. Given the immense size of the deep carbon pool, increased decomposition rates could sustain a long-term positive feedback between respiration and temperature.

[8] We studied decomposition of two types of peat from boreal forest soils. Our goals were (1) to establish a quantitative relationship for the temperature dependence of peat decomposition, particularly at the freeze-thaw transition; (2) to find what components of peat organic matter contribute most to the CO_2 efflux; and (3) to determine whether the relative contribution of these sources changes with temperature. To accomplish these goals, we incubated peat collected from sites dominated by either feather mosses or sphagnum mosses at ∼2°C temperature intervals, from −10°C to +8°C. Following an initial test of methods on unhomogenized samples, peat was homogenized to keep all factors other than temperature constant and to obtain a reliable pattern of temperature dependence.

[9] The CO_2 evolution from homogenized peat at different temperatures was used as a measure of the temperature response of decomposition. We compared radiocarbon measurements of the CO_2 evolved over the incubation with C isotopes [^{13}C and ^{14}C] in soil organic matter fractions such as root and moss detritus and humified material to determine the major components contributing to heterotrophic respiration. The incubations were conducted over a period of 2 months to test how changes in decomposition rates over time affected the observed pattern of temperature dependence.

2. Materials and Methods
2.1. Site Description

[10] Peat samples were collected from a 150-year-old black spruce forest, near Thompson, Manitoba, Canada. The sampling locations were approximately 100 meters to the southwest of the eddy covariance flux tower [NOBS, Northern Old Black Spruce site] that makes up a continuing part of the NASA BOREAS experiment. Soils, soil respiration and ecosystem fluxes at this site have been studied previously [*Trumbore and Harden*, 1997; *Harden et al.*, 1997; *Winston et al.*, 1997; *Rapalee et al.*, 1998; *Goulden et al.*, 1998; *Hirsch et al.*, 2002]. Biomass and carbon stocks at this site vary with drainage. Moderately drained areas are populated with tall, dense black spruce [*Picea mariana*] stands with feather moss [*Hylacomium, Pleurozium*] ground cover. Poorly drained areas have sparse and stunted black spruce trees, with *Sphagnum* moss understory and larger

carbon stores in humic soil horizons. The site is currently losing carbon at a rate of 0.3 ± 0.5 metric tons per hectare per year, and it was hypothesized that carbon losses from warming peat offset carbon gains in overlying moss and trees at this site [*Goulden et al.*, 1998].

[11] Peat samples were collected unfrozen in early October, 1999, from the humified organic horizon (40–45 cm depth) underlying feather moss (moderately well drained) and sphagnum moss (imperfectly to poorly drained) cover. Samples were transported to UC Irvine in a cooler, where they were stored at $+4°C$ until the start of the incubation. Two sets of incubations were performed (Figure 1). The first, on intact feather moss peat samples, was begun within two weeks of sample collection. These samples were not sieved or homogenized so as to minimize disturbance, and a subset of the incubated samples included large pieces of wood or root material. Large variability among replicate samples led us to repeat the experiment with homogenized peats from which large (>2 mm) fragments were removed. This second experiment, conducted using both feather and sphagnum moss peat in spring 2000, provides the majority of data reported here; results are compared with the first feathermoss incubation to address effects of storage and homogenization on our results.

2.2. Incubations

[12] Incubation procedures were identical, except for homogenization. For the first incubation, feather moss peat was cut into sections without removing large pieces of root or bark and incubated intact. In this initial experiment, we saw large variations in CO_2 evolution from replicate samples that were clearly related to differences in the amount of roots and large woody debris between samples. Therefore, in the second incubation, performed ~5 months after sample collection, peat from each of the two sites (feather moss and sphagnum peat) was homogenized and large (>2 mm) roots and pieces of wood were removed. This ensured that the substrate for decomposition was constant and only temperature was allowed to vary. We further introduced a normalization procedure to help account for remaining variation among jars.

[13] Samples were incubated at in situ moisture for peat underlying feather moss, and drained to field capacity for peat underlying sphagnum. In the first incubation, pieces of cut peat were suspended in Teflon film in the incubation jars. In the second incubation, between 60 and 70 g of homogenized peat was placed in a 100 ml Qorpack jar that was then placed on the bottom of 1 L Mason jar. For low temperature incubations [<0°C], two jars were placed one on top of the other inside a 1 L Mason jar to obtain higher concentrations of evolving CO_2. In both incubations, ten milliliters of milliQ water were added to the bottom of each Mason jar (away from contact with the sample) to prevent possible drying. The jars were sealed with an air-tight lid fitted with two stopcocks to permit headspace sampling.

[14] At the end of the first incubation, switching jars among freezers demonstrated that the pattern of variation between replicate jars was consistent regardless of temperature (e.g., a jar with a higher rate of CO_2 evolution at 8°C will have a proportionally higher rate at 6°C. Therefore, in the second experiment, we established normalization coefficients accounting for jar-to-jar variations in CO_2 evolution
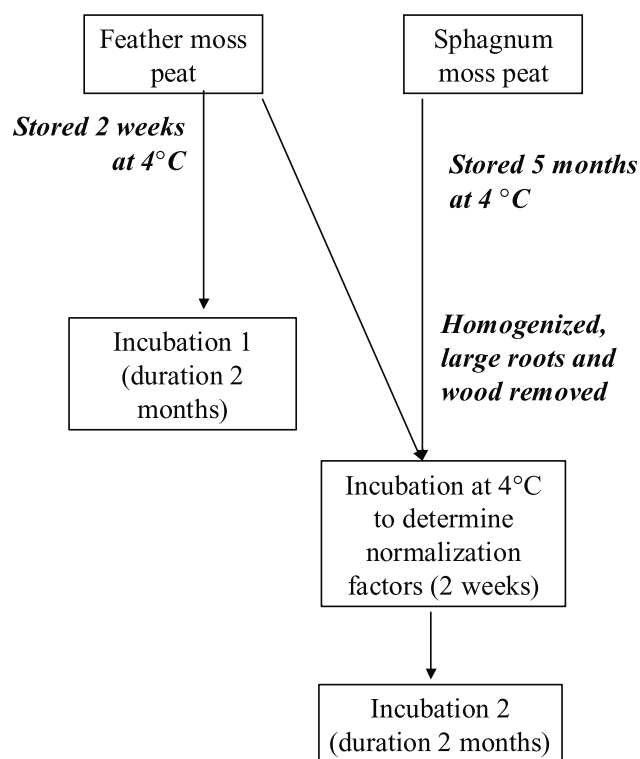

Figure 1. Diagram showing the sequence of sample treatment for the two incubations. Incubation 1 was performed only on feather moss peat. Incubation 2 was performed on homogenized feather and sphagnum moss peat samples that were stored ~5 months at 4°C.

due to remaining inhomogeneities in the soil substrate by incubating jars initially at $+4°C$ for two weeks. The standard deviation of CO_2 evolution per gram organic carbon per day among all jars at this common temperature was 11–15%. Jars that had higher CO_2 evolution rates at $+4°C$ consistently had higher rates at other temperatures as well.

[15] For all incubations, three replicate samples from each site (feather moss and sphagnum) were incubated at each of ten temperatures (−10° to 8°C in 2° increments). On day "zero" of the experiment, the headspace of each jar was scrubbed of CO_2 to remove atmospheric C that would affect isotope signatures. Incubations continued for 2 months with intervals of 1 to 2 weeks between concentration measurements.

[16] CO_2 concentrations were determined using a Shimadzu GC-14A gas chromatograph equipped with a thermal conductivity detector. The GC response was calibrated daily using CO_2 concentration standards spanning the range of concentrations observed in the jars. Air removed from the jars for the CO_2 concentration measurement was replaced by CO_2-free air to keep from contaminating the isotope sampling. We accounted for the effect of dilution in our calculations. The error of the GC-TCD measurements was less than 5%, based on replicate analyses of standards and air samples extracted from the jars.

[17] We used inexpensive household freezers (5 cubic feet), modified to control temperatures from −10 to +8°C. Temperature control was accomplished by cycling each freezer's compressor using a digital controller (OMEGA

CN 7730, OMEGA PR11), with an overall accuracy of ±0.4°C, hooked to a thermocouple inside the freezer. In practice, compressors were switched on every few minutes resulting in a periodic oscillation of air temperature within the freezer of about 1°C. This oscillation was considerably damped within the soil, as demonstrated by RTD probes that were inserted in soil sub-samples. Temperatures were logged continuously. They fluctuated with standard deviation from the mean of less than 0.11°C over the course of the experiment. Temperatures reported here are the means for each freezer over the whole experiment.

[18] Organic carbon content was determined manometrically, from the CO_2 yield of bulk peat samples combusted for graphite target preparation. CO_2 accumulation rates are reported in mg CO_2-C in the jar headspace per gram organic C in the solid peat. The volume of air in the sample-filled jar was determined by measuring the change in jar pressure when air in the jar was allowed to expand into a known, evacuated, volume. Air volume multiplied by the mixing ratio of air was used to calculate the mg CO_2-C in the jar at the incubation temperature.

2.3. Isotope Measurements

[19] CO_2 from incubation jars was collected for ^{13}C and ^{14}C analysis at the end of the 2 months incubation. Gas samples from incubations at t > 0°C were collected on days 56–60, and from incubations at t < 0°C on days 68–69. CO_2 from the jars was collected into a preevacuated 0.5-liter electropolished steel canister, and subsequently purified cryogenically on a vacuum line. One aliquot was saved for ^{13}C analysis and another was reduced to graphite for radiocarbon analysis at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory using the zinc reduction method modified from *Vogel* [1992].

[20] Subsamples of feather moss peat and sphagnum peat were quantitatively divided into size fractions >1 mm (detritus) and <1 mm (fine humified material) by wet sieving. Different constituents of the detrital fraction such as roots, wood, bark, char and individual moss stems were hand-picked from both types of peat. Each of these fractions as well as bulk peat was dried and homogenized. Organic matter was combusted and converted to graphite for radiocarbon measurements following *Trumbore* [1993].

[21] Radiocarbon measurements are reported as $\Delta^{14}C$ (the deviation in ‰ from 0.95 times the oxalic acid standard). The data are corrected for differences in ^{13}C [*Stuiver and Polach*, 1977], and therefore reflect differences in the source or residence time of carbon, rather than mass-dependent fractionation effects. Carbon 13 data are reported as $\delta^{13}C$ (the per mil deviation from the PDB standard). Carbon 13 analyses were made at UCI using a dual inlet isotope ratio mass spectrometer. The accuracy of ^{14}C and ^{13}C measurements are ±6‰ and ±0.02‰, respectively.

2.4. Liquid Water Content

[22] To determine the variation in liquid water as a function of incubation temperature, we measured liquid water content using a *Hydrosense* probe (Campbell Scientific). A 1 L Mason jar filled with homogenized feather moss or sphagnum peat was subjected to freezing and thawing and the change in liquid water content recorded once the temperature had reached a constant value. The

Hydrosense probe signal was calibrated by linear interpolation. The highest Hydrosense reading was assigned liquid water content equal to the volumetric water content determined from the sub-sample of soil by drying, and the reading at −10°C was assumed to be 0% liquid water.

2.5. Determination of Q(10)

[23] The amount of CO_2 increase in the jar (expressed in mg CO_2-C per gram soil C per day) was calculated between sampling days, and normalized by the rate of CO_2 evolution for the same jar evolved at +4°C at the start of the experiment. We calculated the rate of CO_2 evolution per day for three consecutive time intervals, each 10–15 days long. Q(10) values for each time interval were obtained by fitting an exponential of the form Aexp(bT), where T is temperature and A and b are fitted parameters. The Q(10) is the value of this function at temperature T + 10 divided by that at temperature T, or exp(b * 10).

2.6. Determination of Mean Age From Radiocarbon

[24] The radiocarbon content of organic matter reflects the average time since the carbon was fixed by photosynthesis from the atmosphere [*Trumbore*, 2000]. Carbon fixed since the early 1960s has higher ^{14}C than carbon fixed during the previous few centuries due to the incorporation of ^{14}C released by atmospheric thermonuclear weapons testing. Samples with significant amounts of "bomb" carbon have positive ^{14}C values, meaning they have $^{14}C/^{12}C$ ratios greater than that of the 1890 wood used as the ^{14}C standard. The average turnover time of a given organic matter fraction may be estimated using a simple, time-dependent model that tracks C and ^{14}C exchange. This calculation assumes that (1) the organic matter fraction is homogeneous, (2) the time lag between fixation of C from the atmosphere and senescence of plant tissues is known, and (3) either the fraction is at steady state or changing C inventory at a known rate. Samples with negative ^{14}C values, or $^{14}C/^{12}C$ ratios less than that of the 1890 wood standard, have C that has resided in the soil long enough for significant radioactive decay to have occurred. The half-life of radiocarbon is 5730 years, and the average "age" of an organic matter fraction will reflect the relative rates of ^{14}C loss through organic matter decomposition versus radioactive decay [*Torn et al.*, 1997; *Trumbore*, 2000]. More discussion of methods of estimating turnover times from radiocarbon may be found in *Trumbore* [2000], *Gaudinski et al.*, [2000] and *Agnelli et al.* [2002].

2.7. Quantifying Sources of Heterotrophic Respiration

[25] We used an inverse modeling approach to estimate the contribution from different pools of organic matter to CO_2 respired in the incubations. Model code was written using Interactive Data Language (IDL) Version 5.3.2 (MacOS PowerMac) from Research Systems, Boulder, CO. This inverse modeling approach was used previously to predict emissions of C from boreal forest fires and is described more extensively by *Schuur et al.* [2002]. Briefly, the model used the total amount and $^{14}C/^{12}C$ isotope ratio of CO_2 emitted by decomposition to estimate the contribution from organic matter pools that differed in their $^{14}C/^{12}C$ isotope ratio. The model was run separately for incubations of homogenized feather moss peat and homogenized sphagnum peat.

[26] The basic model framework allocated C among pools representing the major pools of soil organic matter (SOM) contained in peat. In feather moss peat, these pools were: fine humified material, fine roots, root hairs, char, and wood plus bark. The sphagnum peat contained the same pools plus an additional moss detritus pool. In the model, C pools were allowed to contribute C to respired CO_2 that reflected the average $\Delta^{14}C$ value of that particular fraction. Charcoal was assumed not to decompose. The isotope values of the C pools were constants derived from laboratory measurements, while the fractions contributing to respired CO_2 by each pool were allowed to vary simultaneously in increments of 10% from 0 to 100%. Solutions were valid when the sum of contributing fractions was equal to 100%, and the sum of weighted $\Delta^{14}C$ matched the isotope values of $CO_2 \pm$ SE from respiration.

[27] The obtained solutions were subsequently filtered applying simple rules to turnover times. Relative turnover times for each C pools were calculated by dividing the size of the pool by its contribution to respiration (pool/flux = turnover time). The rules were (1) relative turnover times of fine roots and root hairs were shorter than relative turnover time of humified material and wood plus bark and (2) fine root and root hair relative turnover time could not equal zero. The first rule is supported by the $\Delta^{14}C$ of the C pools, and the second rule states that at least some amount of the two root pools must be decomposing.

[28] Finally, model permutations that matched both the respiration CO_2 isotopic signature and these rules of turnover times were used to estimate the most likely contribution from each of these pools to the respired CO_2 flux.

3. Results

3.1. Effect of Storage and Sample Pretreatment on CO_2 Evolution Rates

[29] Comparison of the rates of CO_2 evolution with temperature in the two feather moss peat incubations (Figure 2a) and tracking of the relative rate of CO_2 evolution in the $+4°C$ incubations over the ~9 months of the entire experiment (Figure 2b) suggest no large artifacts are associated with sample storage between the two experiments.

[30] Differences in CO_2 evolution rates with time within each incubation experiment are greater than the differences between incubations (Figure 2). The drop in CO_2 evolution rates after the initial 20 days were very similar for the two incubations, and were likely due to a disturbance associated with cutting and/or homogenization of the peat samples. This effect was slightly greater in the second incubation, which was treated more harshly (Figure 2b), and had higher initial rates of CO_2 evolution than the first incubation. Radiocarbon sampled from CO_2 accumulated in the two incubations showed no difference between the two incubation experiments for feather moss (see below).

[31] Sphagnum moss peat incubations were performed only on stored samples. We assume here that effects of storage on CO_2 evolution rates would be similar to those for feather moss peat.

3.2. Effect of Temperature on CO_2 Production Rates

[32] The CO_2 accumulation in the headspace of the jars during incubations was strongly influenced by temperature
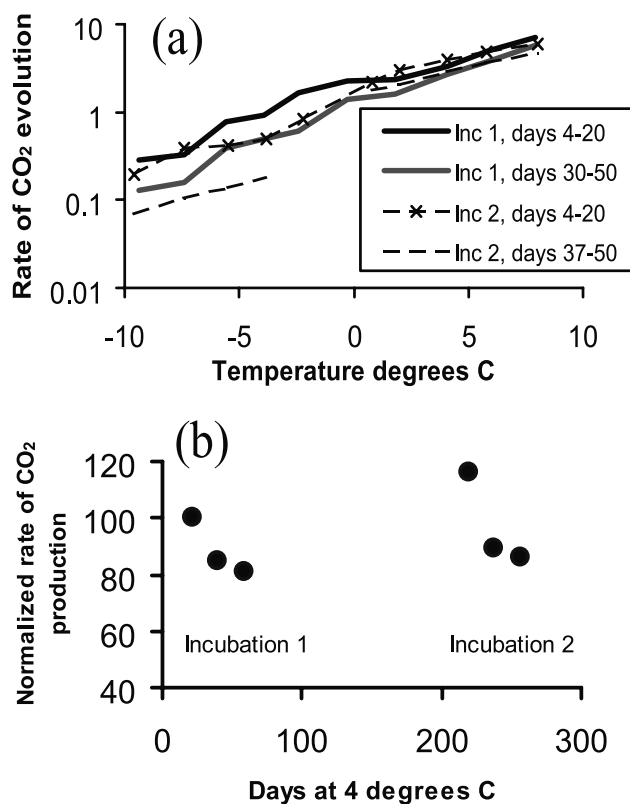

Figure 2. Effect of storage on CO_2 evolution rate in incubations of feather moss peat. (a) Comparison of the rate of CO_2 production by feather moss peat (in mg CO_2 per 100 g of dry peat per day) across the range of temperatures in incubations 1 and 2. Flux data are shown on a log scale to facilitate comparisons across the range of temperatures. (b) Comparison of rates of CO_2 evolution at $4°C$ (the temperature at which peats were stored) between incubations 1 and 2; the mean rate for the first 20 days of experiment 1 is taken as 100%.

(Figure 3). At temperatures above zero, CO_2 evolution rates from sphagnum and feather moss peat were very similar. At temperatures below zero, we observed significant CO_2 evolution from feather moss peat but extremely low CO_2 evolution from sphagnum peat. Temperature sensitivity calculated as the increased CO_2 evolved per $°C$ for each interval of ~$2°C$, was highest in the temperature range from $-2.3°$ to $0.08°C$. Over this temperature interval, the amount of CO_2 evolved per $°C$ rise in temperature is $1.2-1.5$ times greater for feather moss peat and $3-4.2$ times greater for sphagnum peat than for other $2°C$ intervals. This increased sensitivity to temperature coincides with the shift from frozen to thawed conditions.

3.3. Inferred Q(10) Values

[33] Plotting the rate of C accumulation against temperature (Figure 3; normalized for each jar to the rate of CO_2 evolution at $4°C$) emphasizes the differences between decomposition rates above and below the freezing point. No single, uniform temperature relationship can fit decomposition rates for temperatures both greater than and less than $0°C$. We fit exponential curves to CO_2 efflux rates for temperatures $>0°C$ with high (>0.985) R^2 values. For

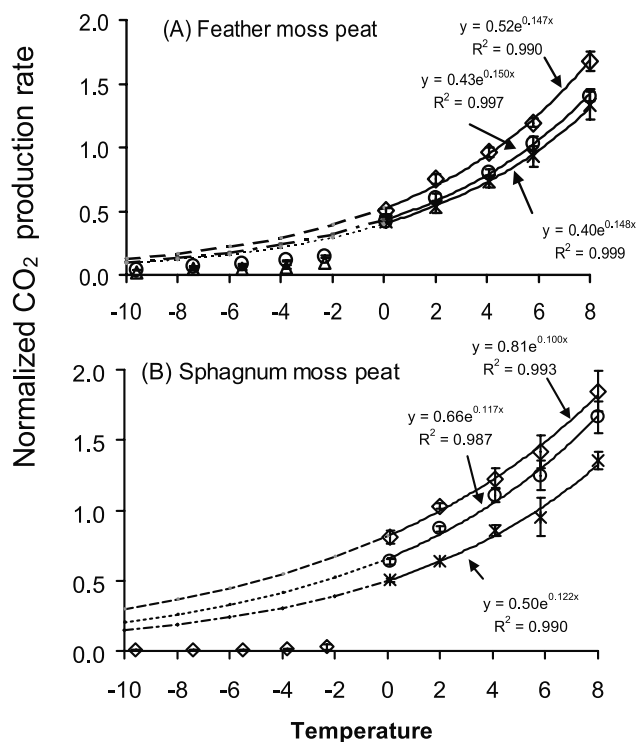**Figure 3.** Temperature dependence (>0°C) of CO_2 efflux for (a) sphagnum and (b) feather moss peat in the second incubation experiment. Rates of CO_2 change are calculated from the increase in CO_2-C in the jar between consecutive measurement periods divided by the time (in days) between the two measurements. Rates are normalized to the efflux observed at 4°C in the preincubation period to reduce variability between replicate jars. Data are shown for three different time periods: days 4–15 (triangles), days 15–30 (circles) and days 30–52 (crosses) for sphagnum and days 4–20 (triangles), 20–32 (circles), and 37–52 (crosses) for feather moss. Points are averages of 2–3 replicate jars, and error bars are standard deviation of the mean. Exponential fits for each period are shown based on incubations at temperatures greater than 0°C only; extrapolations to subzero temperatures show very poor fit.

feather moss peat (Figure 3a), the Q(10)s derived from these exponential fits ranged from 4.3 to 4.5 for incubation 2 (average = 4.4 ± 0.1). The Q(10)s for feather moss peat in incubation 1 (not shown in the Figure 3) ranged from 3.9 to 4.1 (average = 4.0 ± 0.1). For sphagnum peat (Figure 3b), Q(10)s increased over three consecutive ∼2 week sampling periods from 2.7 to 3.4 (average = 3.1 ± 0.3).

3.4. Liquid Water Content

[34] Freezing of water was recorded as a decrease in liquid water content using the *Hydrosense* probe. The initial, room temperature, volumetric water content of incubated samples was 77% in feather moss peat and 88% in sphagnum peat. The maximum rate of change of volumetric water content occurred when the majority of the water froze between ∼−2 and ∼0°C. In feather moss peat, liquid water content changed upon freezing from 59% at −0.01°C to 40% at −0.25°C and to less than 10% at −2°C. In sphagnum peat, liquid water content changed from 80%

at 0.06 to 18% at −0.42°C to 3% at −2.45°C. We observed unfrozen water in excess of 1% in peat samples at temperatures as low as −7.7°C. The drop in liquid water content corresponded to a rapid change in the rate of CO_2 evolution (Figure 4).

3.5. Time Dependence of CO_2 Evolution

[35] CO_2 efflux rates slowed noticeably over the two-month incubation for both types of peat (Figures 2 and 3). Patterns of the relative decrease in CO_2 efflux rates differed markedly for temperatures above and below zero (Figure 5). The rates of CO_2 efflux in jars incubated at temperatures greater than zero (dashed lines/open symbols) decreased in the first month and then leveled off at 60–80% of initial values after about 30 days. In contrast, the rates of CO_2 evolution in jars incubated at temperatures less than zero (solid lines and symbols) continued to decrease through the end of the second month, and showed no signs of stabilizing even though they declined to ∼40% of initial values. Patterns for first and second feather moss peat incubations were the same. Rates of Sphagnum moss CO_2 production below freezing were very low and highly uncertain (Figure 5, bottom panel), but show similar patterns at temperatures above freezing.

3.6. Isotope Data

[36] Radiocarbon CO_2 evolved over the entire period of incubation CO_2 averaged +78.5 ± 10.8‰ for feather moss peat (a mean of 23 measurements over the whole temperature range and during both incubation experiments), and +89.6 ± 3.7‰ for sphagnum peat (a mean of 5 measurements for temperatures above freezing, with no data for the very small amounts of CO_2 evolved below 0°C). The ^{14}C signature of respired CO_2 showed no variation with temperature, even though the amount of CO_2 evolved varied by nearly 100 times between the coldest and warmest temperatures (Figure 6).

[37] Noticeable variation in $\Delta^{14}C$ was observed among individual jars incubated at the same temperature in the pilot study on unhomogenized feather moss peat samples. Peat samples with more abundant fine roots generated more CO_2 with higher $\Delta^{14}C$ than those with large pieces of detritus
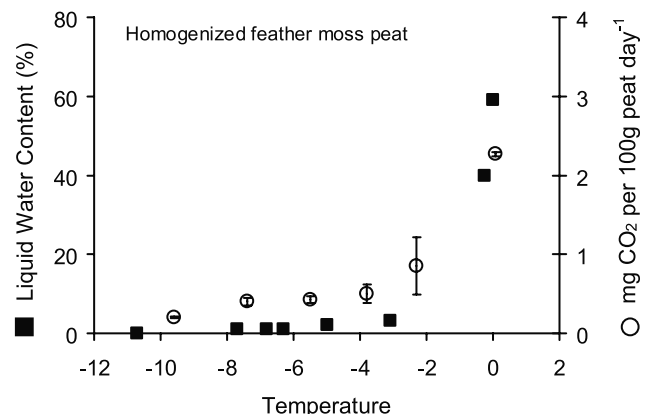

Figure 4. Liquid water content and CO_2 evolution in frozen feather moss peat. Points for CO_2 evolution are averages of 2–3 duplicate jars, and error bars are standard deviation of the mean.
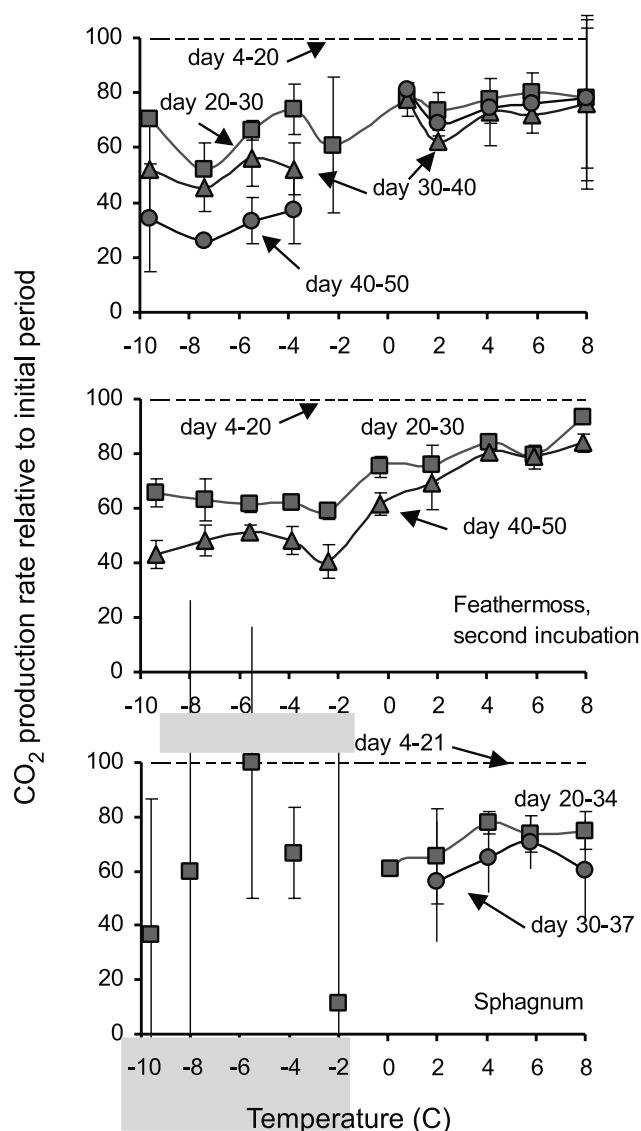
Figure 5. Changes in CO_2 efflux with time for (a) sphagnum and (b) feather moss peat at different temperatures. Rates have been normalized assuming the values for the first 2−3 weeks equal 100%. Error bars are the standard deviation among replicate jars for analyses conducted within each time period. The efflux at temperatures greater than zero decrease and then level off at 60−80% of initial rates after about 30 days. In contrast, the efflux at temperatures less than zero continue to decrease at approximately constant rates and show no signs of leveling off. For sphagnum moss peat, errors in measurement below freezing are large and the amount of CO_2 evolved was very small.

(Table 1). However, the average $\Delta^{14}C$ of evolved CO_2 was the same as in the incubation of homogenized material that occurred ~5 months later. We therefore see no effect of loss of a labile C pool on the isotopic signature of evolved CO_2.

[38] $\delta^{13}C$ values of CO_2 evolved during the incubations did not vary considerably across the temperature range for either feather moss peat ($\delta^{13}C = -26.8 \pm 0.4‰$) or sphagnum peat ($\delta^{13}C = -25.6 \pm 0.2‰$). In the incubation of homogenized feather moss peat samples, there was a

statistically significant difference (ANOVA, p < 0.05) between $\delta^{13}C$ of the CO_2 evolving at $t \geq 0°C$ and at $t < 0°C$. For $t \geq 0°C$, the mean $\delta^{13}C$ for 5 samples was $-26.3 \pm 0.2‰$, and for $t < 0°C$ (5 samples) it was $-30.7 \pm 3.3‰$. $\delta^{13}C$ values did not differ significantly between above-and below-freezing conditions in the earlier, unhomogenized feather moss incubation.

[39] Radiocarbon values of sphagnum and feather moss peat demonstrate that none of the carbon in our samples was older than ~400 years. The $\Delta^{14}C$ values for bulk carbon in homogenized sphagnum and feather moss peat were +20.2‰ and −8.2‰, respectively (Figure 6). Both values reflect a mixture of "bomb" carbon and carbon that likely predated the last fire ~150 years ago. Soil organic matter fractions separated from the bulk organic matter had $\Delta^{14}C$ values ranging from ~+200−+288‰ (corresponding to turnover times of 15−30 years) in fine roots to much lower values in charred organic material (−34‰) and woody debris (−5.1 to −13‰). These oldest components (charred material and woody debris) are likely of pre fire age (>150 years).

[40] The bulk of the organic matter in both peat samples was in the form of fine humified material, with $\Delta^{14}C$ values of −6.4‰ for homogenized feather moss peat and +22.6‰ for sphagnum peat. Turnover times for this bulk material based on $\Delta^{14}C$ would be in the range of 200−500 years; alternatively the humified material could itself represent a mixture of prefire and postbomb material. In feather moss peat, this fine fraction (<1 mm) made up the largest portion
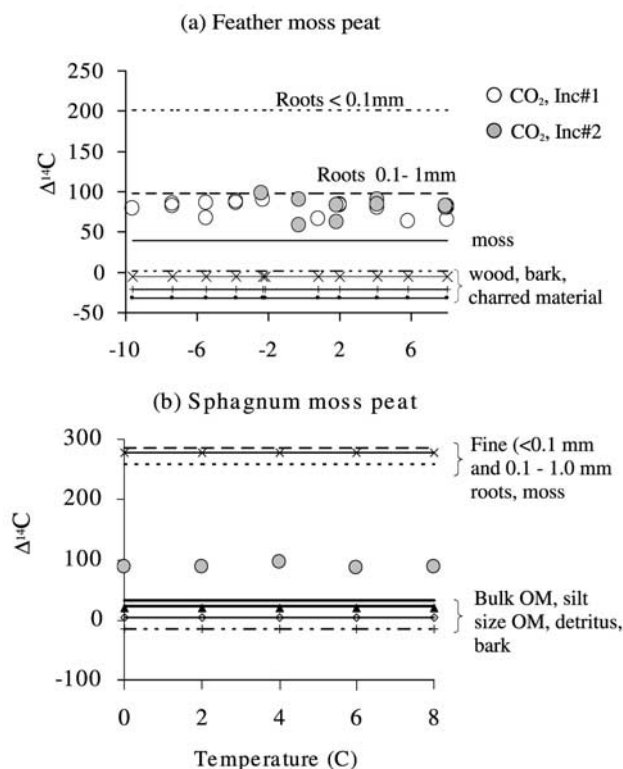

Figure 6. Radiocarbon values of feather moss peat components compared to the isotopic signature of CO_2 evolved in the incubation. Data are reported as $\Delta^{14}C$, the deviation in parts per thousand of the $^{14}C/^{12}C$ ratio in the sample compared to that of the oxalic acid standard.

Table 1. Effect of Substrate Inhomogeneity on Fluxes and Isotopic Values of Respired CO_2 in Feather Moss Peat (Incubation 1)[a]

	Percent Total Organic Carbon					$\Delta^{14}C$ of Incubation Gas at 0°C, ‰	Flux at 0°C, mg CO_2−C/g peat-C per day
	Fraction <1 mm	Fraction >1 mm	Roots <1 mm	Charcoal	Wood and Bark		
JAR 22 (incubation 1)	65	35	17	*4*	*14*	90.2	0.032
JAR 23 (incubation 1)	71	29	7	15	7	58.5	0.006
Homogenized Peat (incubation 2)	75	25	7	*4*	*14*	66.1	0.018

[a] Values given in italics were estimated from a subsample.

of total organic carbon (65–75%), whereas detritus (>1 mm) represented 25–35% of total peat C (Table 2). The relative proportion of detrital components varied significantly in feather moss peat samples prior to homogenization, with 7–17% of total organic carbon in roots, 7–14% in woody debris and bark pieces, and 4–15% in char (Table 2). In homogenized sphagnum peat, humified material and detritus together accounted for 69 and 31% of the total carbon, respectively. Detritus in sphagnum peat consists mostly of sphagnum moss residues and contains far less fine roots and woody debris compared to feather moss peat detritus.

[41] The $\delta^{13}C$ values in different components of feather moss peat ranged from −26.5‰ in humified material to −28.9‰ in larger diameter roots. For sphagnum peat, the $\delta^{13}C$ range was from −26.7‰ in humified material to −28.9‰ in fine roots.

3.7. Modeling of Respiration Source Partitioning

[42] The isotopic signature of CO_2 accumulating in the jar headspaces during the incubation clearly falls between several of the potential respiration sources (Figure 6). The model used estimates the isotopic signature of all possible combinations of sources, then selects those that best fit the observed CO_2 radiocarbon signatures, as described above. Results are given in the last column in Table 2. Although in some cases $\delta^{13}C$ values in organic matter and respired CO_2

might be considered as an additional source constraint, we chose not to use them because preferential respiration of one compound (for example cellulose) might not give a ^{13}C value equal to that of the bulk source material (wood, a combination of lignin and cellulose).

[43] Humified material consisting of decomposed mosses made up 69–75% of the total organic carbon in both peat types. This pool contributes 30% and 50% to the respiration of feather moss peat and sphagnum peat accordingly. In sphagnum peat, roots <1 mm (fine roots and root hairs), with only 5% of TOC contribute ~30% to respiration, and in feather moss peat, where fine roots make up ~7% of TOC, they contribute about 50% to heterotrophically respired CO_2. Wood and bark pieces abundant in the >1 mm detrital fraction of feather moss peat (~14% of TOC) are likely to contribute about 19% to CO_2 efflux. The detrital fraction of sphagnum peat contains less woody debris (~7% of TOC), and a substantial amount of moss residues (~14% of TOC), with likely contribution to respiration of 14% and 3% accordingly.

4. Discussion

4.1. Temperature Dependence of Peat Decomposition

[44] A range of Q(10) values for soil organic matter has been reported from different sites [*Holland et al.,* 2000;

Table 2. Constituents of Homogenized Peat and Their Contribution to Respiration[a]

	$\Delta^{14}C$, ‰	$\delta^{13}C$, ‰	Percent Dry Weight[b]	Percent Total Carbon	Contribution to Respiration,[c] %
Homogenized Feather Moss Peat					
Bulk feather moss peat	−8.2	−26.62	100	100	
Detritus ≥1 mm	25.4	−27.3	16	25	
Humified material <1 mm	−6.4	−26.6	84	75	29.5 ± 18.6
Fine roots 0.1–1 mm	98.3	−27.6	*4*	*6.2*	33.6 ± 17.1
Root hairs <0.1 mm	202.4	−28.3	**	*0.8*	17.1 ± 6.9
Wood	−5.1	−28.4	*10*	*14*	19.1 ± 15.4
Bark	1.9	−28.7	**	combined	combined
Charcoal[d]	−32.3	−27.4	*2*	*4*	0
Incubation gas, t > 0°C	71.8	−26.8	**	0.22	100
Homogenized Sphagnum Peat					
Bulk sphagnum peat	20.2	−26.9	100	100	
Detritus ≥1 mm	33.2	−27.2	17	31	
Humified material <1 mm	22.6	−26.7	83	69	50 ± 8.2
Fine roots 0.1–1 mm	288.1	−27.2	*3*	*4.4*	17.1 ± 4.9
Root hairs <0.1 mm	263.2	−28.9	**	*0.6*	12.9 ± 4.9
Charcoal[d]	−34.5	−27.4	*2*	*5*	0
Bark, wood	−13	−26.3	*5*	*7*	14.3 ± 5.3
Moss residues	*−8.5*		*7*	*14*	2.9 ± 4.9
Incubation gas, t > 0°C	89.6 ± 3.7	−25.6 ± 0.2	**	0.21	100

[a] Values given in italics were estimated from hand-picking of subsets of the total sample.

[b] Two asterisks denote that value in the row above represents the inventory for combined categories (i.e., all roots combined).

[c] Values in the contribution to respiration column are means ± standard deviation derived from computer modeling; means represent mean contribution valid for the majority of solutions found by the model.

[d] Charcoal was assumed not to decompose in the incubations.

Clein and Schimel, 1995], with a general trend of increasing Q(10) at lower temperatures [*Kirschbaum*, 1995]. Data reported by Clein and Schimel for boreal soils (1995) point to (1) large variations in Q(10) values for different substrates and (2) increased temperature sensitivity across the freeze-thaw transition. The temperature response of feather moss in our incubation study is similar to that reported by *Clein and Schimel* [1995] for organic horizons from a white spruce site in Alaska (Table 3), although the absolute rates of CO_2 evolution per gram of incubated organic matter differ between the two studies. Since our data show that no single exponential temperature relationship can well enough describe changes in decomposition above and below $0°C$, we have not attempted to establish a Q(10) value for the temperature interval across freezing point.

[45] Although long-term storage of samples has been shown to decrease the temperature response in incubations [*Holland et al.*, 2000], the disturbance effects associated with starting incubations was greater than differences in CO_2 evolution rates between incubation experiments carried out ~5 months apart (Figure 2b). Further, storage had no effect on the radiocarbon signature of respired CO_2 for feather moss, indicating that the balance of substrates contributing to heterotrophic decomposition stayed the same. The only difference was that $\delta^{13}C$ values of CO_2 respired below $0°C$ in the second feather moss peat incubation were more negative than those in the first.

[46] The Q(10) values we obtained for temperatures $>0°C$ differed significantly for two types of peat (ANOVA, $p < 0.05$), with greater temperature response (Q(10) = 4.4) in feather moss than in sphagnum peat (Q(10) = 3.1). *Goulden and Crill* [1997] report relationships between nighttime soil respiration and 5-cm soil temperature at the NOBS consistent with higher Q(10)s for the feather moss versus sphagnum understory sites (2.5 and 2.0, respectively). Different temperature response was also observed in incubations of tundra soils from different sites [*Christensen et al.*, 1999] and attributed to the different quality of the incubated organic matter. *Boone et al.* [1998] demonstrated that Q(10) values differ for respiration coming from bulk soil, soil lacking roots and soil lacking litter. This implies that differences in substrate quality or proportions of components contributing to respiration will result in site-to-site differences in the temperature sensitivity of decomposition.

[47] In our experiment, detritus retained on a 1 mm sieve contained a higher proportion of fine roots in feather moss peat, and our ^{14}C data suggest a higher proportion (~50%) of CO_2 is derived from root decomposition in feather moss peat as compared to sphagnum peat (~30%). The influence of different amounts of root substrate on decomposition patterns was also observed in replicate samples of unhomogenized feather moss peat (Table 1). Fluxes of CO_2 from the peat sample with a higher proportion of roots (jar 22) were much larger, and had higher ^{14}C values, reflecting considerably higher proportion of root carbon in respired CO_2.

4.2. CO_2 Evolution Below $0°C$

[48] It is well known that soil bacteria adapted to cold (psychrofiles) can grow at temperatures as low as $-12°C$ [*Clein and Schimel*, 1995; *Paul and Clark*, 1996]. Bacterial growth in soil is usually restricted to films of liquid. Thus, if films of liquid water are present in micropores of frozen

Table 3. Comparison of CO_2 Accumulation Rates From the First Month of Various Incubation Experiments[a]

Incubation Temperature	White Spruce Site[b]	Feather Moss Site, BOREAS[c]	Sphagnum Site, BOREAS[c]
$-5°C$	12	5.7	0.5
$-2°C$	24	13	5.6
$+5°C$	100	50	49

[a] Units are mg CO_2-C per gram substrate C per day from 1 month incubations.
[b] *Clein and Schimel* [1995].
[c] This study.

peat, they can be the sites of microbial activity. This is well supported by the correlation between CO_2 release per day and liquid water content in frozen feather moss peat (Figure 4). Increased temperature sensitivity observed in the temperature interval from 0 to $-2°C$ is related to the phase change in the majority of soil water. Liquid water contents we observed at temperatures $<0°C$ were lower than those reported by *Winston et al.* [1997] for mineral soils at similar temperatures, likely because our peat samples contained no clay.

[49] Significant evolution of CO_2 from feather moss peat at temperatures below zero is consistent with winter efflux patterns observed by chambers [*Winston et al.*, 1997] and eddy covariance [*Goulden et al.*, 1998]. Q(10) values at $t < 0°C$ are significantly higher than at $t > 0°C$ (5.8–7.7 and 4.4 accordingly), due to high temperature sensitivity in the temperature range of water-ice transition.

[50] The difference in CO_2 efflux between sphagnum and feather moss below $0°C$ may be caused by physical factors associated with ice formation. The sphagnum peat formed a crust of ice at the surface upon freezing that may have slowed gas transport, while the feather moss, which was drier, did not form similar crust.

[51] The increase in temperature sensitivity of peat decomposition around the freezing point has important implications for modeling boreal peatland responses to warming. Models that use a single Q(10) based on observations made during thaw will overestimate winter fluxes from boreal sites. Thawing of previously frozen peats and increases in the thickness of the active layer will similarly produce higher increases in respiration than would be predicted using Q(10) values established for $t > 0°C$.

4.3. Decline in CO_2 Efflux Over Time

[52] The decrease in CO_2 evolution over the course of a longer-term incubation experiment is a well-known phenomenon [*Holland et al.*, 1995; *Kirschbaum*, 1995]. It is usually explained by either substrate limitation [*Holland et al.*, 1995] or by the initial disturbance of microbial population created by processing the samples [*Kirschbaum*, 1995], or both. We observed stabilization of decomposition rates at $t > 0°C$ (Figure 5), which imply no major substrate limitation. Based on our observed respiration rates for feather moss peat, fine roots (~7% of total carbon) alone could sustain peat decomposition for about 8 years, assuming peat temperature is $4°C$ for 6 months and $0.08°C$ for another 6 months [*Goulden et al.*, 1998]. Diminishing of this pool of more readily respired material may be the cause of the decline in CO_2 evolution rates in long-term warming experiments in Sweden [*Jarvis and Linder*, 2000].

[53] The continued linear decline in CO_2 evolution rates with time observed for frozen peat (Figure 5) reflects substrate limitation. It is likely that at low temperatures microorganisms can only utilize the most easily available carbon, e.g., carbon stored in microbial tissue and soluble carbon in water films. Reserves of this easily available carbon are limited and can be rapidly depleted. Such utilization of microbial biomass for microbial respiration following freeze-thaw has been shown in other studies [*Clein and Schimel*, 1995; *Schimel and Clein*, 1996]. [14]C measurements of CO_2 evolved below freezing cannot help distinguish a shift in substrate from external to internal microbial sources, since internal microbial C stores reflect food sources that apparently do not change with temperature (Figure 6). However, the observed lower ^{13}C values of incubation gas evolved below freezing in the second feather moss incubation experiment support the idea that pools of C for decomposition below and above zero are not identical.

[54] From the observed patterns of rate decrease we can conclude that the ratio of decomposition rate at t > 0°C to decomposition rate at t < 0°C is increasing with time. We can thus expect a contribution of frozen horizons to total CO_2 flux out of the soil to decrease from fall to late winter with the depletion of carbon pool available at t < 0°C. CO_2 fluxes measurements made later in winter will thus reflect greater contributions from deep unfrozen soil horizons with older and more recalcitrant organic matter. This is in good agreement with the fact that ^{14}C values for CO_2 in soil gas in January and February were lower than the values measured in November–December [*Winston et al.*, 1997].

4.4. Sources of Heterotrophic Respiration

[55] The Δ^{14}C values and the total amount of respired CO_2 are consistent with decomposition of a combination of substrates, with large contributions from root and wood detritus, as well as finer, more humified, materials. The relative contributions of these components do not appear to change with temperature across the range we tested (Figure 6).

[56] The radiocarbon signature of respired CO_2 requires significant contributions from at least two substrates. As in other isotope-constrained estimates of soil respiration sources [e.g., *Gaudinski et al.*, 2000; *Trumbore*, 2000; *Wang et al.*, 2000], rapidly decomposing substrates such as roots are major sources even though they make up a small portion of total soil C. Our model requires significant contributions of respired C from the lower-^{14}C humified material, indicating that although this pool is decomposing slowly (as indicated by its low ^{14}C values), there is enough of it to make it an important source of heterotrophic respiration.

[57] The δ^{13}C values of respired CO_2 are somewhat puzzling. If we use model-derived estimates of relative substrate contribution to respired CO_2, we predict lower δ^{13}C values than were observed in the incubation jars. This may be due to preferential microbial use of a ^{13}C-enriched portion of a given substrate (as is the case with cellulose versus lignin).

[58] In the second feathermoss peat incubation experiment, δ^{13}C values of respired CO_2 in jars at temperatures below zero were more negative compared to those at above-zero temperatures. This observation supports the idea that different substrates support CO_2 production in frozen versus unfrozen peat.

4.5. Implications for Boreal Soil Carbon Balance

[59] Our results show that heterotrophic respiration is supported by preferential decomposition of recently fixed carbon that makes a small fraction of total carbon stocks in soil. Failure to account for this can lead to serious misinterpretation of decomposition rates from soil incubation experiments [*Davidson et al.*, 2000]. However, older substrates with slower decomposition rates that make up the most of organic matter in peats still contributed significantly to total CO_2 evolution. Warmer temperatures led to substantial increases from this C source as well as from the less abundant but more highly decomposable detrital C stocks. This indicates the potential for long-term, sustained C losses from soils with warming.

[60] Our results suggest that warming would cause increased decomposition in boreal peats. The relative contribution of different organic matter pools is not expected to change due to temperature increase only, based on our incubation results. However, it may change as the less abundant but more rapidly decomposing substrates (i.e., root detritus) "burn off" within a few years to decades. Longer-term increases in C losses would be sustained by the faster decomposition of the larger but more recalcitrant pool of humified organic matter. Over decades to centuries, increased decomposition could transfer a large amount of C from the soil to the atmosphere. A net loss of C from these humified pools would be difficult to measure directly in the field. At present, these materials contribute only a portion (9–22% [*Trumbore and Harden*, 1997]) of the total heterotrophic respiration at the NOBS site. If the more rapidly cycling pools adjust quickly to new conditions, we would predict long-term, sustained increases in heterotrophic respiration originating from humified materials. This would be further diluted by autotrophic respiration in field measurements, which would make a change in flux difficult to detect.

[61] Changes in the Q(10) for different substrates and across the freezing point mean that no single Q(10) value can be used for soils from tundra to tropical forest. Confounding effects of organic materials of different genesis and quality can explain rather poor R^2 values of regression equations attempting to describe temperature effects in soil respiration across biomes (0.7 in the work of *Lloyd and Taylor* [1994] and 0.5 in the work of *Kirschbaum* [1995]). Since different soil types have different geographic distribution, use of a single Q(10) value for modeling the consequences of global warming will be a source of a huge distortion both in regional and global-scale models.

5. Conclusions

[62] Peat decomposition is clearly temperature dependent. We observed considerable peat decomposition at temperatures below zero that contributes to winter CO_2 fluxes from boreal forest. No uniform temperature relationship could fit equally well decomposition both above and below the freezing point. For temperatures >0°C, decomposition is exponentially related to temperature, with equivalent Q(10) values of 4.4 for feather moss peat and 3.1 for sphagnum peat. The difference in temperature response between the two types of peat under study may be related to differences in substrate quality. Different proportions of organic matter

components that contribute to soil respiration, such as roots, will result in different rates of decomposition and different patterns of temperature sensitivity. Below freezing, the increase in decomposition rates with temperature for feather moss peat was higher than above freezing, with a mean Q(10) of 6.9. The maximums temperature sensitivity of peat decomposition was observed in the interval of water phase transition.

[63] Differences in stable carbon isotope signatures of CO_2 derived from feather moss peat above and below freezing temperatures indicate that the pathways of decomposition above and below freezing point are not identical. These results are consistent with a change in decomposing substrate above and below freezing implied by different patterns of decline in respiration rates. The absence of temperature trend in radiocarbon values of incubation gas does not contradict this conclusion if microbial carbon is the source of decomposition below zero.

[64] The amount of CO_2 evolved during the incubation, and its radiocarbon content, can be used to constrain the partitioning of sources of heterotrophic respiration. Dead fine roots that make a small part of total organic carbon account for ~30% of respiration in sphagnum peat and ~50% of respiration in feather moss peat. Fine humified material representing the bulk of peat organic carbon contributes ~30% and ~50% to respiration of sphagnum peat and feather moss peat accordingly. Woody debris and fresh moss residues contribute the rest of the respired C.

[65] Increasing temperature did not change the $\Delta^{14}C$ of respired carbon, although the amount of C respired increased 100-fold over the range of incubations.

[66] Our results indicate that sustained warming should induce both short-term (decades) and long-term (centuries) increases in heterotrophic respiration from peat soils. The long-term increases in decomposition of fine humified organic matter could be a source of significant amounts of C added from this large organic matter reservoir to atmosphere.

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