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Short-term controls on the age of microbial carbon sources in boreal forest soils

Claudia I. Czimczik¹ and Susan E. Trumbore¹

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[1] One predicted positive feedback of increasing temperatures in the boreal region is carbon (C) loss through enhanced microbial decomposition of soil organic matter (SOM). The degree to which temperature sensitivity for decomposition varies across a range of C-substrates remains uncertain. Using incubations, we tested whether microorganisms shift to more recalcitrant substrates (with longer turnover times) at higher temperatures at low or increased soil moisture. We measured the radiocarbon ($\Delta^{14}\text{C}$) and stable isotope ($\delta^{13}\text{C}$) signature of CO_2 respired from organic soils from six black spruce forests (0 to 150 years since fire). We identified major C substrates contributing to decomposition by comparing $\Delta^{14}\text{C}$ of CO_2 to $\Delta^{14}\text{C}$ of roots, mosses, needles, and wood separated from bulk SOM. The $\Delta^{14}\text{C}$ signatures of these components allow an estimation of their turnover times, further constraining their relative contribution to respiration. Fastest turnover rates were observed for herbaceous litter and needles (annual to <decadal), the longest (>decadal) for mosses, with intermediate turnover times for roots. Dominant microbial C sources in 5 to 40 year old stands were fire remnants and litter of early succession species, while substrates with longer turnover times accounted for a larger proportion of CO_2 in mature stands. At both low and increased moisture levels, the increase in CO_2 efflux at higher temperatures was accompanied by a decline in $\delta^{13}\text{C}$, but no shift in $\Delta^{14}\text{C}$. This suggests that temperature sensitivity is not greater for recalcitrant C and that changes in $\delta^{13}\text{C}$ likely reflect temperature dependence of microbial fractionation processes rather than a substrate shift.

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1. Introduction

[2] The degree to which increased temperatures will cause a positive feedback to warming through enhanced microbial decomposition of SOM remains a large source of uncertainty in predicting future atmospheric CO_2 levels [Prentice *et al.*, 2001]. In particular, considerable debate remains as to whether the sensitivity of decomposition rates is similar for a range of different C substrates [Davidson and Trumbore, 1995; Davidson *et al.*, 2000; Fang *et al.*, 2005; Fierer *et al.*, 2005; Giardina and Ryan, 2000; Knorr *et al.*, 2005].

[3] Underlying this debate is the idea that the main control of the longer term stability of a C substrate in soils is its chemical nature [Krull *et al.*, 2006]. Substrates considered most resistant to microbial decomposition are polymers containing aromatic rings (e.g., lignin) and a range of polymethylenic molecules (e.g., waxes), while less resistant substrates contain hydrolytic bondings [von Lützow *et al.*, 2006]. However, this concept is not generally accepted: In addition to chemical recalcitrance, interactions with the

mineral soil phase (ligand-exchange [Davis, 1982] with Fe-, Al-, Mn-oxides, phyllosilicates and metal ions) and accessibility to microorganisms and their enzymes (physical exclusion via occlusion, intercalation, hydrophobicity and encapsulation or distance) are important controls on SOM stability [von Lützow *et al.*, 2006].

[4] Understanding what types of C substrates can be decomposed at a given temperature is crucial for developing better estimates of total C loss from soils. Roughly 17% of total terrestrial C stocks reside in boreal forest soils [Prentice *et al.*, 2001], in regions that have experienced significant warming in the past century [Pollack *et al.*, 1998; Serreze *et al.*, 2000]. The accumulation of these C stocks since glacial retreat [Harden *et al.*, 1992] is believed to result from a combination of poor substrate quality, cold temperature and poor drainage [Hobbie *et al.*, 2000; Preston *et al.*, 2006]. Most of this C is present in organic layers and not stabilized by interactions with soil minerals.

[5] One way of testing whether microorganisms shift to different C substrates with altered temperature and moisture conditions is to subject soils to manipulated conditions in a controlled incubation. To determine the degree to which C of different ages contribute to microbial respiration, and whether that mix changes with temperature, studies have either taken advantage of a past vegetation change (e.g., shift

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Table 1. Sampling Locations (2 × 3 Cores Per Site, Combined) and Incubation Parameters (2–3 Temperatures, 1–2 Moisture Contents)^a

Last Fire Year	Latitude N Longitude W	Oe Layer			Oa Layer		
		Thickness, cm	Temperature, °C	Moisture % Dry Weight	Thickness, cm	Temperature, °C	Moisture % Dry Weight
2003	55°53'88" N 98°12'96" W	n.p.	n.p.	n.p.	7.8 (2.2)	6.6 or 13.8	51.2 ^b or 299.2 ^c
1998 ^d hummock	56°38'09" N 99°56'54" W	n.p.	n.p.	n.p.	3.3 (1.5)	6.6 or 23.1	60.9 ^b
hollow					2.7 (0.6)	6.6 or 23.1	17.5 ^b
1989 ^d	55°55'0" N 98°57'52" W	n.p.	n.p.	n.p.	5.0 (0.3)	6.6 or 23.1	47.1 ^b
1964 ^d	55°54'42" N 98°22'56" W	4.8 (0.9)	6.6 or 23.1	111.4 ^b	6.8 (3.5)	6.6 or 23.1	95.2 ^b
1930 ^d	55°54'21" N 98°31'29" W	2.6 (1.5)	13.8 or 23.1	108.4 ^b or 400.8 ^c	6.6 (1.4)	6.6 or 13.8	50.0 ^b or 229.4 ^c
1850	55°52'49" N 98°28'43" W	8.0 (1.2)	13.8 or 23.1	211.1 ^b	7.8 (1.3)	6.6 or 13.8	132.99 ^b

^aThickness is given as mean (standard deviation); n.p., soil layer not present.

^bMoisture as during sampling.

^cWetted to field capacity (free draining).

^dAmeriflux sites.

from plants with C3 photosynthetic pathway ($\delta^{13}\text{C} \sim -27\%$) to plants with C4 pathway ($\sim -8\%$) that allows the use of the $\delta^{13}\text{C}$ signature of respired CO_2 to distinguish fresh (enriched in ^{13}C) versus decades-old (depleted) SOM [Biasi *et al.*, 2005; Bol *et al.*, 2003; Waldrop and Firestone, 2004] or used the radiocarbon signature ($\Delta^{14}\text{C}$) of CO_2 [Bol *et al.*, 2003; Cisneros-Dozal *et al.*, 2006; Dioumaeva *et al.*, 2002]. Radiocarbon can be used as a tracer for the last 50 years, because $\Delta^{14}\text{C}$ of atmospheric CO_2 spiked during the 1960s due to above-ground testing of thermonuclear weapons and is subsequently declining as this 'bomb' $^{14}\text{CO}_2$ exchanges with C reservoirs in the oceans and biosphere, and becomes diluted by fossil (>50,000 yrs) CO_2 from combustion processes [Levin and Hesshaimer, 2000]. Some studies used a local ecosystem ^{14}C label (probably due to combustion of ^{14}C -labeled waste) as an additional tracer [Trumbore *et al.*, 2002].

[6] In general, ^{13}C -based measures have interpreted a shift in the $\delta^{13}\text{C}$ signature of respired CO_2 observed for different temperature incubations as evidence of different temperature sensitivities for old (more recalcitrant) versus young SOM [Biasi *et al.*, 2005; Bol *et al.*, 2003; Waldrop and Firestone, 2004]. Studies monitoring $\Delta^{14}\text{C}$ of respired CO_2 have shown no temperature sensitivity [Cisneros-Dozal *et al.*, 2006, 2007; Dioumaeva *et al.*, 2002].

[7] We report the range of $\Delta^{14}\text{C}$ signatures of CO_2 respired in incubations of organic layers for black spruce (*Picea mariana* (P. Mill.) B.S.P.) stands ranging in age from 0 (recent fire) to 150 years since fire. In addition, we compare the isotopic signatures of respired CO_2 to that of bulk C and manually isolated fractions: roots, mosses, needles, and wood.

2. Material and Methods

2.1. Soil Sampling

[8] We sampled six upland sites in various stages of secondary succession after fire in black spruce dominated forests within the BOREAS Northern Study Area near Thompson, MB, Canada (Table 1). The sites are described in more detail in Czimeczik *et al.* [2006].

[9] Organic layers were collected in triplicate at two locations per site in September 2003. Samples were taken by inserting a circular metal frame (i.d. 17.5 cm) from the soil surface into the mineral soil. Living moss was cut from the cores, the remaining material stored at 7°C. The cores were divided into slightly (Oe) and more decomposed organic material (Oa) (Table 1). In the most recent burns (0–14 years since fire) samples identified as Oa layers are dominated by preburn SOM which survived the last fire and a minor component of postfire litter.

2.2. CO_2 Efflux

[10] We incubated all samples at two or three different temperatures in the dark (Table 1). Home-built controllers on commercial refrigerators (as described in [Dioumaeva *et al.*, 2002]) maintained temperatures within the incubation jars at 7, 14 or 23°C ($\pm 0.6^\circ\text{C}$ as monitored by HOBO temperature sensors (BoxCar Pro 4.3)). The incubation temperatures were selected to represent depth-dependent temperature conditions in the organic layers during the growing season (Figure 1). Soil temperatures in the field were measured with precision interchangeable thermistors (EC95H303W Thermometrics, Edison, NJ, USA) encapsulated in thermally conductive epoxy and recorded every 2 hours (CR-10X, Campbell Scientific Inc., Logan, UT, USA).

[11] All samples were incubated with field moisture content so that isotopic signatures would represent conditions close to those in the field. To assess the effects of increasing soil moisture on the rate and isotopic composition of respired CO_2 , we incubated samples from two locations (2003 and 1930 burn) at field capacity as well (Table 1). Field capacity was attained by wetting with deionized water until the soil drained freely. From the 1998 burn, which has a strong micro-topography, we incubated samples from a hummock and a hollow.

[12] Directly prior to incubations, all samples from a given site were combined and homogenized, coarse roots (d. >1 cm) and larger pieces of wood were removed. Out of the combined sample for each site, we incubated about 20 g soil in triplicate. Samples were loosely wrapped in aluminum foil which we punctured to facilitate air flow before

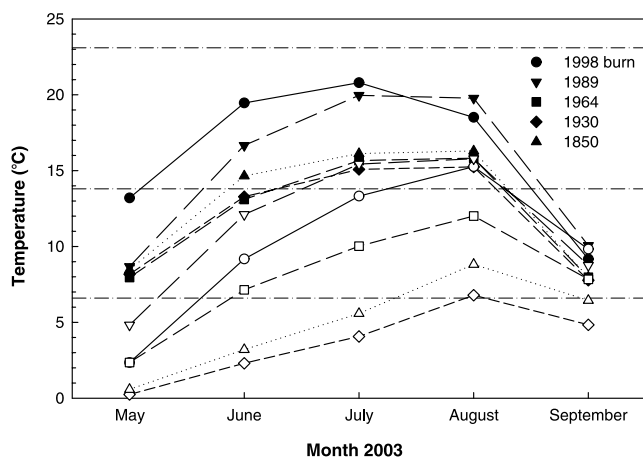


Figure 1. Monthly average temperature during the growing season 2003 at the surface of the organic layers (solid symbols) and the interface between the organic layers and the mineral soil (open symbols). Dashed lines indicate the temperatures at which samples were incubated (7, 14, 23°C).

inserting them into 1 L jars. The jars were initially stored open at 7°C for 24 hours. Then, the jars were flushed with at least three jar volumes of moist CO₂-free air, closed and incubated at 7°C. After the rate of CO₂-efflux at 7°C became constant (5 to 9 days), the jars were moved to the specific incubation temperatures for 7 to 12 days.

[13] The CO₂ concentration in the jars was determined every 1 to 3 days with a LI-6262 CO₂/H₂O Analyzer (LI-COR, Lincoln, NB, USA) as described in *Davidson and Trumbore* [1995]. Five mL of air were sampled from each jar and 1 to 3 mL were injected into a stream of CO₂-free air at a flow rate of about 1 L min⁻¹. Air removed in sampling the jar was replaced with CO₂-free air to maintain jars at atmospheric pressure. Each time the CO₂ concentration in a jar reached 3%, the jar was flushed with moist CO₂-free air.

[14] The volume of air in the jar was determined by change in pressure when attached to a known volume under vacuum. We report CO₂ evolution rate per gram of dry soil in the jar; soil moisture was determined from an aliquot of the homogenized sample used for incubations.

2.3. Isotopic Composition of CO₂

[15] The isotopic composition of CO₂ was determined at the end of the incubation period. We transferred air from the headspace of the incubation jars into evacuated 0.5 L stainless steel containers, and purified CO₂ from the transferred air cryogenically. Roughly 1 mg C was sealed into an evacuated Pyrex tube and reduced to graphite [*Xu et al.*, 2007]. The radiocarbon signature of the graphite was measured with accelerator mass spectrometry (NEC 0.5MV 1.5SDH-2 AMS system) at the Keck-CCAMS facility of UCI [*Southon and Santos*, 2004] and reported as Δ¹⁴C, the deviation (in parts per thousand) of the ¹⁴C/¹²C ratio of the sample (corrected for mass-dependent fractionation to a common δ¹³C of -25‰) from 0.95 times the ¹⁴C/¹²C of the oxalic acid I standard.

[16] A fraction of the CO₂ from each sample was transferred to a He-filled septum-capped vial, and analyzed for its δ¹³C value with an isotope ratio mass spectrometer

(continuous flow, Thermo Finnigan Delta Plus, Waltham, MA, USA).

2.4. Composition of SOM

[17] Following the incubation period, the three replicates of each sample were combined and dried at 60°C. A subsample was sorted into five categories: needles, roots, wood, moss, and amorphous SOM (material too small to be easily identified as one of the four other categories). The components were analyzed for their δ¹³C and Δ¹⁴C signatures as described above, after combustion to CO₂ in evacuated, prebaked, 6 mm quartz tubes with 0.5 mg CuO powder for 2 hours at 900°C.

2.5. CO₂ Efflux Response to Temperature and Moisture (Q₁₀)

[18] We averaged the rate of CO₂ efflux from replicates. We omitted measurements during the first 48 hours of the experiment (to avoid sampling the response to soil homogenization) and measurements 24 hours following flushing with CO₂-free air thereafter, because of higher CO₂ efflux rates at those times indicating incomplete flushing.

[19] For samples incubated at 7°C (same temperature during adjustment and incubation period), the rate of CO₂ efflux remained constant (student's t-test, p < 0.05), and we report the rates averaged over the entire duration of the experiment.

[20] Based on the averages, we calculated the rate of CO₂ efflux (R) with increasing temperature (t) assuming an exponential relationship (1), and derived temperature response (Q₁₀, (2)) curves [*Fang and Moncrieff*, 2001] (Table 2):

$$R = a \times \exp^{(b \times t)}, \quad (1)$$

$$Q_{10} = \exp^{(b \times 10)}. \quad (2)$$

3. Results

3.1. Rates and Isotopic Signature of CO₂ Efflux

[21] The rate of CO₂ efflux from each sample increased with temperature (Figure 2a). Assuming an exponential

Table 2. Correlations ($R = a \times \exp^{(b \times t)}$) Between Rate of CO₂ Efflux (R) and Temperature (t) (R: n = 3 at Each Temperature; t: n = 2 or 3 (2003))^a

Last Fire Year	Moisture	Oe Layer			Oa Layer		
		a	b	Q ₁₀ ^b	a	b	Q ₁₀ ^b
2003	as sampled	n.p.	n.p.	n.p.	1.03 ^c	0.10	2.8
	field capacity				1.53 ^d	0.11	2.9
1998							
hummock	as sampled	n.p.	n.p.	n.p.	0.05	0.13	3.5
hollow	as sampled	n.p.	n.p.	n.p.	0.19	0.11	2.9
1989	as sampled	n.p.	n.p.	n.p.	0.25	0.14	4.1
1964	as sampled	1.79	0.11	3.1	0.57	0.13	3.7
1930	as sampled	3.78	0.07	2.0	1.31	0.04	1.6
	field capacity	3.76	0.10	2.6	1.83	0.09	2.4
1850	as sampled	1.99	0.09	2.4	1.35	0.10	2.6

^aHere n.p., layer not present.

^bQ₁₀ = exp^(b × 10).

^cR² = 1.0.

^dR² = 0.99.

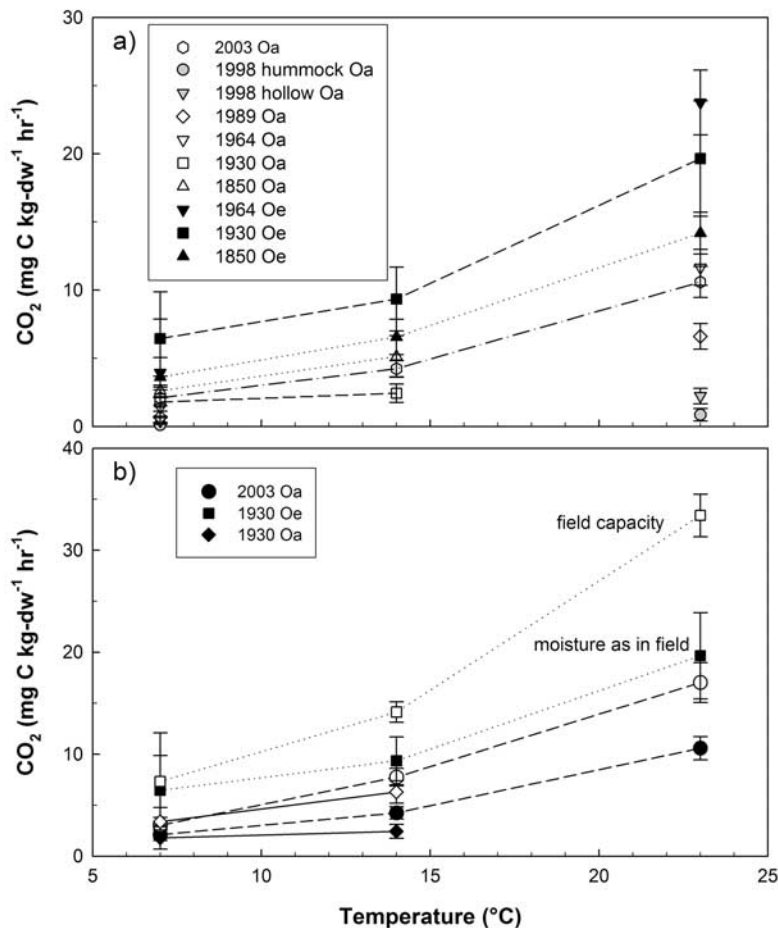


Figure 2. CO₂ efflux at 7, 14, and 23°C from (a) Oe layers (black symbols) and Oa layers (open or grey symbols) and (b) from the 2003 and 1930 burns with a moisture content as sampled in the field (black symbols) and at field capacity (open symbols). Error bars indicate standard deviation (n = 3).

increase, we estimated Q_{10} values between 1.5 and 4.1 (Table 2). Expressed as mg C evolved per unit mass, the flux rates from Oe layers tended to be higher than those from Oa layers, but Q_{10} values were not significantly different between layers. CO₂ effluxes were lowest at the early recovery stages (1998 and 1989 burn) and highest at the 1964 and 1930 burn.

[22] The CO₂ response to increasing temperature was larger at higher moisture contents (Figure 2b). Fluxes from samples wetted to field capacity were significantly higher (student's t-test, $p < 0.05$) than fluxes from field-moist samples at high temperatures, but not at lower temperatures.

[23] $\Delta^{14}\text{C}$ of respired CO₂ showed large differences (up to 300‰) between sites (Figure 3a). However, $\Delta^{14}\text{C}$ of CO₂ respired from a given site or layer did not change significantly (student's t-test, $p < 0.05$) with increasing temperature or moisture (Figures 3a and 3c). The $\delta^{13}\text{C}$ signatures of respired CO₂ varied between -25 and -27 ‰, and decreased with increasing temperature under both, field and increased soil moisture (Figures 3b and 3d).

3.2. Elemental and Isotopic Composition of SOM

[24] The composition of the SOM samples was dominated by amorphous material which accounted for $61 \pm 5\%$ of bulk dry weight in the Oe and $87 \pm 6\%$ in the Oa layer (Figure 4). The C contents of the isolated fractions were similar, ranging from a high of $52.5 \pm 4\%$ C in needles, $46.2 \pm 7\%$ in wood, $48.4 \pm 3\%$ in roots, $41.9 \pm 7\%$ in moss, to a low of $34.8 \pm 13\%$ in the amorphous fraction. In the Oe layer, the amount of C in the amorphous fraction increased with time since fire from 0.2 kg C m^{-2} at the 1964 burn to 0.9 kg C m^{-2} at the 1850 burn. Similarly, C in the moss fraction increased from 0.1 to 0.6 kg C m^{-2} . The root fraction contained $<0.1 \text{ kg C m}^{-2}$ at all sites. In the Oa layer, the amorphous fraction accounted for 0.6 to 2.7 kg C m^{-2} and the moss fraction for 0.01 to 0.3 kg C m^{-2} . The amount of C in the root fraction was low in the early recovery stages (0.05 kg C m^{-2}), but high (0.3 kg C m^{-2}) in the recent burn and older sites, with a maximum at the 1964 burn.

[25] At a given site, $\Delta^{14}\text{C}$ of respired CO₂ showed surprisingly little correspondence with $\Delta^{14}\text{C}$ of the SOM

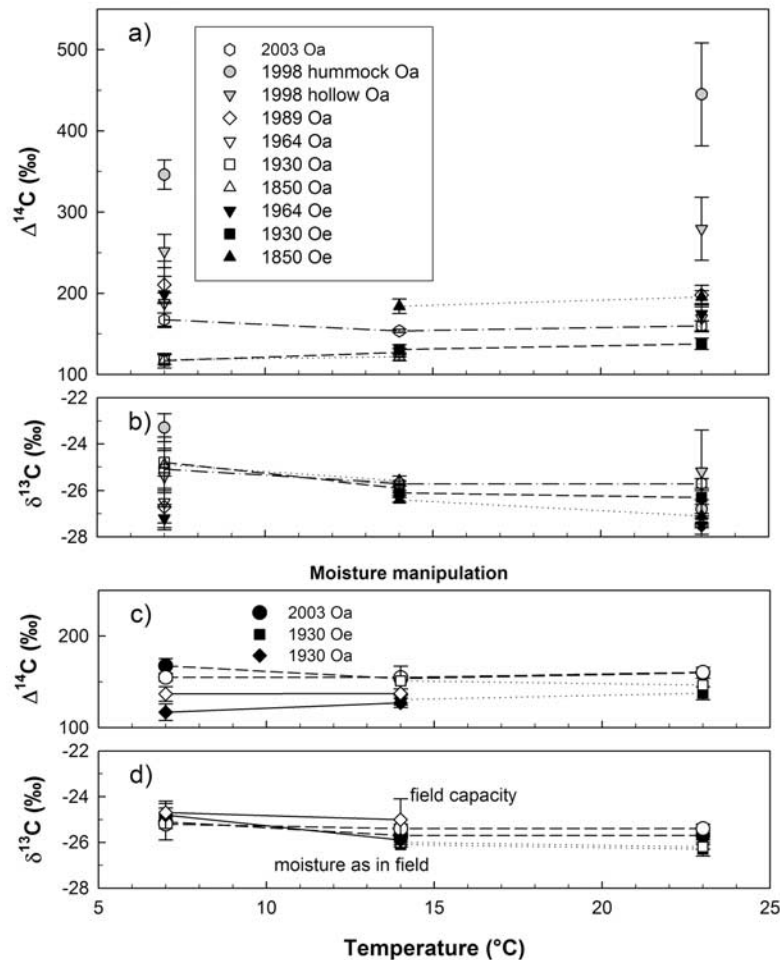


Figure 3. Radiocarbon or $\delta^{13}\text{C}$ signature of CO_2 efflux at 7, 14, or 23°C from (a, b) Oe (black symbols) and Oa layers (open or grey symbols) and (c, d) from the 2003 and 1930-burn sites with a moisture content as sampled in the field (black symbols) and at field capacity (open symbols). Error bars indicate standard deviation ($n = 3$).

fractions (Figure 5). For the youngest stands, the 1998 and 1989 burn (Oa layer) and the 1964 burn (Oe layer), $\Delta^{14}\text{C}$ of respired CO_2 exceeded that of any of the isolated fractions. In contrast, $\Delta^{14}\text{C}$ respired CO_2 from the oldest stands (1930 and 1850 burn) was either slightly less than, or fell within the range of, isolated fractions.

4. Discussion

4.1. Effects of Soil Temperature and Moisture on Microbial C Sources

[26] As expected, we found that CO_2 efflux rates were stimulated by higher temperatures [Davidson and Janssens, 2006] and moisture contents [Skopp *et al.*, 1990]. Our estimated Q_{10} factors are within expected ranges, although their calculations are in most cases based on two data points and are therefore highly sensitive to the chosen model function. Also, Q_{10} values are difficult to transfer to field situations, since correlations between CO_2 efflux from soils and temperature are often confounded by changes in plant activity [Curiel Yuste *et al.*, 2004].

[27] In agreement with other observations [Biasi *et al.*, 2005; Weintraub and Schimel, 2005], increases in CO_2 efflux rates with higher temperature were associated with a decline of $\delta^{13}\text{C}$ of CO_2 . However, this $\delta^{13}\text{C}$ shift was not associated with a significant change in $\Delta^{14}\text{C}$ of CO_2 , implying that microorganisms do not adjust the balance of C substrates when soil temperature changes and different C substrates do not have very different sensitivities to temperature. Similar conclusions have been drawn from incubations of frozen and unfrozen boreal peats [Dioumaeva *et al.*, 2002] and organic layers of temperate forest soils [Cisneros-Dozal *et al.*, 2007], and could also be drawn from incubations of the organic layer-mineral soil interface of a temperate coniferous forest soil [Bol *et al.*, 2003].

[28] Our results indicate that decomposition is not merely regulated by the temperature sensitivity of microorganisms and their enzymes. Instead, decomposition requires the accessibility of organic compounds by specific enzymes which might not be present, because the distribution of active microorganisms within soils is clustered, while organic C is more evenly dispersed. However, we cannot

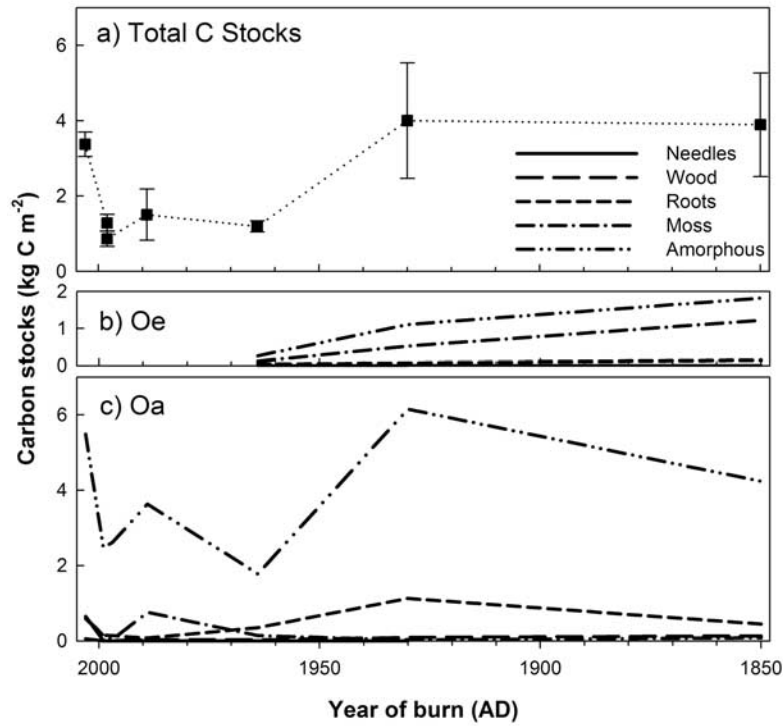


Figure 4. Amount of carbon stored in the (a) organic layers (squares \pm SE, obtained by J. Harden) and within each fraction of the (b) Oe or (c) Oa layer.

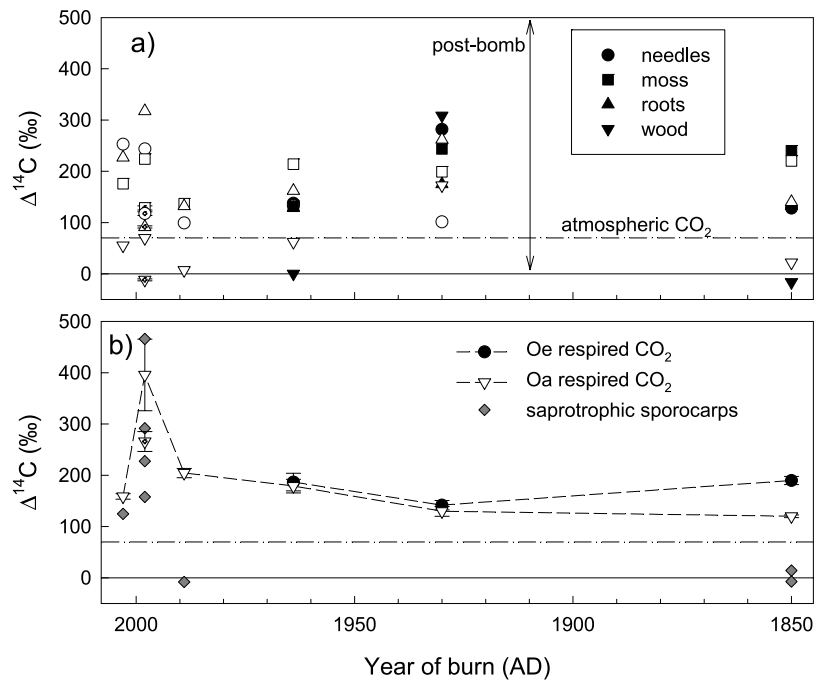


Figure 5. Radiocarbon signatures of (a) of organic matter fractions isolated from the Oe (solid symbols) or Oa layer (open symbols) and (b) CO₂ respired from the Oe or Oa layer and of sporocarps of saprotrophic fungi. For the 1998 burn open symbols represent hummock samples and dotted symbols hollow. The solid horizontal line deviates prebomb and postbomb C, the dashed line indicates atmospheric CO₂ in 2003.

fully exclude that there was no small increase in the proportion of respired CO₂ originating from the decomposition of more recalcitrant C compounds at higher temperature: (1) Most of the CO₂ respired in incubation experiments results from decomposition of fast cycling C pools, and measurements (with and without isotope analysis) are generally not very sensitive in detecting small increases in the decomposition of slow-cycling C pools which only account for a small fraction of the total efflux [Kirschbaum, 1995]; and (2) The $\Delta^{14}\text{C}$ signatures of the different materials making up the bulk C may not be different enough to detect a significant shift (e.g., from roots to moss, see Figure 5a).

[29] It seems likely that the decline in $\delta^{13}\text{C}$ reflects isotopic fractionation during SOM decomposition rather than a shift to more recalcitrant material. More complex SOM, predominantly derived from plants, is often depleted, because its formation involves many enzymatic reactions which discriminate against the heavier ^{13}C isotope. This material, however, should also have longer turnover times in soils and therefore older $\Delta^{14}\text{C}$ signatures, resulting in a shift in the $\Delta^{14}\text{C}$ signature of respired CO₂, which was not observed. Instead, the shift in $\delta^{13}\text{C}$ is likely reflecting the discrimination against ^{13}C during the enzymatic breakdown of SOM, resulting in the depletion of respired CO₂ and the enrichment of ^{13}C in the remaining SOM. $\Delta^{14}\text{C}$ signatures are corrected to a common $\delta^{13}\text{C}$ value of -25% [Stuiver and Polach, 1977] and do not indicate mass-dependant fractionation processes.

[30] Also, the combination of declining $\delta^{13}\text{C}$ and stable $\Delta^{14}\text{C}$ signatures was probably not related to enhanced recycling of C within the existing microbial biomass pool. Recycling is typically associated with declining CO₂ efflux rates, but in this experiment CO₂ efflux rates strongly increased at higher temperatures and did not decline over time.

4.2. Microbial C Sources Along the Chronosequence

[31] The rate of CO₂ efflux per gram of soil was lowest in stands sampled 5–14 years after a fire where SOM was dominated by material that survived the fire: burned remnants of the prefire Oa layer and litter from burned biomass. Even accounting for the higher soil temperatures in the younger stands, heterotrophic respiration rates at these sites are relatively low. This confirms estimates that much of the soil respiration in younger stands is derived from autotrophic sources [Czimczik et al., 2006]. CO₂ efflux was highest in older stands where SOM from new moss and roots, associated with closed canopy, mature forest had accumulated since the last fire.

[32] By incubating organic layers from a range of sites with different fire history (and thus vegetation composition), we covered a wide range of C substrates. Following fire, forest stands undergo a vegetation succession, from a dominance of deciduous tree species (*Salix* sp., *Populus tremuloides* Michx., *Betula papyrifera* Marsh.) for about 40 years to black spruce in mature stands. Understorey vegetation shifts from herbs and ericaceous shrubs to mosses between 40 to 70 years since fire. Generally, moss litter decomposes more slowly than litter of higher plants [Hobbie et al., 2000], foliar litter decomposes faster than woody debris [Moore et al., 2005], and burned SOM decomposes more slowly than unburned SOM [Baldock and Smernik, 2002].

[33] We can draw some conclusions about the contribution of these different fractions to microbial respiration by comparing $\Delta^{14}\text{C}$ of respired CO₂ and isolated SOM fractions to the history of $\Delta^{14}\text{C}$ of atmospheric CO₂: At young burns (5 to 40 years since fire) $\Delta^{14}\text{C}$ of respired CO₂ $\geq 200\%$ require that the majority of the C being respired was fixed between 1960s and 1985 and is at least 18 years old on average. Potential C substrates at the 1998 and 1989 burn are thus fire remnants. As an examples, needles falling from burned trees were clearly an input of a $>200\%$ -C source at the 2003 burn (Figure 5a). At the 1964 burn, another potential C source is litter of early succession species. The absence of herbaceous litter fragments in the isolated fractions indicates that the litter of early succession species decomposes rapidly (within years).

[34] At the youngest recovery stages (1998 and 1989 burn), we could not physically isolate the high $\Delta^{14}\text{C}$ component that was the main C source respired by microorganisms ($\Delta^{14}\text{CO}_2 > \Delta^{14}\text{C}$ of any isolated fraction). This indicates that microorganisms were using a small labile component of SOM fixed between 1960 and 1975, and therefore also derived from burned residues of material fixed before the fire.

[35] At the 1998 burn, the existence of saprophytic fungi which also showed high $\Delta^{14}\text{C}$ values (Figure 5b) confirmed the existence of this C source for microorganisms under field conditions as well as in incubations. Sporocarps were identified according to their combination of $\delta^{15}\text{N}$ ($-5 \pm 4\%$), $\delta^{13}\text{C}$ (-21.8 ± 1) and $\Delta^{14}\text{C}$ signatures [Hobbie et al., 2001; Kohzu et al., 1999].

[36] At sites with $\Delta^{14}\text{C} < 200\%$, the 'age' of respired C is harder to interpret and either indicates that the material was on average younger than 20 years old or represents a mixture of prebomb and postbomb C [Trumbore and Harden, 1997]. We can draw some conclusions about the turnover time of SOM fractions from a comparison of the $\Delta^{14}\text{C}$ and C stock dynamics between the 1930 and 1850 burn: The amount of C in needles and of roots in the Oa layer does not accumulate and their $\Delta^{14}\text{C}$ declines from the 1930 to the 1850 burn (tracking the decline of $\Delta^{14}\text{C}$ of atmospheric CO₂) – indicating intermediate turnover times (years to decades). We can assign longer than decadal turnover times for mosses in both layers and roots in the Oe layer. The amount of C present in the moss and root fractions does not decrease from the 1930 to 1850 burn, and there is no change in $\Delta^{14}\text{C}$ of these fractions. From these estimated turnover times, it seems likely that the overall decrease in $\Delta^{14}\text{C}$ signatures of respired CO₂ with increasing stand age reflects the increasing importance of prebomb (<1960) C.

5. Conclusions

[37] Radiocarbon analyses of SOM, respired CO₂, and sporocarps of saprotrophic fungi suggest that microorganisms in boreal soils access a variety of C substrates. At both low and increased soil moisture conditions, increases in soil temperature resulted in large increases of CO₂ efflux from soils accompanied with a decline in $\delta^{13}\text{C}$ signatures, but no change in $\Delta^{14}\text{C}$. We conclude that increased temperature does not result in significant increase in the use of more recalcitrant C substrates by microorganisms and that

observed changes in $\delta^{13}\text{C}$ signature of CO_2 merely reflect microbial fractionation processes during decomposition.

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References

- Baldock, J. A., and R. J. Smernik (2002), Chemical composition and bioavailability of thermally altered *Pinus resinosa* (Red pine) wood, *Org. Geochem.*, **33**, 1093–1109.
- Biasi, C., O. Rusalimova, H. Meyer, C. Kaiser, W. Wanek, P. Barsukov, H. Junger, and A. Richter (2005), Temperature-dependent shift from labile to recalcitrant carbon sources of arctic heterotrophs, *Rapid Commun. Mass Spectrom.*, **19**, 1401–1408, doi:1410.1002/rcm.1911.
- Bol, R., T. Bolger, R. Cully, and D. Little (2003), Recalcitrant soil organic materials mineralize more efficiently at higher temperatures, *J. Plant Nutr. Soil Sci.*, **166**, 300–307.
- Cisneros-Dozal, L. M., S. E. Trumbore, and P. J. Hanson (2006), Partitioning sources of soil-respired CO_2 and their seasonal variation using a unique radiocarbon tracer, *Global Change Biol.*, **12**, 194–204, doi:110.1111/j.1365-2486.2005.01061.x.
- Cisneros-Dozal, L. M., S. E. Trumbore, and P. J. Hanson (2007), Effect of moisture on leaf litter decomposition and its contribution to soil respiration in a temperate forest, *J. Geophys. Res.*, **112**, G01013, doi:10.1029/2006JG000197.
- Curiel Yuste, J., I. A. Janssens, A. Carrara, and R. Ceulemans (2004), Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity, *Global Change Biol.*, **10**, 161–169, doi:110.1111/j.1529-8817.2003.00727.x.
- Czimczik, C. I., S. E. Trumbore, M. S. Carbone, and G. C. Wiston (2006), Changing sources of soil respiration with time since fire in a boreal forest, *Global Change Biol.*, **12**, 1–15, doi:10.1111/j.1365-2486.2006.01107.x.
- Davidson, E. A., and I. A. Janssens (2006), Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, **440**, 165–173, doi:110.1038/nature04514.
- Davidson, E. A., and S. E. Trumbore (1995), Gas diffusivity and production of CO_2 in deep soils of the eastern Amazon, *Tellus, Ser. B*, **47**, 550–565.
- Davidson, E. A., S. E. Trumbore, and R. Amundson (2000), Soil warming and organic carbon content, *Nature*, **408**, 789–790.
- Davis, J. A. (1982), Adsorption of natural dissolved organic-matter at the oxide water interface, *Geochim. Cosmochim. Acta*, **46**, 2381–2393.
- Dioumaeva, I., S. E. Trumbore, T. A. G. Schuur, M. L. Goulden, M. Litvak, and A. I. Hirsch (2002), Decomposition of peat from upland boreal forest: Temperature dependence and sources of respired carbon, *J. Geophys. Res.*, **107**, 8222, doi:10.1029/2001JD000848 [printed 108(D3), 2003].
- Fang, C., and J. B. Moncrieff (2001), The dependence of soil CO_2 efflux on temperature, *Soil Biol. Biochem.*, **33**, 155–165.
- Fang, C., P. Smith, J. B. Moncrieff, and J. U. Smith (2005), Similar response of labile and resistant soil organic matter pools to changes in temperature, *Nature*, **433**, 57–59.
- Fierer, N., J. M. Craine, K. McLaughlan, and J. P. Schimel (2005), Litter quality and the temperature sensitivity of decomposition, *Ecology*, **86**, 320–326.
- Giardina, C. P., and M. G. Ryan (2000), Evidence that decomposition rates of organic matter in mineral soil do not vary with temperature, *Nature*, **404**, 858–861.
- Harden, J. W., E. T. Sundquist, R. F. Stallard, and R. K. Mark (1992), Dynamics of soil carbon during the deglaciation of the Laurentide Ice Sheet, *Science*, **258**, 1921–1924.
- Hobbie, E. A., N. S. Weber, and J. M. Trappe (2001), Mycorrhizal vs saprotrophic status of fungi: the isotopic evidence, *New Phytol.*, **601**–610.
- Hobbie, S. E., J. P. Schimel, S. E. Trumbore, and J. R. Randerson (2000), Controls over carbon storage and turnover in high-latitude soils, *Global Change Biol.*, **6**, suppl. 1, 196–210.
- Kirschbaum, M. U. F. (1995), The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage, *Soil Biol. Biochem.*, **27**, 753–760.
- Knorr, W., I. C. Prentice, J. I. House, and E. A. Holland (2005), Long-term sensitivity of soil carbon turnover to warming, *Nature*, **433**, 298–301.
- Kohzu, A., T. Yoshioka, T. Ando, M. Takahashi, K. Koba, and E. Wada (1999), Natural ^{13}C and ^{15}N abundance of field-collected fungi and their ecological implications, *New Phytol.*, **144**, 323–330.
- Krull, E. S., C. W. Swanston, J. O. Skjemstad, and J. A. McGowan (2006), The importance of charcoal in determining the age and chemistry of organic carbon in surface soils, *J. Geophys. Res.*, **111**, G04001, doi:10.1029/2006JG000194.
- Levin, I., and V. Hesshaimer (2000), Radiocarbon - A unique tracer of global carbon cycle dynamics, *Radiocarbon*, **42**, 69–80.
- Moore, T. R., J. A. Trofymow, M. Siltanen, C. Prescott, and C. W. Group (2005), Patterns of decomposition and carbon, nitrogen, and phosphorus dynamics of litter in upland forest and peatland sites in central Canada, *Can. J. For. Res.*, **35**, 133–142, doi:110.1139/X1104-1149.
- Pollack, H. N., S. Huang, and P.-Y. Shen (1998), Climate change record in subsurface temperatures: a global perspective, *Science*, **282**, 279–281.
- Prentice, I. C., G. D. Farquhar, M. J. R. Fasham, M. L. Goulden, M. Heimann, V. J. Jaramillo, H. S. Khesghi, C. Le Quéré, R. J. Scholes, and D. W. R. Wallace (2001), The carbon cycle and atmospheric carbon dioxide, in *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, edited by R. A. Houghton et al., pp. 183–237, Cambridge Univ. Press, New York.
- Preston, C. M., J. S. Bhatti, L. B. Flanagan, and C. Norris (2006), Stocks, chemistry, and sensitivity to climate change of dead organic matter along the Canadian boreal forest transect case study, *Clim. Change*, **74**, 223–251, doi:210.1007/s10584-10006-10466-10588.
- Serreze, M. C., J. E. Walsh, F. S. I. Chapin, T. Osterkamp, M. Dyrgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, and R. G. Barry (2000), Observational evidence or recent change in the northern high-latitude environment, *Clim. Change*, **46**, 159–207.
- Skopp, J., M. D. Jawson, and J. W. Doran (1990), Steady-state aerobic microbial activity as a function of soil water content, *Soil Sci. Soc. Am. J.*, **54**, 1619–1625.
- Southon, J., and G. M. Santos (2004), Ion source development at the KCCAMS Facility, University of California, Irvine, *Radiocarbon*, **46**, 33–39.
- Stuiver, M., and H. A. Polach (1977), Reporting of ^{14}C Data, *Radiocarbon*, **19**, 355–363.
- Trumbore, S., J. B. Gaudinski, P. J. Hanson, and J. R. Southon (2002), A whole-ecosystem carbon-14 label in a temperate forest, *Eos Trans. AGU*, **83**, 267–268.
- Trumbore, S. E., and J. W. Harden (1997), Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study area, *J. Geophys. Res.*, **102**, 28,817–28,830.
- von Lützow, M., I. Kögel-Knabner, K. Ekschmitt, E. Matzner, G. Guggenberger, B. Marschner, and H. Flessa (2006), Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions - a review, *Eur. J. Soil Sci.*, **57**, 426–445, doi:410.1111/j.1365-2389.2006.00809.x.
- Waldrop, M. P., and M. K. Firestone (2004), Altered utilization patterns of young and old soil C by microorganisms caused by temperature shifts and N additions, *Biogeochemistry*, **67**, 235–248.
- Weintraub, M. N., and J. P. Schimel (2005), The seasonal dynamics of amino acids and other nutrients in Alaskan Arctic tundra soils, *Biogeochemistry*, **73**, 359–380, doi:310.1007/s10533-10004-10363-z.
- Xu, X., S. E. Trumbore, S. Zheng, J. R. Southon, K. E. McDuffee, M. Luttgen, and J. C. Liu (2007), Modifying a sealed tube zinc reduction method for preparation of AMS graphite targets: reducing background and attaining high precision, *Nucl. Instrum. Methods Phys. Res., Sect. B*, **259**, 320–329.

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