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Changing sources of soil respiration with time since fire in a boreal forest

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Abstract

Radiocarbon signatures ($\Delta^{14}C$) of carbon dioxide (CO_2) provide a measure of the age of C being decomposed by microbes or respired by living plants. Over a 2-year period, we measured $\Delta^{14}C$ of soil respiration and soil CO_2 in boreal forest sites in Canada, which varied primarily in the amount of time since the last stand-replacing fire. Comparing bulk respiration $\Delta^{14}C$ with $\Delta^{14}C$ of CO_2 evolved in incubations of heterotrophic (decomposing organic horizons) and autotrophic (root and moss) components allowed us to estimate the relative contributions of O horizon decomposition vs. plant sources. Although soil respiration fluxes did not vary greatly, differences in $\Delta^{14}C$ of respired CO_2 indicated marked variation in respiration sources in space and time.

The ^{14}C signature of respired CO_2 respired from O horizon decomposition depended on the age of C substrates. These varied with time since fire, but consistently had $\Delta^{14}C$ greater (averaging $\sim$120‰) than autotrophic respiration. The $\Delta^{14}C$ of autotrophically respired CO_2 in young stands equaled those expected for recent photosynthetic products (70‰ in 2003, 64‰ in 2004). CO_2 respired by black spruce roots in stands $>$40 years old had $\Delta^{14}C$ up to 30‰ higher than recent photosynthates, indicating a significant contribution of C stored at least several years in plants.

Decomposition of O horizon organic matter made up 20% or less of soil respiration in the younger ($<$40 years since fire) stands, increasing to $\sim$50% in mature stands. This is a minimum for total heterotrophic contribution, since mineral soil CO_2 had $\Delta^{14}C$ close to or less than those we have assigned to autotrophic respiration. Decomposition of old organic matter in mineral soils clearly contributed to soil respiration in younger stands in 2003, a very dry year, when $\Delta^{14}C$ of soil respiration in younger successional stands dropped below those of the atmospheric CO_2.

Keywords: black spruce, boreal forest, chronosequence, fire, radiocarbon, soil respiration

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Introduction

Globally, the flux of carbon dioxide (CO_2) from soils (soil respiration) was estimated to average $80.4 \pm 0.4\,\mathrm{Pg\,C\,yr^{-1}}$ during 1980–1994, with the boreal forest contributing $4.12\,\mathrm{Pg\,C\,yr^{-1}}$ (Raich *et al*., 2002). Northern latitudes, including boreal forests, have warmed significantly over the last 40–50 years, with air temperature during winter and spring increased by 0.2–0.3 °C, accompanied by increased precipitation in autumn and winter (Pollack *et al*., 1998; Keyser *et al*., 2000; Serreze *et al*., 2000). Soil respiration is predicted to increase with rising temperature despite changes in the timing and distribution of precipitation (Raich *et al*., 2002), implying that northern soils may already be a net source of carbon (C) to the atmosphere.

Soil respiration is made up of two main sources: the CO_2 produced by microorganisms decomposing organic matter (heterotrophic respiration) and CO_2 respired by plant roots or mosses (autotrophic respiration). Predicted responses of soil respiration to warming often are based on empirical relationships between soil temperature and total respiration, and may be inaccurate predictors of future change if autotrophic and heterotrophic respiration respond differently to warming. Increases in decomposition with temperature have the

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potential to add large amounts of C to the atmosphere (Knorr *et al*., 2005), since boreal soils hold about 23% (338–471 Pg C) of global soil C (IPCC, 2001). Alternatively, increases in plant productivity associated with warming, while increasing autotrophic respiration, may end up storing more soil C if litter inputs increase more than decomposition losses (Janssens *et al*., 2001).

Boreal forests are fire-adapted ecosystems, and, averaged over centuries, fire is as important as decomposition in returning soil C to the atmosphere in these ecosystems (Harden *et al*., 2000). The response of boreal forests to climate change are likely to be dominated by changes in fire regime. Today's fire frequencies (area burnt per year) in Canada are lower than estimates of preindustrial fire (ca. 1750–1850) derived from proxy data (Bergeron *et al*., 2004): the positive effect of increasing temperature on fire frequency seems to be compensated by an increase in precipitation frequency and amount. Also, fire detection and suppression have become more efficient during the last 50 years. Although fires today occur less frequently than historical averages, the area burned by large forest fires ($>$200 ha), which account for 97% of the area burned each year, has increased over the past four decades (Gillett *et al*., 2004). One confounding factor for predicting fire frequency and forest C balance is that the climate change predicted for this century in conjunction with changes in forest management may result in changing vegetation composition (Chapin *et al*., 2004a, b).

Increased fire frequency implies a shift in the age structure of boreal forests towards younger stands, which in turn may affect the distribution and overall age of soil respired CO_2 across the landscape. The goal of this study was to quantify how total respiration is partitioned into autotrophic and heterotrophic sources in boreal forests, and how the importance of these sources varies during the growing season, interannually, and with time since fire in a boreal forest.

Our study focuses on black spruce (*Picea mariana* B.S.P.) forests, which occupy the largest area of the North American boreal forest. Boreal forests are subject to large seasonal changes in air temperature, ranging from 30 °C in the summer to −60° in the winter, with large interannual variations. The amplitudes of seasonal and interannual temperature change declines with soil depth and with time since fire because of the insulation of the soil by moss cover.

Within a given stand, soil respiration fluxes are expected to increase with increasing temperature, and to peak in late July or early August (Wang *et al*., 2003). Although seasonal dynamics of root production are not well understood for boreal forests, autotrophic respiration is positively correlated to temperature and above ground productivity, and we can assume rates will peak in early to mid-summer (Ruess *et al*., 2003). The source of C respired by roots should shift from stored C pools in early spring (Cisneros-Dozal *et al*., 2006) to recent photosynthetic products in the peak growing season (Högberg *et al*., 2001). Because soils warm slower than air temperatures, heterotrophic respiration should peak after maximum air temperatures, in the fall when soils are warmest. We, therefore, predict a shift in the make-up of soil respiration from autotrophic to heterotrophic sources during the course of the growing season.

Differences in the response of photosynthesis and respiration to interannual or long-term changes in climate will affect stand-level C balance. Goulden *et al*. (1998) hypothesized that the annual C balance of a mature black spruce forest is very sensitive to the duration and depth of soil frost as this determines the annual heterotrophic CO_2 flux. We expect that soil warming may enhance decomposition of old C in the mineral soil. However, respiration fluxes are also affected by soil moisture. We can assume moisture limitations to mainly reduce respiration of mosses and microorganisms, while trees can obtain water from deeper soil layers. Hence, we might predict lower soil respiration fluxes overall in warm, dry years, with a greater contribution from autotrophic respiration.

Soils undergo large shifts in temperature and moisture during forest regeneration following fire (Chapin *et al*., 2004a). After fire, death of the standing biomass and combustion of organic layers (living moss and soil organic matter) reduce the shading and insulation of the soils. The deciduous species (*Salix* sp., *Populus tremuloides* MICHX., *Betula papyrifera* MARSH.) regenerate vegetatively and attain canopy dominance early in the succession. Black spruce grows from seed and gains dominance late in the succession. With ongoing succession and better insulation because of accumulation of mosses, the soils cool.

Autotrophic respiration should recover with vegetation productivity following fire, and reach a maximum in stands that are several decades old. Ecosystem net primary productivity (NPP) is higher during the early deciduous stage of forest succession than during the coniferous stage. But the fraction of C allocated below ground is higher during the coniferous stage when soil temperatures and nutrient mineralization rates are lower (Gower *et al*., 2001). In black spruce stands, fine root production can account for up to 56% of ecosystem NPP, while mosses account for the largest fraction (20%) of aboveground NPP (Ruess *et al*., 2003). For our study region, Bond-Lamberty *et al*. (2004b) showed that the production of fine and medium-sized roots, which account for most of the root respiration flux, peaked when black spruce reaches canopy closure and declined in more mature stands by 50–70%, together with ecosystem NPP (Litvak *et al*., 2003).

In contrast, heterotrophic respiration is expected to peak very early in the succession because of rapid decomposition of fire residues while soils are warm, and then decline as fire residues disappear (Schulze *et al*., 2000; Litvak *et al*., 2003; Wang *et al*., 2003). After the initial peak, heterotrophic respiration should increase with a time lag following the increase in NPP as substrates for decomposition accumulate. Cooler soil temperatures may slow decomposition, partly offsetting the larger stores of decomposing soil C; overall, we expect greater importance of heterotrophic respiration in older stands.

We use the ^{14}C signature (Δ^{14}C) of respired CO_2 as a tool to separate soil respired C into autotrophic and heterotrophic components. Δ^{14}C is a measure of the time elapsed since CO_2 was fixed by plants from the atmosphere (Trumbore, 2006). Because of the production of ^{14}C by above ground nuclear weapon testing in the 1950s and 1960s, Δ^{14}C of atmospheric CO_2 peaked in the northern hemisphere in 1963–1964 at about 900‰. Subsequently, Δ^{14}C of the atmospheric CO_2 and, therefore, recent photosynthetic products has declined as this 'bomb' $^{14}CO_2$ exchanges with C reservoirs in the oceans and biosphere, and becomes diluted by fossil ($>50\,000$ years) CO_2 from combustion processes. The present rate of decline is 5–6‰ yr^{-1} (Levin & Hesshaimer, 2000). As an example, if Δ^{14}C of respired CO_2 is 30‰ higher than that of contemporary atmospheric CO_2, we estimate that the respired C was fixed on average 5–6 years ago. If Δ^{14}C of respired CO_2 is below 0‰, most of the C must have been fixed before the bomb tests (1950); the more negative Δ^{14}C, the longer ago the CO_2 was fixed. The detection limit for ^{14}C dating is about 50 000 years.

We normally assume that the main C sources contributing to heterotrophic respiration can span a range of different ages (Trumbore & Harden, 1997), while autotrophic respiration of plant roots and bryophytes is recently fixed C (Ekblad & Högberg, 2001). The relative contributions of heterotrophic and autotrophic sources to soil respiration can be calculated by comparing Δ^{14}C of CO_2 respired from the soil surface (R_s), with Δ^{14}C of CO_2 derived from decomposition of organic matter (R_h), and respiration by roots and bryophytes (R_a):

$$\Delta^{14}C_{R_s} = (1-a)\Delta^{14}C_{R_h} + a\Delta^{14}C_{R_a}. \qquad (1)$$

We applied this approach (which has also been discussed by Gaudinski *et al*. (2000), Cisneros-Dozal *et al*. (2006), Schuur & Trumbore (2006), Trumbore (2006)) in 2003 and 2004 growing seasons across a range of sites that differed in time since fire. We made the further assumption that most of the CO_2 derived from decomposition will come from substrates found in the relatively thick O horizons in these soils; this is especially true for mature black spruce stands with large amounts of C and an insulating moss layer that keeps the underlying soil cold and moist.

Materials and methods

Site description

The field sites were located within the BOREAS Northern Study area near Thompson, Manitoba, Canada. We studied six upland sites in various stages of secondary succession after large stand replacement fires in black spruce-dominated forests (Table 1). These sites have also been the site of continuous eddy covariance measurements (Litvak *et al*., 2003), and studies of soil respiration and net primary production (Bond-Lamberty *et al*., 2003; Wang *et al*., 2003). Soils (Boralfs) are all developed from glacial Lake Agassiz sediments with underlying permafrost (H. Veldhuis, pers. com.). Organic horizon thicknesses varied from an average of 9 cm in recently burned stands which had a patchy cover from the remnants of unburned organic layers, to 25 cm in mature black spruce stands with moss cover. Mineral *soil bulk densities* increased with depth and varied between 0.7 and 1.5 g cm^{-3}. Silt and clay made up $>95\%$ of all mineral soils (except the 1850 burn which had 15% sand below 19 cm); however, clay contents at the 1989 and 1964 burn were higher (78–90%) than those at the 1998 burn (37–85%), 1930 burn (35–69%) or 1850 burn (54–82%). Differences among mineral soils diminish with increasing depth.

While we attempted to make the best possible selection of sites so as to allow substitution of space for time to study how sources of soil respiration vary with succession, we acknowledge the potential limitations of the 'chronosequence' approach. Data on soil C content and vegetation characteristics fall well within the range found in a larger study of soils in this region conducted as part of the BOREAS experiment (Harden *et al*., 1997; Trumbore & Harden, 1997; Rapalee *et al*., 1998). In any case, our results are illustrative of how soil respiration sources vary across the boreal landscape in this part of Manitoba.

Isotope samples were collected during the growing season (May–September) of 2003 and 2004. Compared with 2004, the mean air temperature in 2003 at Thompson airport (55°48′ N, 97°52′ W, data source Environment Canada) from May to August was up to 7 °C higher, and about 1 °C cooler in September (Fig. 1). Total precipitation in 2003 from May to September was 262.8 mm compared with 194.8 mm in 2004.

Table 1 Locations and sampling dates of CO_2 concentration in soil pits, soil respiration and root respiration fluxes in stands in age sequence

Last stand replacing fire* (Year)	Latitude (N)/longitude (W) of eddy flux tower	Vegetation composition		Sampling dates			
				Soil CO_2 profile		Respiration	
		Dominant tree cover	Dominant ground cover	Concentration	Δ^{14}C sample	Soil surface	Roots
2003	55° 53′ 88″/	No living trees	*Alnus crispa*	n.m.	n.m.	09/2003	09/2003
	98° 12′ 96″		(Aiton) Pursh	n.m.	n.m.	05/2004	05/2004
			Epilobium augustifolium L.	n.m.	n.m.	07/2004	n.m.
				n.m.	n.m.	09/2004	n.m.
			Dicentra sp.				
			Rosa sp.				
1998†	56° 38′ 09″/	No large trees	*A. crispa*, *Ledum groenlandicum*	07/2003	07/2003	07/2003	07/2003
	99° 56′ 54″		Oeder,	09/2003	09/2003	09/2003	09/2003
			E. augustifolium,				
			Rosa sp.				
1989†	55° 55′ 0″/	*Picea mariana*	*A. crispa*,	07/2003	07/2003	n.m.	07/2003
	98° 57′ 52″	B.S.P.	*L. groenlandicum*	09/2003	09/2003	09/2003	09/2003
		Pinus banksiana	*E. augustifolium*	05/2004	n.m.	05/2004	05/2004
		Lamb.	*Rosa* sp.	07/2004	07/2004	07/2004	07/2004
		Populus tremuloides		09/2004	09/2004	09/2004	09/2004
		Michx.					
		Salix sp.					
1964†	55° 54′ 42″/	*P. mariana*	*L. groenlandicum*	07/2003	07/2003	07/2003	07/2003
	98° 22′ 56″	*P. banksiana*	*Rosa* sp.	09/2003	09/2003	09/2003	09/2003
		Salix sp.	*Vaccinium oxycoccus* L.	05/2004	n.m.	05/2004	05/2004
		Betula papyrifera		07/2004	07/2004	07/2004	07/2004
		Marsh	Peat (*Sphagnum* sp.)	n.m.	n.m.	09/2004	09/2004
			and feather mosses				
1930†	55° 54′ 21″/	*P. mariana*	*L. groenlandicum*	07/2003	n.m.	n.m.	n.m.
	98° 31′ 29″		*Rosa* sp.	09/2003	09/2003	09/2003	09/2003
			V. oxycoccus	05/2004	05/2004	05/2004	05/2004
			Peat and feather mosses	07/2004	07/2004	07/2004	07/2004
				09/2004	09/2004	09/2004	n.m.
1850‡	55° 52′ 49″/	*P. mariana*	*L. groenlandicum*,	07/2003	07/2003	n.m.	07/2003
	98° 28′ 43″		*Rosa* sp.	09/2003	09/2003	n.m.	09/2003
			V. oxycoccus,	05/2004	05/2004	n.m.	n.m.
			Peat and feather mosses	07/2004	07/2004	n.m.	07/2004
				09/2004	09/2004	n.m.	09/2004

*Litvak *et al*. (2003), Michael Goulden (personal communication, 2005).

†Ameriflux sites.

‡Very close to site BOREAS Northern Old Black Spruce (NOBS†), but better drained.

n.m. = not measured.

Closure of the moss layer occured in the 1964 burn, black spruce reached canopy dominance and closure at the 1930 burn.

Field installations

In September, 2002, one soil pit was instrumented and backfilled at each site, except the 2003 burn site, which has no soil profile data and was added to the study after a fire in July 2003 (Table 2). Soil gas probes were made using high-density porous PTFE tubing (1/4″ OD, approximately 20 cm length; International Polymer Engineering, Tempe, AZ, USA). A stainless steel rod was inserted inside the PTFE tubing to make the probes stiff enough to install. This rod also minimized the dead volume contained within, and consequently, the volume required to sample air representative of the soil pore space surrounding the probe. These probes were inserted horizontally to their full length at various depths into the face of each soil pit.

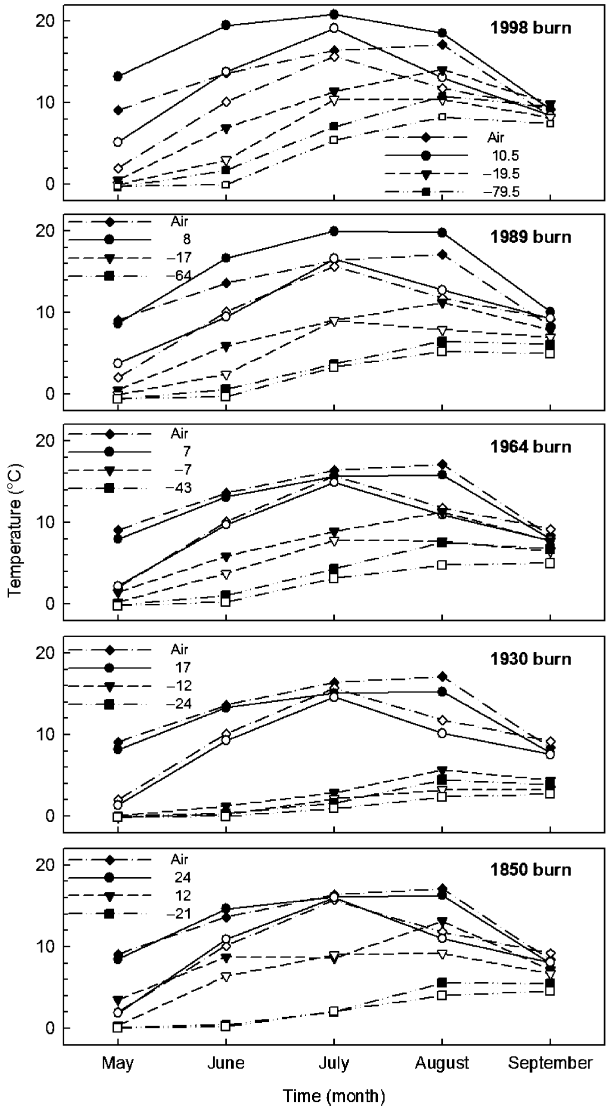

Fig. 1 Seasonal distribution of temperature within the organic layers (positive depths in cm) and the mineral soil (negative depths) with time since fire during a warmer (2003, filled symbols) and a cooler (2004, open symbols) growing season. As a comparison, air temperature data from Thompson airport is shown at each site.

Stainless steel tubing (1/16″ OD) was used to access the PTFE tubing from above the soil surface and was connected to the PTFE and capped with Swagelok fittings. Precision interchangeable thermistors (model EC95H303W Thermometrics, Edison, NJ, USA) encapsulated in thermally conductive epoxy, and TDR soil moisture probes (model CS616 Campbell Scientific Inc., Logan, UT, USA) were inserted horizontally at the same depths. There were no deep moisture probes inserted at the 1989 and 1983 burn, because the profile was water saturated in September 2002. Surface temperature and moisture conditions were monitored with an additional thermistor and a fuel moisture sensor (model CS505, Campbell Scientific Inc.). Temperature and moisture were recorded every 2 h using a data logger (model CR10X, Campbell Scientific Inc.) continuously from deployment through 2004.

Gas sampling and measurements

In 2003 and May 2004, we measured the CO_2 concentration at various soil depths in syringe samples using a LI-800 or LI-820 infrared gas analyzer (Licor, Lincoln, NB, USA) as described by Davidson & Trumbore (1995). In July and September 2004, we flushed the air in each soil tube directly through an infrared gas analyzer for a few minutes at $0.1\,L\,min^{-1}$. We recorded the highest CO_2 concentration with a LI-1400 data logger as the concentration in the profile. For deeper probes, we sampled soil CO_2 for $\Delta^{14}C$ analysis at high concentrations by connecting the probe tubes via a stainless steel capillary (0.05″ ID), which restricted the flow rate so that one to four evacuated 0.5 L stainless steel flasks were filled in 4–5 h (Gaudinski *et al.*, 2000). For shallow probes with lower CO_2 concentrations, we pumped the soil air ($0.1\,L\,min^{-1}$) through Drierite to an activated molecular sieve 13X trap that quantitatively removes CO_2 to capture $>0.5\,mg\,C$.

The rate of CO_2 efflux from the soil surface (soil respiration) was measured by placing a PVC chamber lid (inner diameter of 26 cm) onto a chamber base that was preinstalled in the soil. We circulated chamber headspace air through an infrared gas analyzer for about 6 min at $0.5\,L\,min^{-1}$, and recorded the rate of change of CO_2 in the chamber headspace every 1 s. The chamber lid was vented to prevent pressure gradients between the chamber and the surrounding air. Three chamber bases were inserted into the soil organic layer at each site 1 day (2003 and 1998 burn), 2 months (1989 and 1930 burn) or 1 year (1964 and 1850 burn) before the first measurement, and then left in their position during the remaining time of the experiment. Living mosses were not disturbed in this process, so our measurements of soil respiration include a contribution from moss autotrophic respiration. We attempted to minimize the cutting of roots during chamber base installation. At the 1850 burn, we found that chamber bases had been cut into the mineral soil, removing all living roots; we do not report measurements of CO_2 or $\Delta^{14}C$ fluxes from this site. At sites where coarse woody debris was present on or in the forest floor, we included it in one of the three chambers.

To collect CO_2 for ^{14}C samples, we circulated the air in the chamber headspace through sodalime for 30 min ($0.5\,L\,min^{-1}$) to remove most of the CO_2 derived from

Table 2 Depth of temperature, moisture and gas probes in soil profiles

Last stand replacing fire (Year)	Depth of probes		
	Temperature	Moisture*	Gas
	cm†		
2003		None	
1998	10.5, 7.5, 4.5	5.5 FR	10.5, 7.5, 4.5
	−0.5, −4.5, −19.5, −49.5, −79.5	−0.5, −79.5	−0.5, −4.5, −19.5, −49.5, −79.5
1989	8, 5, 1	3.5 FR	8, 5, 1
	−6, −17, −26, −42, −64	−6	−6, −17, −26, −42, −64
1964	7, 5, 1	3 FR, 2	7, 5, 1
	−7, −23, −43, −63, −73	−7, −23, −43, −63	−7, −23, −43, −63, −83
1930	17, 11, 6, 1	6 FR	17, 11, 6, 1, 0
	−1, −12, −24, −38	−1, −12, −24, −38	−1, −12, −24, −38
1850	24, 17, 16, 12	12 FR	24, 17, 16, 12
	−1, −8, −21, −36	−8	−1, −8, −21, −36

*FR is fuel moisture sensor.

†Positive numbers indicate that the probes are in the organic layers, negative that they are in the mineral soil.

ambient air. Then we closed the tubing on the chamber lid and let the CO_2 respired from the soil accumulate for ≥ 30 min. The CO_2 was trapped by circulating the chamber air ($0.5\,\mathrm{L\,min^{-1}}$) through Drierite to a molecular sieve trap and back to the chamber for 15 min. For more details, see Gaudinski *et al*. (2000), Cisneros-Dozal *et al*. (2006).

CO_2 fluxes (in $\mathrm{mg\,C\,h^{-1}\,m^{-2}}$) were calculated from the slopes of the concentration vs. times curves, the system volume, and the surface area covered by the chamber. Molar fluxes were based on concentrations adjusted for temperature at atmospheric pressure.

Measurements of C isotopes in the laboratory

To isolate the CO_2 from the gas samples, we connected the flasks or molecular sieve traps to a vacuum line. Traps were heated to 630 °C for 45 min to release the CO_2 which was purified cryogenically. A fraction of the CO_2 from each sample was transferred to a He-filled septum-capped vial, and analyzed for its $\delta^{13}C$ value with an isotope ratio mass spectrometer (continuous flow, Thermo Finnigan Delta Plus, Bremen, Germany). Enough CO_2 to yield 0.6–1 mg C was frozen and sealed into an evacuated 9 mm Pyrex tube. This tube contained 25 mg Zn and 17 mg TiH_2 powder at the bottom. Approximately 2.5 cm above the bottom, we suspended a 6 mm Pyrex tube containing 5 mg Co powder. Both tubes were prebaked for 3 h at 500 °C and 4 h at 550 °C. The CO_2 was catalytically reduced to graphite for 3 h at 500 °C and 4 h at 550 °C. $\Delta^{14}C$ of the graphite was measured using an accelerator mass spectrometer at the Keck-CCAMS facility of UCI (Southon & Santos, 2004).

Either incomplete removal of initial air or leaks in our air circulation system occasionally added air to our chamber samples, which we detected as a $\delta^{13}C$ signature that not sufficiently depleted in ^{13}C (> -20‰). In such cases, we corrected $\Delta^{14}C$ of all CO_2 samples from chamber and root incubation measurements as described in Gaudinski *et al*. (2000). Assuming that each CO_2 sample consisted of CO_2 respired from the soil or an incubation sample and of CO_2 from ambient air we calculated the proportion of ambient air present in each sample:

$$\mathrm{Fraction_{air}} = \frac{\delta^{13}C_{\mathrm{sample}} - \delta^{13}C_{\mathrm{respired}}}{\delta^{13}C_{\mathrm{air}} - \delta^{13}C_{\mathrm{respired}}}, \qquad (2)$$

where the value of $\delta^{13}C_{\mathrm{respired}}$ was the lowest of $\delta^{13}C$ value of all replicate samples with $\delta^{13}C < -20$‰ from the same site. If no replicate sample was available, we used a $\delta^{13}C$ value of -22. If the proportion of air was > 0.4, the sample was excluded from further analysis.

The corrected $\Delta^{14}C$ value of the respired CO_2 was calculated using (2) as

$$\Delta^{14}C_{\mathrm{respired}} = \frac{\Delta^{14}C_{\mathrm{sample}} - \mathrm{fraction_{air}}\Delta^{14}C_{\mathrm{air}}}{1 - \mathrm{fraction_{air}}}, \qquad (3)$$

where $\Delta^{14}C_{\mathrm{respired}}$ was the corrected $\Delta^{14}C$ signature of CO_2 produced in the soil, $\Delta^{14}C_{\mathrm{sample}}$ was the signature of CO_2 collected from chambers or incubations, and $\Delta^{14}C_{\mathrm{air}}$ was the signature of ambient air.

The CO_2 collected from soil probes is a mixture of CO_2 produced in the soil and air (Hirsch *et al*., 2002). Its

$\Delta^{14}C$ signature reflects this mixing, especially in moss layers that exchange CO_2 rapidly with the atmosphere; no correction for a contribution of CO_2 from air was applied.

Heterotrophic and autotrophic respiration

We used an isotope mass balance equation (1) to calculate the contribution of heterotrophic (R_h) and autotrophic (R_a) sources to soil respiration (R_s), where a was the fraction of autotrophic respiration. The propagation of errors was calculated as described by Phillips & Gregg (2001).

We defined $\Delta^{14}C_{R_h}$ as the $\Delta^{14}C$ of CO_2 respired from organic layers during the one-time laboratory incubations using methods described by Dioumaeva *et al.* (2003). In the field, we sampled organic material from the Oe (slightly decomposed; living moss removed) and Oa layers (more decomposed) using triplicate cores of 17.5 cm diameter in September 2003.

Samples were stored at 7 °C for at least 2 months to allow roots (we did not remove fine roots) to die. Before the incubation, samples were homogenized and coarse roots ($>$1 cm) and larger pieces of wood were removed. About 20 g of soil was incubated at field moisture content, which was about 17 wt% for Oe and 7–24% for Oa layers, in 1 l jars in the dark at 7, 14, and 23 °C. Samples were incubated in two batches. After CO_2 flux rates became constant (batch 1 after 7 days, batch 2 12 days), we let the CO_2 accumulate in each jar and sampled it with an evacuated 0.5 l stainless steel flask. We will report on the results of temperature and moisture manipulations of these incubations elsewhere. Isotopic signatures were not affected by these manipulations, though the rate of CO_2 evolution clearly was (see also Cisneros-Dozal *et al.*, 2006).

For the young sites (2003 to 1989 burn), where the Oe layer had burned off, we assumed that $\Delta^{14}C_{R_h}$ equaled $\Delta^{14}CO_2$ respired from the Oa layer. For the older sites (1964 to 1850 burn), we used flux–temperature relationships to calculate the appropriate respiration flux for the Oe and Oa layer using field temperatures. These fluxes were used to weight isotopic signatures of CO_2 evolved from both layers so as to obtain a flux-weighted $\Delta^{14}C_{R_h}$.

We assume that $\Delta^{14}C_{R_h}$ did not change throughout the sampling period. Given the several months waiting period between sampling and measurement, we have removed organic matter that decomposes very rapidly, which we assume would have $\Delta^{14}C$ values close to those of recent photosynthetic products. Hence, our method would exlude the influence of some or all of the rapidly cycling organic matter from our heterotrophic component; in calculations this fraction would be combined with the 'autotrophic' end member. Our estimates of the heterotrophic component of soil respiration are conservative, because we assume in the mass balance (1) that the contribution of CO_2 from the decomposition of organic matter in the mineral soil was zero. Steep CO_2 gradients with depth and the lack of correspondence in $\Delta^{14}C$ of CO_2 in the deeper soil pore space with $\Delta^{14}C$ of the surface fluxes suggest that the contribution of mineral soil CO_2 to the surface flux was generally very small, and most of the heterotrophic CO_2 flux originates from the organic layers (see also Hirsch *et al.*, 2002). Small amounts of decomposition-derived CO_2 from deeper soil layers would tend to dilute the $\Delta^{14}C$ of the heterotrophic end member (see Results, below).

The signature of autotrophic respiration ($\Delta^{14}C_{R_a}$) was calculated from field incubation as the average of the $\Delta^{14}C$ of root- and moss-respired CO_2 for a given growing period, except at the 2003 burn were all mosses had died and we only used $\Delta^{14}C$ of root-respired CO_2. This average was not flux weighted, because we could not scale root and moss CO_2 fluxes to stand area or relative biomass contribution. Also, the $\Delta^{14}C$ of root-respired CO_2 varied strongly from season to season and we did not get an estimate for each season from each stand.

In 2003 we sampled a representative mixture of fine roots ($<$2 mm) from all species present at a site by excavating all roots in 20 cm × 20 cm squares from three to four locations within the stand. In 2004, we sampled fine roots ($<$1 mm) of black spruce trees only. Roots were identified by following them from a spruce tree. Roots were extracted from the ground, rinsed with water and placed in air tight plastic container of 2020 cm^3 volume. The containers were placed into the organic layer to mimic initial the temperature conditions of the roots. We flushed the container (0.5 L min^{-1}) with CO_2-free air for 10 min, let the root-respired CO_2 accumulate for $\geq$ 2 h, and then circulated the air in the container through Drierite to a molecular sieve trap and back to the container for 10 min at 0.5 L min^{-1}. Dates of soil and root respiration measurements for each site are given in Table 1. Undisturbed living moss was cut out of the ground, incubated and sampled, using similar methods, but in the dark, in May 2004. During each sampling campaign, we also collected two to three samples of ambient air in a well mixed area of each site by pumping air (0.5 L min^{-1}) through Drierite to a molecular sieve trap for 30 min. This was used as a measure for $\Delta^{14}C$ of recently photosynthetic products.

Our estimate of $\Delta^{14}C_{R_a}$ is an estimate of 'fast cycling carbon'. It includes the respiration of microorganisms decomposing plant exudates in the rhizosphere which may or may not be correlated to root growth, because the $\Delta^{14}C$ of rhizosphere microorganisms-respired CO_2 cannot be distinguished from root or moss respiration.

Results

Soil temperature and moisture

Soils underwent large seasonal and smaller interannual changes in temperature which were most pronounced in young regenerating stands (Fig. 1). The upper part of the organic layers reached a maximum of 21 °C at the 1998 and 1989 burn with shallower organic layers and open canopies, but only 15 °C in moss layers at the older sites with closed canopy (Fig. 4c). The maximum soil surface temperature coincided with the maximum air temperature in July if living moss was absent (1998 burn). At sites where living moss was present (1989 to 1850 burns) maximum soil surface temperatures were reached in July 2003 and August 2004. Air and soil organic layer temperatures from May to August were higher in 2003 than in 2004. Temperatures in the mineral soil increased from May to September. Mineral soils warmed more in 2003 than in 2004. The young stand warmed more than the older stands (Fig. 1).

Changes in soil moisture were also largest in most recently burned stands. Seasonally, the volumetric water content in the organic layer (measured by fuel moisture sensors) varied between 23% and 70% at the 1998 and 1989 burn, with a minimum in July, but only between 58% and 71% in the older, closed-canopy stands. The volumetric water content in the upper mineral soil (<20 cm) at all sites was 10–30% in May and 15–40% in July and September. The deeper mineral soil (>20 cm) at the 1998 and 1964 burn had volumetric water contents of 40% in May and 60% in July and September. The deep soil water content at the 1930 burn increased throughout the growing season with temperature from 15% in May to 40% in September.

The overall drier conditions in 2003 were associated with lower soil water content, which was up to 20% lower than in 2004 at all depths and for all sites. The interannual variation in soil moisture was as high as the observed seasonal changes.

Soil profile CO_2 concentrations and $\Delta^{14}C$ signatures

In the organic layers, CO_2 concentrations and their $\Delta^{14}C$ did not change significantly with stand age on seasonal and interannual time scales (Fig. 2). The signatures were dominated by postbomb C (>0‰) and similar to that of CO_2 obtained from root and moss incubations. Hirsch *et al.* (2002) demonstrated that CO_2 concentrations in mosses are affected by wind speed and are highly variable over time.

In the mineral soils, CO_2 concentrations increased with soil temperatures. The CO_2 concentrations in the faster warming soils of the 1998 to 1964 burn reached a maximum of 0.2–0.4% (100 mol mol^{-1}) in the upper 20 cm in July. Below 20 cm CO_2 concentrations increased from July to September, except at the 1989 burn where concentrations did not change. Maximum concentrations

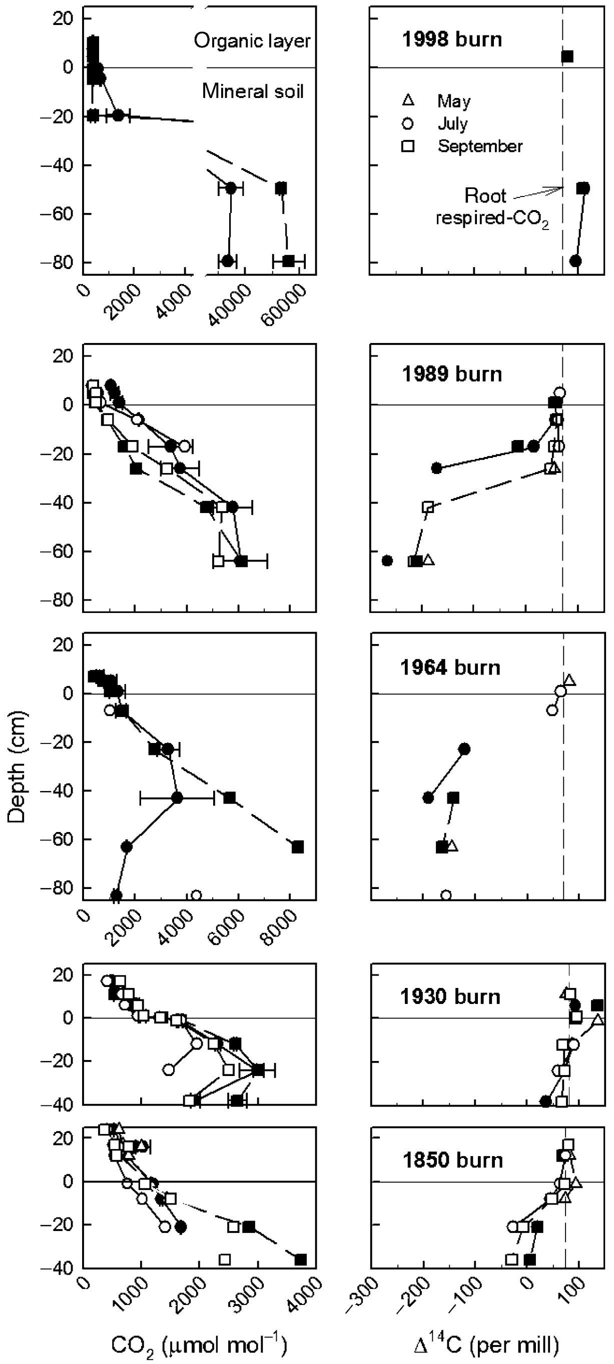

Fig. 2 Distribution of CO_2 and its $\Delta^{14}C$ signature with soil depth at different times since fire during a warmer (2003, filled symbols) and a cooler (2004, open symbols) growing season. The dashed vertical line indicates the $\Delta^{14}C$ of root-respired CO_2. (Error bars indicate standard deviation.)

were $>5\%$ at the 1998 burn, 0.6% at the 1989 burn, and 0.8% at the 1964 burn. Δ^{14}C of CO_2 below 20 cm was dominated by postbomb C (>0‰) at the 1998 burn, and by very old C (<-100‰) at the 1989 and 1964 burn. In the slower-warming soils of the 1930 and 1850 burn, CO_2 concentrations increased from July to September within the entire mineral soil and reached a maximum of 0.3–0.4%. Δ^{14}C below 20 cm ranged from −50–50‰, indicating a mixture of prebomb and postbomb sources.

As concentrations increased during the growing season at all sites, Δ^{14}C of soil CO_2 increased. There were no interannual changes in the CO_2 concentrations or Δ^{14}C at the 1989 burn, and insufficient data was collected to identify trends at the 1998 and 1964 burn. At the 1930 and 1850 burn, however, the CO_2 concentration at a given depth and its Δ^{14}C were higher in 2003 than in 2004.

Soil respiration

Soil respiration reached 60 $\mathrm{mg\,C\,m^{-2}\,h^{-1}}$ at the 2003 burn, increased with stand age to 145 $\mathrm{mg\,C\,m^{-2}\,h^{-1}}$ at the 1964 burn, and declined to 120 $\mathrm{mg\,C\,m^{-2}\,h^{-1}}$ at the 1930 burn (Fig. 3a). However, differences between sites in a given month were not significant because of large spatial variability. Also, fluxes showed a strong seasonal trend being lowest in May and highest in July. But flux increases at a given site from May to July were not significant, except at 1930 burn (Student's *t*-test, $P<0.05$). Decreases from July to September were also not significant, except at the 1964 burn in 2003 (Student's *t*-test, $P<0.05$). There were no significant differences (at $P<0.05$ level) in fluxes between 2003 and 2004 at any site in any month.

At all sites, the CO_2 respired from the soil surface was dominated by C with Δ^{14}C indicative of C fixed after 1950 (>0‰). Values were higher ($\sim$ 100‰) at the 2003 and 1930 burn sites than at the 1998 to 1964 burn sites ($\sim$ 80‰; Fig. 4a). There were no significant seasonal changes in Δ^{14}C of respired CO_2 at any site. However, Δ^{14}C at the 2003 burn decreased throughout the growing season during 2004. In 2003, the mean Δ^{14}C of respired CO_2 at any given site was lower than in 2004, although the differences were not significant. Minimum Δ^{14}C for soil respired CO_2 were observed in September 2003 at the 1998, 1989 and 1964 burn sites; Δ^{14}C at the 1989 burn at that time was lower than that of the ambient atmospheric CO_2.

Respiration partitioning

$\Delta^{14}C_{R_h}$ (not including living moss) was dominated by bomb-C at all sites and higher than that of ambient CO_2 which was 70‰ in 2003 and 64‰ in 2004 (Fig. 4c).

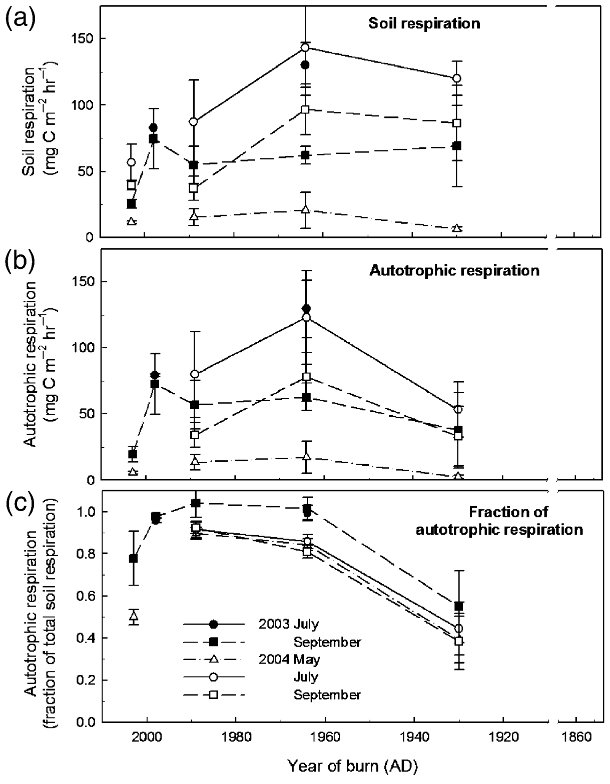

Fig. 3 (a) Soil respiration at the soil surface, (b) autotrophic respiration (CO_2 respired by roots, mosses, and microorganisms feeding on plant exudates), and (c) autotrophic respiration as a fraction of soil respiration with time since fire during a warmer (2003) and a cooler (2004) growing season.

In 2003, we measured Δ^{14}C of CO_2 respired by roots of all regrowing tree species present at the 1998 to 1964 sites (including both deciduous and young coniferous trees). These isotopic signatures were close to those measured for CO_2 in ambient air (Fig. 4b). Δ^{14}C of CO_2 respired from living moss also equaled that of CO_2 in ambient air in both 2003 and 2004.

At the 2003, 1930, and 1850 burn sites, where black spruce trees were the dominant vegetation, we measured CO_2 respired from black spruce roots in 2003 and 2004. In 2004, we also measured Δ^{14}C of CO_2 respired from black spruce roots only at the 1998, 1989, and 1964 burn (these were identified by tracing roots from small black spruce trees). Δ^{14}C respired from black spruce roots ranged from values close to those of CO_2 in ambient air to values that were up to 30‰ higher. The largest differences between root respired and atmospheric-$\Delta^{14}CO_2$ values were detected in stands where large spruce trees were present (2003, 1964 to 1850 burn). We also observed higher Δ^{14}C values in black spruce roots more frequently in 2003 than in 2004.

The isotope mass balance (1) suggested that very little of the soil respiration in early succession stages (1998 to

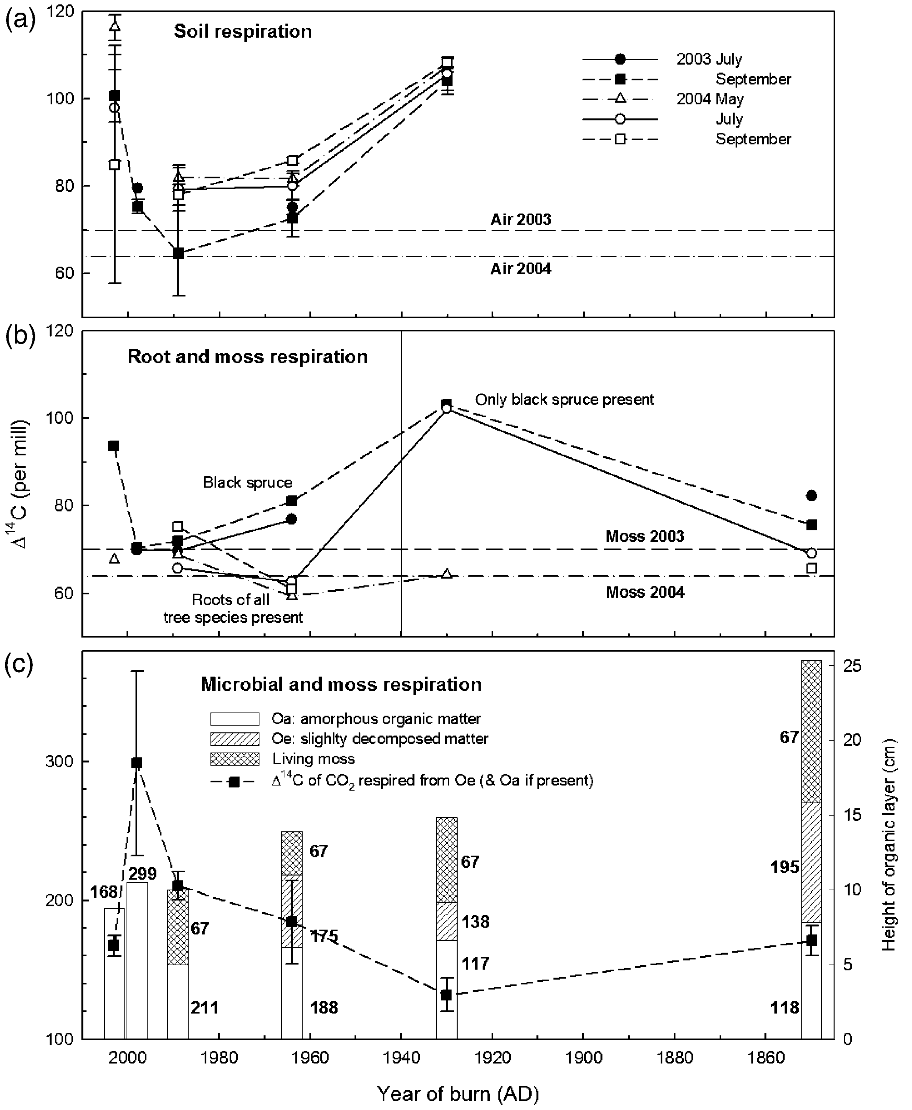

Fig. 4 Seasonal changes in $\Delta^{14}C$ of CO_2 respired (a) from the soil surface, and (b) by tree roots and mosses with stand age in 2003 (filled symbols) and 2004 (open symbols). Root respiration represents all tree species present at a site in 2003, but only black spruce in 2004. CO_2 respired by mosses had the same $\Delta^{14}C$ as CO_2 in ambient air. (c) Composition of organic layers (bars), and $\Delta^{14}C$ of CO_2 respired from individual layers (numbers near bars), and from Oe and Oa layers (squares) with time since fire. (Note the different scales for the ordinates.)

1964 burn) originated from O horizon decomposition sources (<20%) (Fig. 3b and c). The contribution from heterotrophic sources in the O horizon increased to 40–50% in stands where black spruce had reached canopy dominance and closure (1930 burn and probably the 1850 burn). Respiration with the ^{14}C signature of autotrophic respiration followed a trend with time since fire similar to that of total soil respiration with a maximum 40 years since fire (Fig. 3b). As for soil respiration, seasonal differences in respiration sources were not significant at a given site. However, at the 2003 burn black spruce root-respired CO_2 accounted for 80% of the soil respiration 1 month after the fire in September of 2003 and decreased to 50% in May of 2004; in July and September 2004, we could not detect a CO_2 flux from roots.

In 2003, a drier and warm year, the contribution of O horizon decomposition to soil respiration was less at all sites than in 2004. At the 1989 and 1964 burn, the mass balance does not work, which indicates that our two end members (root/moss respiration and O horizon decomposition) are not bracketing observed ^{14}C signatures in soil respiration (which were lower than the ^{14}C of root/moss respired CO_2). The only source of CO_2

with a Δ^{14}C lower than that of atmospheric CO_2 at these two sites was the deep mineral soil (Figs 2 and 4).

Discussion

Heterotrophic respiration from the organic layers

Δ^{14}C of heterotrophic respiration ($\Delta^{14}C_{R_h}$) depends on a number of factors that vary with time since fire, including the age of the organic C accumulated since the last fire, the character of that organic matter (herbaceous litter vs. mosses), and the temperature conditions that determine the relative weighting of decomposing substrates found at different soil depths. Across all sites, heterotrophic respiration was dominated by C fixed since 1950 (positive $\Delta^{14}C_{R_h}$). The highest $\Delta^{14}C_{R_h}$ were observed at the 1998 burn (300‰), indicating that most of the C currently decomposing at this site had accumulated between 1960 and 1980 (i.e. before the recent fire) when Δ^{14}C of atmospheric CO_2 was >300‰. In contrast, $\Delta^{14}C_{R_h}$ at the 1850 burn included decomposition of C fixed both before and after 1950. Decomposition rates are higher earlier in the succession when the input is dominated by biomass from forbs and deciduous trees, and slower after the moss has regrown (Trumbore & Harden, 1997). $\Delta^{14}C_{R_h}$, thus, depends on the successional stage of each stand compared with 1963, when Δ^{14}C of atmospheric CO_2 peaked.

Incubation studies have shown that $\Delta^{14}C_{R_h}$ does not change over a wide temperature range (Dioumaeva *et al*., 2003). Thus, we did not expect $\Delta^{14}C_{R_h}$ to change seasonally. However, temperature and moisture conditions can change the rate of CO_2 production. When temperature and moisture interact with the differences in Δ^{14}C of organic substrates with depth in organic horizons, changes in the overall $\Delta^{14}C_{R_h}$ can be expected. For example, in the very dry summer of 2003, Δ^{14}C of total soil respiration dropped below Δ^{14}C of atmospheric CO_2. This can only have happened if the dry surface layers we incubated contributed less to overall soil respiration than the diffusion of ^{14}C-depleted CO_2 from deeper in the soil. Hence the $\Delta^{14}C_{R_h}$ we derived from incubations reflect the isotopic signature for relatively humid conditions, and the contribution of O-horizon decomposition to soil respiration underestimates the total heterotrophic contribution to soil respiration.

Autotrophic respiration

The variability of Δ^{14}C of root-respired CO_2 ($\Delta^{14}C_{R_a}$) at a given site was much larger than that of organic layer-respired CO_2 or of soil respiration. $\Delta^{14}C_{R_a}$ of root-respired CO_2 from deciduous and young black spruce trees was near that of atmospheric CO_2 at all times, confirming that recent photosynthates were fueling autotrophic respiration in some boreal trees (Högberg *et al*., 2001). In contrast, roots of black spruce trees ≥ 40 years old either respired CO_2 from recent photosynthetic products or from an internal storage pool with an average age of at least 5 years (30% divided by the 6‰/year rate of decline of ^{14}C in atmospheric CO_2). Similar values were obtained in incubations of black spruce roots in Alaskan boreal forest by Schuur & Trumbore (2005).

We did not find the expected seasonal trend in the use of stored (i.e. higher Δ^{14}C) C, with a larger proportion of storage-derived C in the spring and a dominance of recent photosynthates in the summer and fall as proposed by Ekblad & Högberg (2001). Instead, storage use appeared to be greater in the warmer year, 2003, which might be related to higher maintenance respiration under temperature stress (Marshall & Waring, 1985; Marshall, 1986). The presence of a large storage pool would also explain why we were able to measure CO_2 respired from black spruce roots at the 2003 burn until May 2004, although the trees had died in the fire in July 2003. The respiration of dying roots accounted for 50–80% of the soil respiration flux. However, $\Delta^{14}C_{R_a}$ decreased with time in contrast to our hypothesis that the roots would use up younger C stores first. More measurements are needed to resolve the C pools used by roots under various conditions.

Gradients of temperature, CO_2, and Δ^{14}C in the mineral soils

In the warmer soils of the early succession stages, CO_2 concentrations below 20 cm were higher and CO_2-depth-gradients were steeper than in the cooler soils of late succession stages. CO_2 concentrations in mineral soils reflect the balance of production and transport. Previous work using radon to estimate gas exchange rates in mineral soils at these sites showed that gas transport rates are very slow in these moist, clay rich soils (Hirsch, 2001). In particular, the soils of the early succession stages had lower porosity and diffusivity resulting from the presence of soil horizons with bulk densities $>1.3\,g\,cm^{-3}$ (K. Manies personal communication, 2005). Hence, high CO_2 concentrations at these sites can indicate decreased gas transport as much as enhanced production of CO_2 at higher temperatures.

At sites where Δ^{14}C of CO_2 was negative in the pore space of mineral soils, Δ^{14}C values increased over the growing season with temperature and CO_2 concentrations (Fig. 2). These results are in agreement with earlier studies of winter time CO_2 concentrations (Winston *et al*., 1997). CO_2 in the mineral soil originates from decomposition of organic matter and from root respiration. CO_2 production from decomposition should be enhanced at higher temperatures (Knorr *et al.*, 2005), however, incubation studies suggest that the $\Delta^{14}C$ of CO_2 derived from decomposition is independent of temperature or moisture variation (Dioumaeva *et al.*, 2003; Cisneros-Dozal *et al.*, 2006). Therefore, increased $\Delta^{14}C$ values likely reflect increased autotrophic respiration. If we assume that the source of respiration at colder temperature was decomposition of organic matter only, and the new source is autotrophic respiration (70‰), we can calculate the autotrophic contribution using Eqn (1). For example, the increase in $\Delta^{14}C$ at 60 cm depth from July to September 2003 at the 1989 burn could be explained by a contribution of 17% from the autotrophic source. The increase at 40 cm at the 1850 burn from September 2003 to 2004 could be explained by a contribution of 35%. This is in accord with results by Hirsch *et al.* (2002) who showed that $\Delta^{14}C$ of CO_2 in the deep soil in a poorer-drained area of the 1850 burn decreased in late September, when NPP and autotrophic respiration probably had declined because of cold air temperatures, while decomposition of mineral soil C was enhanced as soil continued to warm.

Soil respiration

We found no peak in soil respiration from the decomposition of fire residues as measured in Siberian Scots pine forests (Schulze *et al.*, 2000). Soil respiration fluxes were low in young regenerating stands, increased with stand age to a maximum at 1964 burn, which was the most productive site of the chronosequence (Litvak *et al.*, 2003), and declined as stands reached maturity. This pattern confirmed measurements by Wang *et al.* (2003) who previously measured soil respiration fluxes of similar magnitude for comparable soil temperatures in the same area.

Our results show that soil respiration during early stand development (5–40 years) originates mainly from autotrophic sources, with no pulse of heterotrophic respiration. The selection of our field sites (time since fire) would not allow us to detect a pulse in the contribution of heterotrophic sources immediately after fire (1–4 years). However, we witnessed the invasion of forbs and resprouting of shrubs and deciduous trees in the 2003 burn within months after the fire. This suggests that autotrophic sources contribute significant amounts to soil respiration early in the succession.

In general, the contribution of autotrophic sources was found to increase with increasing productivity across the chronosequence. Upon reaching a stand age of 70 years heterotrophic and autotrophic sources contributed equally to soil respiration. Schuur & Trumbore (2005), using similar methods, showed that autotrophic respiration contributed 37–53% of total soil respiration in mature (>100-year-old) black spruce stands in Alaskan boreal forests, in accord with our estimate for a closed canopy (73 years since fire) black spruce stand.

Our seasonal estimate of autotrophic respiration in <40-year-old sites are much higher than those obtained at the same (or very similar) sites by Bond-Lamberty *et al.* (2004c) using a trenching experiment. They estimated that root respiration on an annual basis contributed <40% to total respiration at all times since fire, peaking in importance at the 1930 burn. The differences are due to two factors. First, trenching removes both root and rhizosphere respiration contributions, while our incubations of O horizons (which included fine roots) may include the ^{14}C signature of some of the rhizosphere component. This would tend to make our estimates of autotrophic respiration smaller, as we include the rhizosphere in our heterotrophic endmember, while Bond-Lamberty *et al.* (2004c) include it in their autotrophic endmember.

Second, the CO_2 derived from decomposition of older organic matter in mineral soils was not included in our estimate of $\Delta^{14}C_{R_h}$. Radiocarbon signatures of soil CO_2 in mineral soils are at or below atmospheric $\Delta^{14}CO_2$ values for all but the 1998 burn site. Failure to include a significant contribution from decomposition of old organic matter in our estimate of $\Delta^{14}C_{R_h}$ implies that the value of $\Delta^{14}C_{R_h}$ used in our mass balance was too high and, therefore, that we have underestimated the contribution of heterotrophic respiration by incubating the O horizons alone. This is clearly a factor in 2003 at the 1989 and 1964 burn sites; these are also the two sites with the oldest CO_2 in airfilled pore space (see Fig. 2). In 2004, when litter was wetter on the days we sampled, the fluxes and $\Delta^{14}C$ of soil respiration are higher. For older sites with much thicker moss layers and colder and wetter mineral soils, the $\Delta^{14}C$ of CO_2 in the mineral soil indicated little contribution from decomposition of old organic matter found in these horizons. Schuur & Trumbore (2006) found that the CO_2 evolved during incubations of mineral soils from mature black spruce stands contributed little compared with O horizon decomposition. Hence, in mature stands, and in the 1998 burn where $\Delta^{14}C$ of soil CO_2 is higher than atmospheric $\Delta^{14}CO_2$ values, our estimates of heterotrophic and autotrophic respiration are more robust than for the 1989 and 1964 burn sites.

We cannot rule out that we underestimated the contribution of decomposition since our method includes any decomposition of organic matter in the organic layer of mineral soil with a $\Delta^{14}C < \Delta^{14}C_{R_h}$ and $\geq \Delta^{14}C_{R_a}$ in the autotrophic endmember. Nevertheless, we can estimate the missing contribution from the decomposition of old C (Δ^{14}C <0‰) in mineral soils at the 1989 and 1964 burn in 2003 if we assume that decomposition of O horizon C did not contribute to the soil respiration flux because of moisture limitations. In the mass balance (1), we assume that $\Delta^{14}C_{R_h}$ is the lowest measured Δ^{14}C of mineral soil CO_2 (-266‰ at the 1989 burn, -190‰ at the 1964 burn). This calculation suggests that decomposition of old mineral soil C contributed 1–3% to total soil respiration. If we further assume a constant soil temperature and, thus, contribution of this source during July to September, $240\,\mathrm{g\,C\,m^{-2}}$ would be respired during the period between 10 and 40 years since fire ($2.73\,\mathrm{mg\,C\,m^{-2}\,h^{-1}} \times 24\,\mathrm{h} \times 122$ days $\times$ 30 years).

On a global scale, the proportion of autotrophic respiration is positively correlated with temperature and productivity (Bond-Lamberty *et al*., 2004a). Our results show that time since disturbance is potentially an important confounding factor in this relationship. Support for higher contributions of autotrophic respiration come from the fact that our estimates include plant respiration from living mosses as well as plant roots. Further, it has been observed that plant respiration makes up a larger fraction of photosynthesis in black spruce forests (Ryan *et al*., 1997, 2004). These authors showed that the C use efficiency of trees, the ratio of NPP to NPP plus autotrophic respiration, is species specific and lower for black spruce than for temperate conifers.

At a given site, soil respiration rates followed a seasonal trend exhibiting the lowest fluxes in May and the largest fluxes in July, corresponding to the temperature increase in the organic layers. This was in accord with earlier measurements showing that soil respiration is positively correlated with shallow mineral soil depth temperature (Wang *et al*., 2003). The autotrophic CO_2 flux followed a similar trend showing increases in autotrophic respiration corresponding to increased in plant productivity (Goulden *et al*., 1998).

Productivity, which must be reflected in autotrophic respiration, can differ dramatically from day to day with changes in air and surface soil temperature and moisture throughout the growing season (Ekblad & Högberg, 2001; Bowling *et al*., 2002). Since autotrophic sources seem to dominate soil respiration within the first 40 years following fire, we can expect daily changes of similar magnitude in soil respiration. Our data indicate the importance of O horizon decomposition to the soil respiration flux in older stands; changes in the moisture of this layer can also occur rapidly and affect soil respiration. Consequently, more frequent measurements at each site are needed to make annual budgets, understand seasonal changes in soil respiration, and determine the magnitude of interannual differences across the chronosequence.

Conclusions

Soil respiration in a central Canadian black spruce forest did not show a large pulse of heterotrophic respiration from the decomposition of fire residues. We did find evidence of decomposition of old C substrates in the mineral soils of recently burned, warmed soils 10–40 years postfire, but these sources contributed a maximum of 3% to growing season surface soil respiration fluxes or $\sim 240\,\mathrm{g\,C\,m^{-2}}$ of C loss from mineral soil organic matter over three decades.

In contrast, soil respiration fluxes were dominated by autotrophic respiration (rhizosphere and mosses) for 40 years after fire and underwent large seasonal and smaller interannual variations following changes in shallow soil temperature and plant productivity. The contribution of heterotrophic respiration from the O horizons increased when black spruce and feather mosses gained canopy and ground dominance (70 years since fire). Seasonal and interannual variations in respiration were smaller in older stands, because changes in soil moisture and temperature are buffered by the thick insulating moss layer.

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