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Spatiotemporal analysis of black spruce forest soils and implications for the fate of C

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[1] Post-fire storage of carbon (C) in organic-soil horizons was measured in one Canadian and three Alaskan chronosequences in black spruce forests, together spanning stand ages of nearly 200 yrs. We used a simple mass balance model to derive estimates of inputs, losses, and accumulation rates of C on timescales of years to centuries. The model performed well for the surface and total organic soil layers and presented questions for resolving the dynamics of deeper organic soils. C accumulation in all study areas is on the order of 20–40 gC/m^2/yr for stand ages up to ~200 yrs. Much larger fluxes, both positive and negative, are detected using incremental changes in soil C stocks and by other studies using eddy covariance methods for CO_2. This difference suggests that over the course of stand replacement, about 80% of all net primary production (NPP) is returned to the atmosphere within a fire cycle, while about 20% of NPP enters the organic soil layers and becomes available for stabilization or loss via decomposition, leaching, or combustion. Shifts toward more frequent and more severe burning and degradation of deep organic horizons would likely result in an acceleration of the carbon cycle, with greater CO_2 emissions from these systems overall.

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1. Introduction

[2] High northern latitude soils contain 50% of the world's soil organic carbon (C) [*McGuire et al.*, 2009; *Tarnocai et al.*, 2009], much of it stored in the organic layers of subarctic boreal forests and peatlands. In boreal forests, large changes in soil C stocks occur when fire consumes these organic horizons [*Kasischke and Johnstone*, 2005]. Burning is typically followed by a gradual accumulation of the shallow organic layer. Given the role of boreal forests in the global climate system [*Chapin et al.*, 2000], it is essential to quantify C fluxes over timescales of stand replacement [*Bhatti et al.*, 2003; *Kashian et al.*, 2006]. Although recent research has studied the amounts of C released from boreal fires [e.g., *Flannigan et al.*, 2009; *Turetsky et al.*, 2011], fewer empirical studies have focused on the accumulation of soil C following fire [e.g., *Camill et al.*, 2009; *Trumbore and Harden*, 1997]. Therefore, modeling efforts typically rely on sparse data from only one region or site when modeling C cycling of boreal forests in response to fire.

[3] Soil carbon is recognized and modeled as a mixture of dynamic and static pools that are typically represented by a mixture of these pools within a set depth [*Parton et al.*, 1994] or by using temporal vegetation shifts that impact the soil pools [*Trumbore et al.*, 1995]. Northern soils, however, present a rather different physical and biogeochemical structure because of the upward accumulation of organic horizons, a structure that challenges the concept of separate C pools of a fixed depth or with fixed mixtures of substrate inputs. Moreover, the upward accumulation of organic horizons exerts major feedbacks on soil thermal properties and the ground temperature regime [*O'Donnell et al.*, 2009]. Therefore, in boreal forest soils, carbon turnover and decomposition change with respect to both pool dynamics and to vertical structure as it changes over the course of stand replacement.

[4] Models for soils and ecosystems have been greatly improved by chronosequence studies in which space-for-time substitutions apply to both landform [*Viereck*, 1970] and fire [*Bond-Lamberty et al.*, 2004]. Our understanding of spatiotemporal variations of soil and vegetation C of boreal forests has expanded as well because of the combination of spatial and temporal variations nested in the chronosequence design. Detecting changes in soil C stocks over time, however, is a challenge because of spatial variation in both the local and landscape-scale features that govern soil C storage and because of historical variations in other variables not shared by all sites. For example, spatial variation of C stocks

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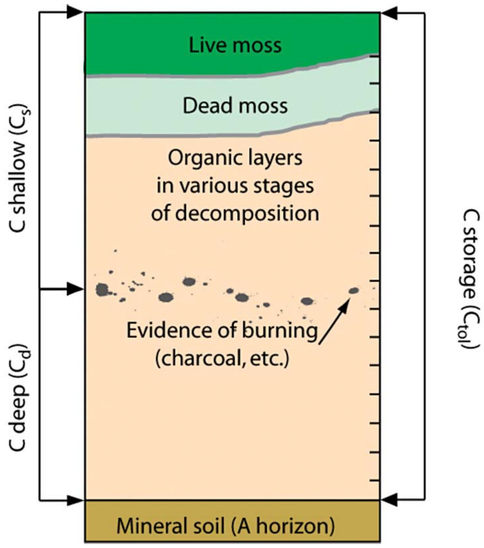

Figure 1. Diagram of shallow C (C_s), showing C that has accumulated since the last fire; deep C (C_d), which includes C remaining from previous burn cycles; and the carbon in the total organic layer (C_{tol}) in a post-fire black spruce landscape.

in black spruce forests are related to soil drainage class (including the presence of permafrost), topography, burn intensity, vegetation class, and the timing of previous burns [*Johnson et al.*, 2011; *Mack et al.*, 2008; *Turetsky et al.*, 2005; *Yi et al.*, 2009]. While some studies have recognized the near-constant rate of C accumulation in post-fire soil organic layers [*Kane and Vogel*, 2009; *O'Neill et al.*, 2006; *Turetsky et al.*, 2011], few studies have addressed whether accumulation is generalizable or whether spatial variations are too great to detect such a signal in soil C stocks. Moreover, if our goal is to better understand how C accumulation is linked to the dynamics of succession and regrowth, then capturing attributes of depth, input, and loss in our analysis is also important.

[5] In order to improve estimates for carbon uptake and loss in response to disturbance across the North American boreal forest biome, four soil chronosequences of fire disturbance were established in Alaskan and Canadian boreal forests to constrain C accumulation in shallow and deep organic-soil horizons. Soil C stocks (in gC/m^2) were calculated for soil horizons above the charred layer, reflecting organic C accumulation since the time of burn, herein called shallow C or C_s (Figure 1). Soil C that remained post-fire is referred to as deep C or C_d (Figure 1), with the total sum of shallow and deep organic-layer C referred to as total C or C_{tol}. These data were input into a simple mass balance model and used to constrain long-term inputs and losses to C_s, C_d, and C_{tol}. Our objectives were to robustly quantify post-fire C accumulation in the context of C_s and C_d; to compare our stock-based rates of C exchange to rates based on other methods of estimating C accumulation and loss in these ecosystems; and to improve upon our understanding of soil C and its fate at a variety of temporal and spatial scales.

2. Methods

2.1. Study Area and Site Descriptions

[6] Fire chronosequences, in which black spruce (*Picea mariana* (Mill.) BSP) ecosystems had stand-replacing fires at various times in the past, were identified and sampled in four study areas in Alaska, USA, and Manitoba, Canada (Figure 2). The Thompson, Manitoba, study area is located within the northern study area (NSA) of the Boreal Ecosystem Atmosphere Study (BOREAS) [*Sellers et al.*, 1997] and represents sites of a subsequent study (FIRES-ExB) of black spruce/feathermoss stands in various stages of recovery from stand-replacing fires. The Hess Creek study area is located in interior Alaska approximately 150 km north of Fairbanks and is underlain by ice-rich eolian silt of the Pleistocene [*O'Donnell et al.*, 2011]. The Delta Junction study area is located on flat to nearly flat glaciofluvial and eolian deposits approximately 150 km southeast of Fairbanks [*Péwé and Holmes*, 1964]. The Taylor Highway study area is located in interior Alaska, north of the city of Tok, where parent material consists of metamorphic rocks on steeper topography.

[7] Data were collected from 316 profiles covering 24 stand ages over nearly 200 yrs (see Table S3 in Text S1 of the auxiliary material).[1] For each study area at least five ages since time of last burn, which varied from <1 yr to >100 yrs,

[1]Auxiliary materials are available in the HTML. doi:10.1029/2011JG001826.

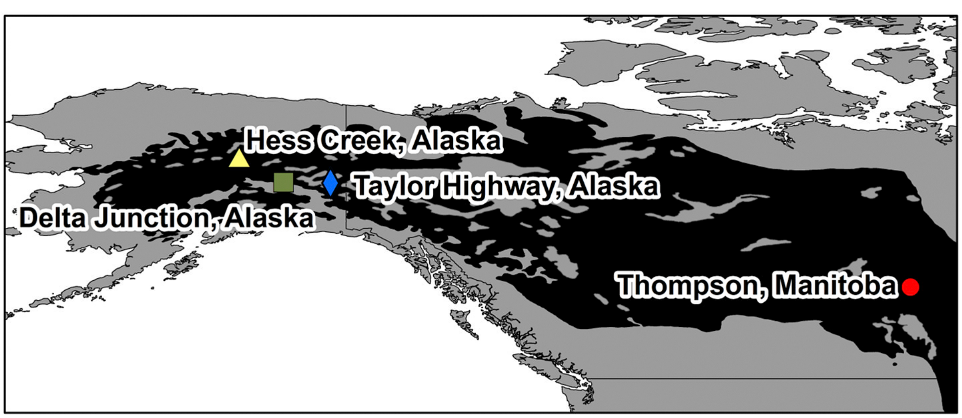

Figure 2. Map of study sites. The area shaded in black is the boreal forest biome.

Table 1. Site Characteristics of Four Black Spruce Chronosequences in Alaska and Manitoba[a]

Site Characteristics	Delta Junction, AK	Hess Creek, AK	Taylor Highway, AK	Thompson, MB
Stand ages (yrs)	2, 7, 19, 27, 45†, 50†, 116	4, 14, 17, 40, 98, 148, 198	4, 18, 20, 22, 42, 132	0, 5, 8, 14, 22, 39, 73, 153
Number of soil profiles	77	89	50	100
Latitude (°N)	63.9	65.6	63.4	55.9
Elevation (m)	429	289	867	259
Slope (%)	0–2	3–9	6–9	0–3
Mean summer temperature (°C) ‡	13.5	13.8	12.3	14.2
Mean winter temperature (°C) ‡	−20.2	−24.8	−19.7	−22.4
Growing season length (days) ‡	174	163	170	N.D.
Annual precipitation (mm) ‡	383	310	351	517
Parent material	silt over glaciofluvial outwash	silty loess	silty loess over bedrock	lacustrine clay and silt
Soil drainage class	somewhat poorly	somewhat poorly	well to moderately well	moderately well
Active layer depth (cm), mature stands	∼70	∼50	∼40	>100
Thickness of silt cap (m)	∼1	>10	<0.3	>3

[a]A single dagger (†) indicates that the same stand was sampled two different times. A double dagger (‡) indicates that the mean climate data for Alaska were taken from the Parameter-Elevation Regression of Independent Slopes Model (PRISM), a product of the Spatial Climate Analysis Service at Oregon State University (1961–1990) [*Daly et al.*, 2001]. For Thompson, Manitoba, the Canadian Climate Normals (1971–2000) for the Thompson station (http://climate.weatheroffice.gc.ca/) were used.

were sampled. Study areas varied in climate, topography, soil drainage class, and parent material (Table 1). In study areas with slopes >5% (Hess Creek and Taylor Highway), sampling sites were located on north-facing slopes with the exception of one Hess Creek profile, which was located on a south-facing slope. In all study areas, mosses and forbs colonized stands <5 yrs post-fire; black spruce and mosses dominated the vegetation of mature stands [*Bond-Lamberty et al.*, 2002; *Mack et al.*, 2008]. The vegetation of mid-successional stands (10–100 yrs in age) varied in the amount of deciduous tree and moss type. NPP was characterized at Delta Junction, AK [*Mack et al.*, 2008], and Thompson, Manitoba [*Bond-Lamberty et al.*, 2004], and ranged from about 150 to 300 gC/m^2/yr in mature stands in both study areas. Eddy covariance was measured over a 3 yr period at the Thompson study area [*Goulden et al.*, 2006] and over a 1–2 yr period for two sites in the Delta Junction study area [*Welp et al.*, 2007].

2.2. Carbon in Shallow, Deep, and Total Organic Layers

[8] At each site we described and measured the thickness of organic-soil layers within a soil profile along linear transects (using the nomenclature of *Manies et al.* [2004]), with plots spaced every 5–20 m depending on the extent of the stand and the heterogeneity of vegetation. Additionally, over one third of these profiles were sampled for bulk density and chemical characterization. For profiles described but not sampled, we developed linear regression models for predicting soil C storage (gC/m^2) on the basis of organic layer thickness (cm) for each horizon type using data from the Thompson, Hess, and Delta Junction study areas (see Text S1 in the auxiliary material). Observed versus predicted regressions of soil organic C from withheld observations (25% of data) resulted in R^2 values from 0.73 to 0.93 (Table S1 in Text S1), demonstrating that our predictive equations function well for estimating C storage from field descriptions. For all profiles, we calculated cumulative C storage in total organic layers (C_{tol}), and where possible we calculated C storage in the shallow layers above the uppermost charcoal layer (C_s) and the deep organic layers below the uppermost charcoal layer (C_d). We infer that C_s is a measure of carbon accumulated since the last burn and that C_d is, initially, a measure of unburned detritus accumulated over previous burns (Figure 1).

[9] Where between-area comparisons were made, we generalized time since fire into five categories, 0–14, 15–49, 50–99, 100–149, and 150–200 yrs. Analysis of variance (ANOVA) tests were run in Statistica (version 7.1, StatSoft Inc., Tulsa, Okla.) using the Fisher Least Significant Difference test to evaluate significant differences among means. Generalized models for annual rates of carbon recovery over the time span of the chronosequence were estimated from the following simple first-order equation for the soil:

$$dC/dt = I - kC, \tag{1}$$

where dC/dt is net carbon exchange (gC/m^2/yr), I is the C input to the system (gC/m^2/yr), t is time (yr), k is a decomposition coefficient (yr^{-1}), C is the soil C stock in gC/m^2 [*Harden et al.*, 1997]. We solved equation (1) for each site individually and all sites combined for C_s, C_d, and C_{tol} using plots of C against stand age (time-since-fire). The best fits were for C_s and C_{tol} (see auxiliary material for C_d information). For C_s, equation (1) was solved by plotting C_s (gC/m^2) against stand age (time since fire in yrs) while assuming the intercept is zero:

$$C_s(t) = I_s/k_s\left(1 - e^{-k_s t}\right). \tag{2}$$

This approach is a single-pool model of soil carbon for C_s, the recovered organic layer after fire, and it does not include organic C in the below-char organic or mineral layers, nor does it partition C into fast and slow pools. For total C (C_{tol}), equation (1) was solved by plotting C_{tol} (gC/m^2) against stand age (yr), but we did not assume the intercept to be zero ($C_o > 0$)

$$C_{tol} = I_{tol}/k_{tol}\left(1 - e^{-k_{tol} t}\right) + C_0 e^{-k_{tol} t}. \tag{3}$$

Therefore, C_0 represents the unburned organic soil at the time of the fire (C_d at time 0). Inputs (I_{tol}) were constrained to be $\geq I_s$. This approach is also a single-pool model of soil C but does not include organic C in mineral soil horizons.

[10] Model fits for equations (2) and (3) were generated by TableCurve 2D (version 5.01, Systat, Inc., San Jose, Calif.),

Table 2. C Stocks for Shallow C (C_s), Deep C (C_d), and Total Organic Layer C (C_{tol}) for Stand-Age Classes Among the 4 Study Sites[a]

	Age class	All sites	Delta Junction, AK	Hess Creek, AK	Taylor Highway, AK	Thompson, MB
C_s (g/m^2)	0–14 yrs	104 A	56 b	90 a,b	0 a,b	180 a
	15–49 yrs	807 A	320 c	1083 a,b	508 b,c	1423 a
	50–99 yrs	2305 B	1550 b	2005 b	—	3603 a
	100–149 yrs	2314 B	2620 a	3397 a	2007 a	—
	150–200 yrs	4190 C	—	2571 a	—	4676 a
C_d (g/m^2)	0–14 yrs	3155 A	3162 b	4780 a	468 c	1480 c
	15–49 yrs	2698 A	3563 a	2469 a,b	3105 b	1536 b
	50–99 yrs	1185 B	317 b	3676 a	—	407 b
	100–149 yrs	3251 A	3168 a	2757 a	3366 a	—
	150–200 yrs	3105 A	—	8618 a	—	1451 b
C_{tol} (g/m^2)	0–14 yrs	3410 A	3322 b	4922 a	468 a	2137 a
	15–49 yrs	3329 A	3308 a	3662 a	3857 a	2698 a
	50–99 yrs	4446 A	2606 c	7636 a	—	3516 b
	100–149 yrs	5755 B	5891 a	5404 a	5884 a	—
	150–200 yrs	8416 C	—	11590 a	—	6753 b

[a]Uppercase letters within columns indicate statistical similarities among stand ages and lowercase letters indicate statistical similarities among study sites, with errors and sample number information shown in the auxiliary material (Table S2 in Text S1).

in which an equation solver is used to indicate I, k, and C_0 using a best-fit procedure. The resulting TableCurve equations were used to calculate the C stocks of C_s and C_{tol} on an annual timestep. There were 316 profiles available for C_{tol} and 229 profiles for C_s calculations.

[11] Radiocarbon was measured on untreated, homogenized soil for select soil profiles by vacuum sealing a homogenized sample containing about 1 mg C with cupric oxide and elemental silver in a quartz tube and combusting at 850°C. The CO_2 produced was purified cryogenically and reduced to graphite using a modified reduction method with titanium hydride, zinc, and cobalt catalyst [*Vogel*, 1992] for samples from Thompson and Delta. For Hess samples, this method was modified in order to improve precision [*Xu et al.*, 2007]. The graphite target was measured directly for ^{14}C at W. M. Keck C Cycle Accelerator Mass Spectrometer (AMS) Laboratory at the University of California Irvine. The ^{14}C data are expressed in Delta notation (δ^{14}C), which is the deviation in the ^{14}C/^{12}C in parts per thousand (‰) from a standard (^{14}C/^{12}C standard = 1.176×10^{12}), with a correction for possible fractionation based on ^{13}C [see *Stuiver and Polach*, 1977]. A δ^{14}C of approximately 0‰ represents the ^{14}C/^{12}C of atmospheric CO_2 in the year 1890. After ~1954, C fixed by plants and input to soil was subjected to enrichment of the atmosphere by aboveground weapons testing.

2.3. Changes in C Stocks Over Incremental Timesteps

[12] We also calculated the change in C stocks (gC/m^2) over incremental timesteps between stand ages for each stand (Table S3 in Text S1), including across-study area comparisons. These values were then averaged using the same five age classes utilized for the statistical tests (see section 2.2).

3. Results

3.1. Variations in C Stocks Across Regions and Stand-Age Classes

[13] Stocks of C_s were significantly different among age classes (df = 1, F = 14.16, p-value = 0.0002) and had an age class by study area interaction (df = 8, F = 2.87, p-value = 0.0047). This interaction was in part a result of greater C_s in Thompson (as compared to Delta Junction and Taylor Highway, 0–14 yrs; Delta Junction and Hess Creek, 50–99 yrs; and Hess Creek, 150–200 yr) (Table 2). Both within study areas and overall, C_s increased as a function of stand age (Figure 3a) as dictated by equation (2). Model fit was good (adj. R^2 values ranged from 0.52 to 0.70, all p-value < 0.01) (Table 3).

[14] Stocks of C_{tol} also had a significant age class by study area interaction (df = 8, F = 5.30, p-value < 0.0001), largely owing to the higher stocks at Hess Creek (as compared to all study areas, 0–14 yrs; Thompson and Delta Junction, 50–99 yrs; and Thompson, 150–200 yrs) (Table 2). Both within study areas and overall, C_{tol} increased as a function of stand age (Figure 3b), as dictated by equation (3). Model fit was significant (adj. R^2 values ranged from 0.07 to 0.29, all p-value < 0.02) (Table 3).

[15] Stocks of C_d had a significant age classes by study area interaction (df = 8, F = 4.7, p-value = 0.0003), due to the higher stocks at Hess Creek (as compared to all study areas, 0–14 yrs; Delta Junction and Thompson, 50–99 yrs, and Thompson, 150–200 yrs) (Table 2). In the 15–49 yr-old age class Taylor Highway and Delta Junction had higher C_d stocks than either Hess Creek or Thompson (Table 2). Equations (1)–(3) were unable to describe C_d dynamics over time, both within individual study areas and for all study areas combined (adj. R^2 values ranged from 0.00 to 0.06, all p-value > 0.04).

3.2. Dynamics of Soil C Based on Stand-Age Chronosequences

[16] Because model fits of C_s (equation (2)) and C_{tol} (equation (3)) were significant for each of the four study areas and for all study areas combined (see section 3.1), we examined the model parameters further. Annual coefficients for I_s, k_s, I_{tol}, and k_{tol} were not significantly different among study areas based on the overlapping 95% confidence intervals (Table 3). Therefore, the combined-study-area model was used to evaluate temporal variations in C_{tol} and C_s over the chronosequence.

[17] The combined-study-area model of C_s demonstrated an increase over the course of stand replacement from 0 to

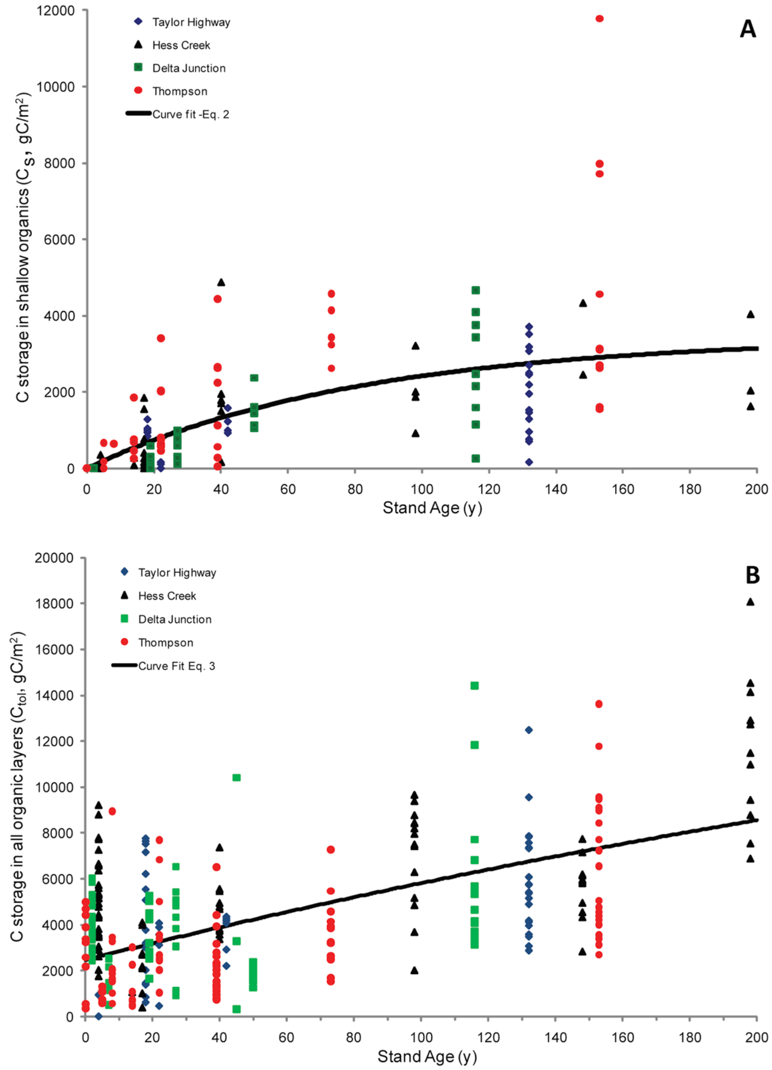

Figure 3. Carbon stocks for organic soil layers in the four chronosequences, showing stand age trends in (a) shallow (C_s), and (b) all organic soil layers (C_{tol}). C_s was calculated as C stock in organic soil layers above recognizable char from the most recent burn. Line fit from equation (2) (C_s) or equation (3) (C_{tol}) using TableCurve software for all sites combined. Data for C_d are not shown because the model fit was not significant.

Table 3. Input and Decay Constants for Shallow and Total Organic Soil C Accumulations[a]

Site	I_s (gC/m^2/yr)	k_s (yr^{-1})	I_{tol} (gC/m^2/yr)	k_{tol} (yr^{-1})	C_0 (gC/m^2)	Average net C Accumulation (gC/m^2/yr)
Delta Junction, AK	24 (13–34)	0.0005 (−0.0079–0.0090)	24 (−148–196)	0.0009 (−0.0407–0.0424)	2887 (1895–3879)	20
Hess Creek, AK	51 (29–72)	0.0173 (0.0062–0.0285)	51 (−11–112)	0.0021 (−0.007–0.0111)	3145 (2252–4038)	29
Taylor Highway, AK	26 (5–46)	0.0086 (−0.0068–0.0243)	147 (−147–441)	0.0246 (−0.0298–0.0790)	2038 (−1448–5525)	20
Thompson, MB	59 (30–88)	0.0095 (−0.0002–0.0193)	59 (5–112)	0.0038 (−0.0065–0.0142)	1449 (553–2346)	30
All sites	42 (24–59)	0.0121 (0.0064–0.0178)	42 (24–147)	0.0020 (0.0009–0.025)	2475 (1449–3145)	29 (20–40)

[a]Shallow stocks C_s were fit to stand ages (equation (2)) to derive I_s and k_s. Total organic stocks C_{tol} were fit to stand ages (equation (3)) to derive I_{tol}, k_{tol}, and C_0 for separate and combined chronosequences. Average net C accumulation rates were calculated from model fits of annual stock change. In the parentheses are 95% confidence intervals (model parameters) or minimum/maximum values (net C accumulation values). Goodness of fit (adj. R^2) values were as follows: C_s (equation (2)): Delta Junction = 0.70 (p-value < 0.001); Hess Creek = 0.62 (p-value < 0.001); Taylor Highway = 0.52 (p-value < 0.01); Thompson = 0.55 (p-value < 0.001); and all sites = 0.55 (p-value < 0.001). C_{tol} (equation (3)): Delta Junction = 0.07 (p-value = 0.02); Hess Creek = 0.31 (p-value < 0.001); Taylor Highway = 0.16 (p-value < 0.01); Thompson = 0.29, and all sites = 0.28 (p-value < 0.001).

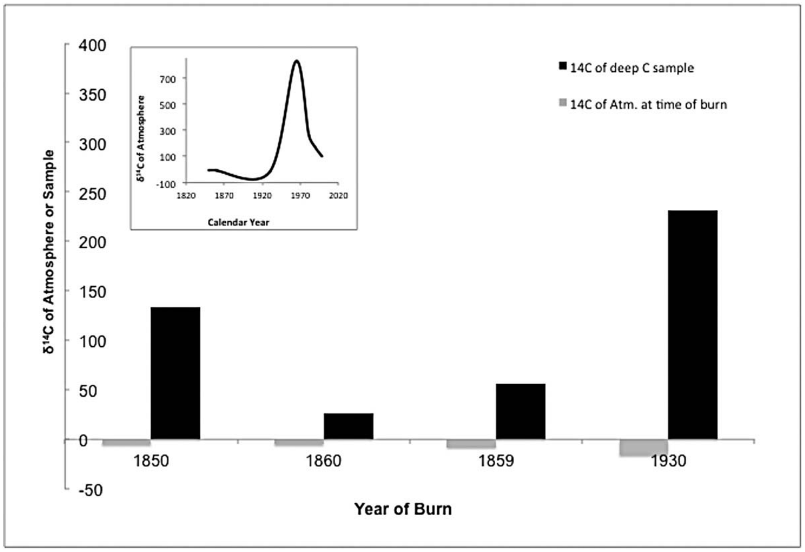

Figure 4. Radiocarbon of deep organic horizons (C_d) and of the atmosphere (inset). A value above zero indicates C enriched by weapons testing. Enrichment of soil radiocarbon occurred via plant input since 1954. Data are from sites within study areas: Thompson (*Manies et al.* [2006], 1930 and 1850 sites); Delta Junction (*Manies et al.* [2004], 1860 site), Hess Creek (*O'Donnell et al.* [2011], 1859 site).

about 4000 gC/m^2 (Figure 3a). I_s averaged 42 gC/m^2/yr (ranging from 24 to 59), and k_s averaged 0.0121 yr^{-1} or a turnover time of 83 yrs (ranging from 56 to 160 yrs) (Table 3). (For comparison, see *Trumbore and Harden* [1997], which had inputs to the surface soil of 60 gC/m^2/yr $\pm$ 30 gC/m^2/yr and 0.011 yr^{-1} $\pm$ 0.007 yr^{-1} for k_s). Rates of C_s accumulation varied ~fivefold between newly burned stands (0–14 yrs; 39 $\pm$ 2 gC/m^2/yr) and very mature stands (150–200 yrs; 5 $\pm$ 1 gC/m^2/yr). Intermediate-aged stands (50–99 yrs) accumulate C_s about three times faster than very mature (150–200 yrs) stands (Table 3).

[18] The combined-study-area model for C_{tol} (equation (3)) also increased with stand age from ~2500 to 8500 gC/m^2 (Figure 3b). I_{tol} was on average 42 gC/m^2/yr (ranging from 24 to 150), and k_{tol} was 0.002 yr^{-1} or turnover time of 500 yrs (ranging from 40 to 1100 yrs). The intercept was 2500 gC/m^2 (ranging 2200 to 2700 gC/m^2). Rates of C_{tol} accumulation did not vary much by age class, ranging from 36 gC/m^2/yr ($\pm$0.3 gC/m^2/yr) for the newly burned (0–14 yrs) stands to 26 gC/m^2/yr ($\pm$1 gC/m^2/yr) for the very mature stands (150–200 yrs).

3.3. Soil Radiocarbon

[19] C_d samples from sites that burned before 1954 were enriched by bomb-spike ^{14}C during the time between burning and the time of sampling (Figure 4). Enrichment was highest for oldest (age of 150, from ~1850) and youngest (age 74, from ~1930) stands from depths of 21 cm and 17 cm, respectively.

4. Discussion

4.1. Is the Heterogeneity of Soil C Stocks Related to Stand Age?

[20] Temporal shifts in spatial variability may help to elucidate the influence of burning, succession, and decomposition on heterogeneity. Despite variations in site conditions such as permafrost, slope, and drainage (Table 2), variations in C_{tol} across stand age and study area typically are within 40%–60% of the mean (based on values from Table S2 in Text S1). The contributions from C_s and C_d to such variations shift depending on stand age. Coefficients of variation (CV, or standard deviation/mean) were the highest (>1.2) for C_s in stands <49 yrs old and the highest for C_d (>1.2) in stands between 49 and 99 and >149 yrs old. Forest floor burning has been shown to be a heterogeneous process [*Harden et al.*, 2003; *Shetler et al.*, 2008] that is reflected as legacy carbon (C_d at time 0). In stands <14 yrs, the CV of C_d is about 0.7, while the CV of C_s is 2.2. Thus, while spatial variations in burning are great, the variation in early plant colonization (both in coverage and species) introduces significantly more heterogeneity to those young stands. As stands mature, C_s becomes less variable (CV = 0.5 for 50–99 yrs), likely reflecting a more pervasive organic horizon thickness that promotes consistent and cooler temperatures [*Carrasco et al.*, 2006; *O'Neill et al.*, 2006]. Meanwhile, C_d variations increase over the course of succession, perhaps reflecting spatial variations across the study areas in fire legacies as well as variations in root input and decomposition. The stand-age shifts in C stock heterogeneity demonstrated here likely have major impacts on the variability of gaseous and dissolved C fluxes and their sources, whether derived from root, moss, or heterotrophic respiration, variability that was noted by *Czimczik et al.* [2006]. Despite the spatial heterogeneity of soil C stocks observed across stand ages, the signal of C accumulation over time-since-disturbance is clear, as evidenced by goodness of fit for the C_s and C_{tol} models (Table 3).

4.2. Do C Accumulation Rates Change as Stands Age?

[21] Despite the spatial variations in C stocks, total C accumulation rates were roughly constant over time and

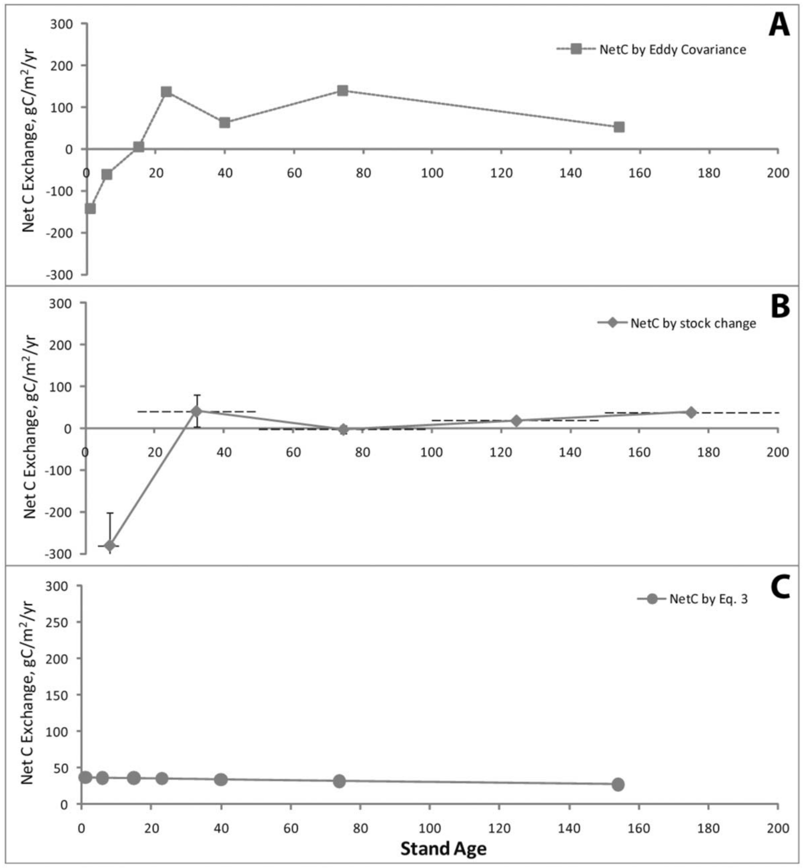

Figure 5. Net C balance based on (a) eddy covariance (Thompson only); (b) incremental soil stock change (all site combinations of all study areas from Table S3 in Text S1 of the auxiliary material), where the *x* axis error bars represent the range of the age class and *y* axis error bars are standard errors; and (c) from equation (3) (Thompson only).

within 20 to 40 gC/m^2/yr for all study areas. Across these study areas, the C_{tol} intercept indicates that 2500 +/− 250 gC/m^2 remains as unburned organic matter. Our models for total organic layer carbon (C_{tol}) reflect significant relationships between stand age and C_{tol} stocks within each study area and across combined study areas overall. Near-linear accumulation for C_{tol} of ∼20 to 40 gC/m^2/yr is supported by other studies of North American boreal forests [*Kane and Vogel*, 2009; *O'Neill et al.*, 2006; *Turetsky et al.*, 2011]. By contrast, the shallow soil's (C_s) portion of C_{tol} reflects rates of accumulation that decline fivefold over the course of stand replacement, a nonlinear trend that is consistent with a simple model of constant inputs and fractional decomposition (equation (2)). In contrast to the constant inputs assumed in the soil model, NPP of aboveground vegetation for the study areas in Delta Junction [*Mack et al.*, 2008] and Thompson [*Bond-Lamberty et al.*, 2004] were not constant over stand replacement. Clearly, more information is needed to elucidate interactions among above- and below-ground processes.

[22] The combination of a near-linear trend of C_{tol} (Figure 3b) and the declining rate of accumulation of C_s (Figure 3a) infers that C_d stocks likely increase over time in a way that compensates the difference in trends between C_{tol} and C_s. A decline in C_d in young stands is more consistent with initially warmer soils post-fire [*Kane and Vogel*, 2009; *O'Donnell et al.*, 2010; *O'Neill et al.*, 2006] and with measures of C flux by eddy covariance at the Thompson study area [*Goulden et al.*, 2011]. In these early stand ages soil C is destabilized via decomposition and leaching. An increase in deep C, however, favors inputs from roots, litter, and DOC to C_d layers as well as a slowing of decomposition as C_d becomes cooler, wetter, and further from the surface. Radiocarbon measurements of C_d (Figure 4) clearly demonstrate that some new inputs occur in these mid to late successional stages. For example, stands that burned between 1850 and 1930 were 25–100 yrs old when the atmosphere was first enriched by weapons testing in 1954. Yet these stands have C_d samples that are highly enriched with ^{14}C relative to the atmosphere at the time of burning (Figure 4). C_d dynamics deserve further investigation to address the complex feedbacks among rates of burial, temperature shifts in decomposer communities, root colonization, priming, and the allocation of nutrients and carbon. Meanwhile, our model results of C_s and C_{tol} can help to constrain the net changes of C_d for moderately well to somewhat poorly drained black spruce ecosystems.

4.3. How Do Rates of Net C Accumulation Relate to Long-Term C Fate?

[23] Models of net C accumulation derived from equations (1)–(3) show pervasive, clear signals across the study areas,

but these rates are small compared to other measures of net C accumulation (NetC). Eddy covariance CO_2 measurements of NetC (Net Ecosystem Production or NEP) at the Thompson site, for example, which comprise all sources and sinks of C, including aboveground carbon, have much larger NetC rates (−150 to +140 gC/m^2/yr) (Figure 5a) [*Goulden et al.*, 2011] than were found using soil models of equations (1)–(3) (20–40 gC/m^2/yr) (Figure 5c). Another method for estimating NetC used by *Goulden et al.* [2011] was based on incremental changes in soil C stocks, which we calculated for our sites for the full array of stand ages across all study areas (Table S3 in Text S1 and Figure 5b). For both eddy covariance and incremental stock changes, NetC rates decline as ecosystems progress from young to older stands (Figures 5a and 5b). All three methods converge at similar values in the oldest stands (+27 to +52 gC/m^2/yr). The discrepancy in the rates of NetC for early stand ages is likely due to the fact that eddy covariance and stock-change NetC rates are greatly impacted by spatial variation (i.e., differences in burn severity), differences in C sources and sinks (i.e., in the case of eddy covariance, C accumulation in aboveground components that have not yet entered soil), and interannual variations in climate that influence C processing. By contrast, NetC rates in older stands and/or on longer time scales represent longer-term averages over timescales during which variations can cancel each other out. This concept of short-term, high-amplitude variations and longer-term, lower-amplitude variations in NetC exchange rates is consistent with the comprehensive studies reported by *Roulet et al.* [2007] for the Mer Bleue boreal peatland in which the authors found that interannual variations in NetC rates by eddy covariance were quite large (−14 to +89 gC/m^2/yr over 6 yrs), with the majority of this variation ascribed to interannual variations in seasonal climate. Variations of longer term and deeper pools of NetC were found by Roulet and others to be smaller (∼14 to 22 gC/m^2/yr), with these variations in rates ascribed to large scale differences in physiographic and drainage conditions.

[24] Similarly, inputs and losses of C also vary depending on the temporal scale examined. Annual NPP is on the order of 200 to 300 gC/m^2/yr for the Thompson and Delta study areas [*Goulden et al.*, 2011; *Mack et al.*, 2008], whereas our model based long-term inputs to the soil system are <60 gC/m^2/yr (Table 3, I_{tol}), much less than average annual NPP. Therefore, only ∼15%–25% of NPP enters the long-term soil pools, the remaining either is stored aboveground or is cycled back to the atmosphere as respiration. In Thompson, about 20%–40% of NPP was ascribed to the forest floor, consistent with our soil input term (I_{tol}), and another 20%–40% is ascribed to storage in wood and vegetation [*Goulden et al.*, 2011, auxiliary material]. Similarly, annual-scale scale measurements of soil C loss (heterotrophic respiration, or R_h) at Thompson were estimated at ∼160 gC/m^2/yr [*Goulden et al.*, 2011], while this paper's century-scale estimates of *k*C were ∼38 gC/m^2/yr (Figure S1 in Text S1), about one fourth of the annual flux. The discrepancies between NPP and *I* (equation (1)) and R_h and *k*C (equation (1)) suggest that black spruce forests receive large amounts of C (>80%) that cycle over decadal timescales and are transient relative to the persistence of soil C stocks (Figure S1 in Text S1). Over millennial timescales, C accounting would also need to include combustion losses, which are on the order of 1 [*Balshi et al.*, 2007] to 25 gC/m^2/yr [*Turetsky et al.*, 2011], resulting in 0%–20% of ecosystem NPP being sequestered over millennial timescales.

5. Implications

[25] A number of recent studies indicate that the North American boreal forest biome is undergoing an increase in fire activity [*Flannigan et al.*, 2009; *Gillett et al.*, 2004] with a shift toward shorter fire return intervals [*Bergeron et al.*, 2004] that occur seasonally later and with more severe burning [*Turetsky et al.*, 2011]. Fire regime shifts have consequences for not only combustion but also for production [*Mack et al.*, 2004] and decomposition [*O'Donnell et al.*, 2011] with a net effect of accelerating C cycling [*Kimball et al.*, 2007] as plant and soil processes respond to the new regime. Our annual to decadal modeling perspectives and associated data provide important constraints on the complexities of net C accumulation in these landscapes. While 20–40 gC/m^2/yr likely accumulate over the course of succession (Table 3), combustion estimates reduce this rate even further. Shifts in fire—including severity, return interval, and successional cover—will likely play an important role in the net C balance. Given the significant contribution of both the shallow and deep organic layers to both biogeochemical and thermal controls of black spruce systems, there is great importance in understanding and constraining the mechanisms that sustain and control the C cycling of these horizons.

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