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Succession-driven changes in soil respiration following fire in black spruce stands of interior Alaska

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Abstract. Boreal forests are highly susceptible to wildfire, and post-fire changes in soil temperature and moisture have the potential to transform large areas of the landscape from a net sink to a net source of carbon (C). Understanding the ecological controls that regulate these disturbance effects is critical to developing models of ecosystem response to changes in fire frequency and severity. This paper combines laboratory and field measurements along a chronosequence of burned black spruce stands into regression analyses and models that assess relationships between moss succession, soil microclimate, decomposition, and C source-sink dynamics. Results indicate that post-fire changes in temperature and substrate quality increased decomposition in humic materials by a factor of 3.0 to 4.0 in the first 7 years after fire. Bryophyte species exhibited a distinct successional pattern in the first five decades after fire that corresponded to decreased soil temperature and increased C accumulation in organic soils. Potential rates of C exchange in mosses were greatest in early successional species and declined as the stand matured. Residual sources of CO_2 (those not attributed to moss respiration or humic decomposition) increased as a function of stand age, reflecting increased contributions from roots as the stand recovered from disturbance. Together, the field measurements, laboratory experiments, and models provide strong evidence that interactions between moss and plant succession, soil temperature, and soil moisture largely regulate C source-sink dynamics from black spruce systems in the first century following fire disturbance.

Abbreviations: ΔR – non-microclimate driven changes in respiration; B – burned material; BD – bulk density; C – carbon; C_O – control material.; FD – fibric decomposition; F(T) – flux associated with a given incubation temperature; F_T – field CO_2 flux; HD – humic decomposition; MR – moss respiration; RF – temperature functions for respiration; RR – residual sources of respiration; T – temperature; T_h – thickness of soil layer; WHC – water holding capacity

Introduction

Boreal forest ecosystems contain between one-quarter and one-third of global soil carbon (200–500 Gt C) (Gorham 1991; Dixon et al. 1994) and are subject to periodic disturbance by wildfire. In addition to the immediate release of stored soil C during combustion and the subsequent reduction in C inputs from primary production, fire can also alter soil physical and biogeochemical properties (e.g., soil temperature, moisture, substrate quality) that regulate soil C exchange over longer time scales. Recent studies in Alaskan black spruce systems have suggested that changes in the local energy balance may result in post-fire biogenic emissions of C that equal or exceed the amount of CO_2 released during combustion (Auclair and Carter 1993; Richter et al. 2000; O'Neill et al. 2003), potentially transforming large areas of the landscape from net C sinks to net sources. Gillett et al. (2004) showed that the doubling of annual area burned in the Canadian boreal forest region between the 1960s and 1990s was correlated to warming in this region, and modeling studies by Stocks et al. (1998, 2000) and Flannigan et al. (2005) using GCM-predicated climates indicate that this trend is likely to continue in the future. Understanding the ecological controls that regulate the magnitude and duration of these disturbance effects is critical to developing models of ecosystem response to climate-driven changes in fire frequency and severity.

In boreal soils, CO_2 flux from the ground surface represents the difference between photosynthetic uptake by surface mosses and the sum of heterotrophic, root, and moss respiration. Mature upland boreal black spruce forests (*Picea mariana* (Mill.) BSP) in Canada and Alaska have been shown to function as a net C sink; that is, the amount of C respired from the soil is less than the amount of C taken up each year in moss, shrub, and tree NPP (Harden et al. 1997, 2000; Yarie and Billings 2002; Bond-Lamberty et al. 2003; Bond-Lamberty et al. 2004). Immediately following fire, fixation of C by vegetation is minimal to non-existent, while rates of decomposition may be stimulated as a result of warmer soil temperatures and changes in soil drainage (Van Cleve and Yarie 1986; Richter et al. 2000; O'Neill et al. 2002). The ecological significance of these post-fire C emissions depends upon the ways in which the ecological and biophysical factors regulating production, consumption, and decomposition change as a soil recovers from fire disturbance.

A special feature of boreal black spruce forests is that bryophytes, and not vascular plants, represent the dominant source of C inputs in many systems. The annual productivity of forest mosses in Alaska may exceed that of black spruce foliage by as much as four-fold (Van Cleve et al. 1983). In central Canada, "feathermoss" and *Sphagnum*-dominated areas of the landscape were found to contain two to five times the amount of C stored in living and dead black spruce trees (Harden et al. 1997; Goulden et al. 1998). Moss species typical of mature forest stands have high heat and moisture holding capacities and thereby regulate soil moisture, temperature, and nutrient availability (Viereck 1975; Skre and Oechel 1981). Understanding the patterns of species distribution, the rates at which moss communities colonize sites after fire, and the effects of this colonization on soil temperature and CO_2 flux is essential to understanding the dynamics of post-fire C exchange.

O'Neill et al. (2003) evaluated CO_2 flux along an age-sequence of burned black spruce stands to assess the magnitude of post-fire C emissions in the first 140 years after disturbance. In this study, we combine portions of this earlier work with additional experimental data into regression-based models that: (1) partition field CO_2 fluxes into heterotrophic and autotrophic sources, (2) assess how the contributions from different components of soil CO_2 flux change as a function of time since disturbance, and (3) evaluate feedback mechanisms between moss species, soil microclimate, and C source-sink dynamics.

Materials and methods

Field measurements along the chronosequence

Studies were conducted along a chronosequence of burned black spruce stands located in the eastern Tanana River Valley of Alaska (Table 1). Details of the chronosequence, experimental design, and methods were reported in O'Neill et al. (2003). Sampling sites were limited to stands with soils of similar texture, drainage class, ground vegetation, and slope position. Soils in the paired mature stands were characterized by highly developed, moss-derived organic profiles overlying well-drained subsoils, with the maximum depth of thaw in mature stands remaining within the organic profile throughout the growing season. At the time of chronosequence establishment (1997), stand ages were 1, 3, 7, 10, 41, 80, and 140 years. Stand age was determined by historical record for recent burns and by tree ring counts for more mature stands following the methods described in Johnstone and Kasischke (2005). Ring counts were obtained from tree stem disks or increment cores sampled 15–20 cm above the soil surface and just above the swollen portion of the trunk base. Trees were assumed to have grown for a minimum of 5 years before reaching the height of the tree-ring sample.

Within each stand, CO_2 fluxes from the forest floor surface were measured weekly throughout a growing season (May–September) at 10 sampling points spaced 10-m apart along a 50- by 10-m grid using a dynamic closed gas exchange system (EGM-1, PP Systems). Living moss and vegetation were not removed prior to measurement to limit disturbance and the subsequent potential for enhanced decomposition and disturbance of root biomass. Concurrent with each CO_2 measurement, soil temperature was measured at 10 and 20-cm below the forest floor surface and soil moisture potential was measured using a granular matrix sensor (Watermark Irrometer, Riverside CA) placed immediately above the mineral soil boundary.

Table 1. Location and site characteristics for stands along a black spruce chronosequence measured from May to September, 1997.

Stand age	Soil description	Status	Depth of maximum seasonal thaw (cm)	Mean CO_2 flux (g CO_2 m^{-2} h^{-1})	Mean temp. at 10 cm (°C)	Mean temp. at 20 cm (°C)	Thickness of organic soil profile (cm)[a]	C storage in the upper organic profile (Mg C ha^{-1})[b]
1	Coarse-silty, mixed, non-acid pergelic cryaquept/cryaquent	Burned	70.56 ± 0.68	0.34 ± 0.17 (159)	6.8 ± 2.3 (140)	5.1 ± 1.9 (141)	19.8 ± 2.0	–
		Control	16.05 ± 0.62	0.58 ± 0.24 (160)	5.1 ± 3.1 (149)	2.5 ± 1.9 (136)	–	–
3	Coarse-silty, mixed, non-acid aeric cryaquept	Burned	> 100	0.38 ± 0.17 (126)	12.5 ± 2.0 (120)	11.0 ± 1.9 (109)	5.7 ± 3.5	10.94 ± 6.31
		Control	20.10 ± 1.14	0.72 ± 0.36 (132)	9.3 ± 2.8 (120)	2.7 ± 1.7 (110)	–	–
7	Coarse-silty, mixed, non-acid pergelic cryaquept/cryaquent	Burned	> 100	0.51 ± 0.27 (175)	10.0 ± 3.0 (154)	9.0 ± 2.5 (129)	10.6 ± 3.0	22.29 ± 13.30
		Control	22.91 ± 2.35	0.58 ± 0.26 (190)	5.6 ± 3.1 (165)	2.7 ± 1.8 (141)	22.3 ± 4.1	–
10	Coarsesilty over sandy-skeletal, mixed typic cryrochrept	Burned	> 100	0.47 ± 0.22 (90)	9.5 ± 2.6 (90)	7.4 ± 2.4 (80)	4.7 ± 2.1	23.35 ± 12.11
		Control	40.25 ± 1.57	0.82 ± 0.35 (85)	7.2 ± 3.2 (87)	3.6 ± 2.3 (80)	–	–
41	Not classified	Burned	–	–	–	–	11.1 ± 3.2	18.65 ± 12.16
		Control	–	–	–	–	13.1 ± 2.6	–
80	Coarse-silty, mixed, non-acid pergelic cryaquept/cryaquent	Control	22.91 ± 2.35	0.58 ± 0.26 (190)	5.6 ± 3.1 (165)	2.7 ± 1.8 (141)	22.3 ± 4.1	34.29 ± 7.73
140	Loamy, mixed, non-acid histic pergelic cryaquept	Control	23.3 ± 0.74	0.92 ± 0.37 (130)	11.0 ± 3.0 (100)	5.6 ± 2.1 (90)	33.5	56.93 ± 13.47

Data reported in O'Neill et al. (2000, 2003). Values represent mean ± 1 s.d.; the number of samples is provided in parentheses. Dashed lines indicate that a variable was not measured at this site.

[a] Organic profile thickness does not include moss; reported in Zhuang et al. (2003).

[b] Moss + Fibric horizons only.

C storage along the chronosequence was estimated by collecting twenty 40-cm^2 cores within each stand and measuring the thickness of the organic horizons (moss, fibric, humic). Conversion factors for estimating the C content of each horizon were determined by excavating ten 40-cm^2 soil cores at randomly located sampling points within four burned and four control plots. Two cubes were cut from the center of each organic horizon for determination of volumetric moisture content and bulk density. Oven-dry samples were ground to 60-mesh and analyzed for total C by combustion (Perkins Elmer 2400 Series II CHNS/O Analyzer). A representative C content for each horizon was determined as the product of the mean C concentration (%C) and the mean bulk density (g cm^{-3}). C contents were multiplied by the mean thickness of each horizon to determine C storage.

Moss cover and C exchange

Within each chronosequence stand, percent-cover of moss species was measured at 20 randomly selected points along two 50-m transects using a 1-m^2 wooden frame with a 10-cm flexible grid. Percent cover was estimated as the number of grid squares occupied by a species. Species that did not cover an entire 10×10 cm square were assigned a value of 1%. Percent-cover data were used to identify two early successional (*Ceratodon purpureus* and *Polytrichum juniperinum*) and three late successional moss species (*Hylocomium splendens*, *Pleurozium schreberi*, and *Sphagnum* spp.). Five samples of each species were collected from the 3 and 140-year-old stands, rinsed, and placed in collars constructed of 5- to 8-cm lengths of 30-gauge galvanized steel stove pipe (12.8-cm diameter). Collars were attached to the base of a 22.9 cm diameter aluminum pan using a silicon adhesive and the pan outside of the collar filled with 1-cm of water to ensure an air-tight seal.

Net photosynthesis was measured with a transparent, small-canopy cuvette (CPY-2, PP Systems) instrumented with a stirring fan, a PAR sensor, and an air temperature sensor. Net respiration was determined by measuring the CO_2 concentration within the cuvette at 8 s intervals over a 2-min period. Gross respiration rates were determined by covering the cuvette to prevent light from reaching the moss sample. Photosynthetic uptake of CO_2 was estimated as the difference between gross and net respiration. CO_2 exchange was measured at intervals to capture temperature and light responses. Moisture contents were held constant throughout the experiment by adding distilled water with a spray bottle until samples reached field capacity (the maximum amount of water held on the surface after draining against gravity for 1 h) and adding additional water as necessary throughout the experiment to maintain a constant sample weight.

Temperature–moisture incubations

Relative responses of CO_2 exchange to temperature and moisture were determined by incubating humic material from an 80-year-old black spruce stand and humic/char material from a stand burned within 2 weeks of sampling (mid-July, 1998). Ten replicate samples of the entire organic profile were excavated using a 40 cm^2 corer. In the control stand, humic layers were removed and analyzed separately; the entire thickness of the organic profile (consisting of char and humic materials) was sampled in the burned stand. Due to the consumption of moss and fibric horizons in the burned stand, the humic horizon provided the best basis for direct comparison of burned and unburned materials. An abrupt color and texture boundary allowed for distinguishing the boundary between the humic and mineral soil. Replicate cores were combined and roots >2 mm diameter removed. Samples were air dried and stored at 4 °C until analyzed.

Burned and control organic materials (15 g oven-dry weight) were placed into chambers and incubated for 500 h at four moisture contents (25%, 50%, 75%, and 90% of water holding capacity (WHC)) and four temperatures (0, 4, 10, and 22 °C); each combination of temperature and moisture was incubated in triplicate. Incubation chambers consisted of 500-ml glass jars wrapped in aluminum foil with rubber septa (20-mm diameter) inserted into the lids to create air-tight sampling ports. During the first 500 h of the incubation, chambers were covered with a 0.4- to 0.5-mm thick food-quality plastic film that permitted gas exchange but prevented moisture loss. At the beginning of the sampling period, the film was removed and the chambers were sealed with the metal lids. A glass syringe was inserted into the chamber, filled and evacuated 10 times to facilitate mixing, and 10 ml of gas withdrawn from the headspace. Samples were collected every 3 h over a 12-h period and the rate of change in CO_2 concentration used to calculate flux (μmol CO_2 g C^{-1} h^{-1}). CO_2 concentration was determined using a Shimadzu TOC 5000A Total Organic Carbon Analyzer. Q_{10} values were calculated for the 0–22 °C range following:

$$Q_{10} = \left[\frac{k_2}{k_1}\right]^{10\times(T_2-T_1)^{-1}} \tag{1}$$

where k_2 and k_1 are the rate constants observed at temperatures T_2 and T_1.

Three replicate samples of burned and control organic material were analyzed for pH (water and 0.01 M $CaCl_2$) and total C and N concentration (dry combustion, Perkins Elmer 2400 Series II CHNS/O Analyzer). Exchangeable Ca, Mg, Na, and extractable P were extracted with Mehlich III solution, with cations analyzed by atomic adsorption spectrophotometer and P by Murphy–Riley colorimetry.

Statistical analysis

Multiple comparison procedures were performed with the software package SigmaStat (SyStat Software Inc., Richmond CA). For comparisons of groups with normal distributions and equal variances, a one-way analysis of variance (ANOVA) was performed to test for differences in mean values of the different groups. If significant differences between mean values were found, than Tukey's test (T-method) of all pair-wise multiple comparisons was used to identify specific differences between groups. Probability and significance levels were set to 0.05. Trend analysis was conducted using simple linear regression with temperature and moisture content as the independent variables and the mean of the replicate samples as the dependent variable (SigmaPlot 8.0, SPSS Inc.). When data appeared to depart from the linear model and there was ecological justification, nonlinear curve fitting was performed using the Gauss–Newton method of least squares estimation procedure. The level of significance for all analyses was $p < 0.05$.

Regression analyses and models

In order to assess the potential contributions of moss, root, and heterotrophic respiration to soil CO_2 fluxes measured along the chronosequence, we developed a series of regression analyses and models based on: (1) temperature and moisture relationships determined from incubations and moss photosynthesis studies, and (2) the seasonal patterns of temperature and moisture measured in the field. CO_2 fluxes measured in the field (F_T) were divided into three components: (1) moss respiration (MR), (2) decomposition of humic materials (HD), and (3) residual respiration (RR), following:

$$F_T = \mathrm{HD} + \mathrm{MR} + \mathrm{RR} \tag{2}$$

Potential contributions from decomposition of humic materials (HD) were derived from incubations. C flux rates (g CO_2 g oven dry weight soil^{-1} h^{-1}) were converted to units of area (g CO_2 m^{-2} h^{-1}) using the mean bulk density of humic samples collected for C storage (0.365 g cm^{-3}). In order to account for steep temperature gradients as a function of depth, the mean thickness of humic material measured at each site was divided into 1-cm increments. An exponential regression of measured soil temperature on depth was used to estimate mean soil temperature within each 1-cm increment on each sampling date. HD was then modeled as:

$$\mathrm{HD} = \sum T_{\mathrm{d}} \times F(\mathrm{T}) \times \mathrm{BD} \times T_h \tag{3}$$

where T_{d} is the soil temperature at a given depth determined by regression analysis (°C), F(T) is the incubation flux associated with that temperature (g CO_2 g dry soil^{-1} h^{-1}), BD is the bulk density (g dry soil m^{-3}), T_{h} is the thickness of the soil layer (m), and the summation is across all humic soil layers. Based on field measurements collected concurrent with the field CO_2 flux measurements, mean moisture contents of 75% and 50% WHC were assumed for control and burned soils, respectively. Estimates for HD were made in the 3, 7, 11, 80, and 140 year-old burned black spruce stands for all dates on which field measurements of temperature and CO_2 flux were collected. Weekly estimates for each site were averaged over the growing season, and the potential contribution of humic decomposition to total soil CO_2 flux estimated by dividing the modeled HD by the mean soil CO_2 flux measured in the field.

An upper limit for the contribution of individual moss species to total CO_2 flux (MR_S) was determined by applying the mean weekly surface temperature (T) to the temperature functions for respiration (R_F) determined for each moss species (Equation 4). MR_S was multiplied by the proportion of the site occupied by that species (P_M) and summed across all moss species present to estimate the potential contribution from mosses at each site (MR) (Equation 5).

$$\mathrm{MR_S} = T \times R_F \tag{4}$$

$$\mathrm{MR} = \sum \mathrm{MR_S} \times \mathrm{P_M} \tag{5}$$

Residual respiration (RR) represents CO_2 from root activity as well as contributions from fibric organic horizons (in control stands) and mineral soils (in burned stands). RR was estimated by subtracting MR and HD from mean surface soil CO_2 flux at each site.

$$\mathrm{RR} = \mathrm{F_T} - (\mathrm{MR} + \mathrm{HD}) \tag{6}$$

Sensitivity analyses were conducted to test assumptions of: (1) soil moisture, (2) bulk density, and (3) decomposition of fibric materials. Equations and parameters are summarized in Tables 7 and 8. Sensitivity analyses for soil moisture evaluated how HD varied as a function of the temperature and moisture response curves determined during incubation studies. Bulk density was allowed to vary within the range reported by O'Neill et al. (2003). The assumption that fibric decomposition was negligible relative to HD was tested by adding an additional decomposition source to the model (FD) that was allowed to vary between 0 to 100% of HD (g dry soil^{-1} basis). Determination of fibric soil temperature as a function of depth was determined following approach outlined above for HD. FD was then estimated as a fractional proportion of the predicted HD for that temperature. FD estimates were adjusted to 0.11 g cm^{-3} to reflect the measured difference in bulk density between humic and fibric materials.

Results

Soil CO_2 flux, soil temperature, and carbon accumulation

CO_2 flux, soil temperature, and C storage along the chronosequence were reported in O'Neill et al. (2003). A summary of findings directly related to the present research is presented in Table 1. Across the 140-year chronosequence, mean soil respiration increased as a function of stand age from $0.34 \pm 0.17_{\mathrm{s.d.}}$ g CO_2 m^{-2} h^{-1} in the first year after fire to $0.92 \pm 0.37_{\mathrm{s.d.}}$ g CO_2 m^{-2} h^{-1} in the 140-year-old stand. This pattern of increasing soil respiration as a function of stand age resulted from an initial reduction in root and moss activity immediately following the fire followed by the reestablishment of understory species as the stand recovered. During this same time period, C storage in the upper organic profile (moss and fibric horizons) increased from $10.9 \pm 6.3_{\mathrm{s.d.}}$ Mg C ha^{-1} in the 3-year-old stand to $56.9 \pm 13.5_{\mathrm{s.d.}}$ Mg C ha^{-1} in the 140-year-old stand. Removal of insulating mosses and darkening of the soil surface caused an elevation of soil temperatures and increased thaw in permafrost active layers which gradually declined as the stands recovered from disturbance.

Moss cover

C. purpureus colonized the soil within the first year after fire and remained the dominant bryophyte ground cover for stands less than 40-years-old (Table 2). *P. juniperinum* also appeared early in the successional

Table 2. Percentage of ground covered by bryophyte species along a black spruce chronosequence.

Species	Mean % cover						
	Stand age (y)						
	1	3	7	10	41	80	140
C. purpureus	0.0	59.4 ± 6.4 (95%)	26.2 ± 5.9 (90%)	35.5 ± 5.5 (95%)	0.0	0.0	0.0
P. juniperinum	0.0	0.4 ± 0.3 (20%)	0.1 ± 0.1 (5%)	3.9 ± 0.9 (55%)	0.0	0.0	0.0
H. splendens	0.0	0.0	0.0	0.0	1.6 ± 0.5 (40%)	57.5 ± 7.7 (95%)	54.5 ± 6.2 (100%)
P. schreberi	0.0	0.0	0.0	0.0	15.8 ± 3.6 (95%)	4.0 ± 1.6 (45%)	11.8 ± 2.8 (65%)
Sphagnum spp.	0.0	0.0	0.0	0.0	0.0	3.8 ± 3.9 (5%)	6.2 ± 3.3 (30%)

Values represent the mean ± 1 s.d. of 20 replicate samples. The number in parentheses indicates the percent of plots that contained individuals of that species.

sequence but never comprised more than 4% of the ground cover. The two feathermoss species, *P. schreberi* and *H. splendens* were present in all stands greater than 40-years-old. By 80 years, these two species covered more than 60% of the ground surface. *Sphagnum* spp. (predominantly *S. fuscum* and *S. magellanicum*) occurred only in mature stands (80 and 140 years) and was highly localized in extent.

Moss C exchange

Linear regressions of field-measured respiration on temperature were significant for all species and explained 29 to 81% of the variability in the data, with the strongest correlations found in the early successional species, *C. purpureus* and *P. juniperinum* (Figure 1; Table 3). These species also exhibited the

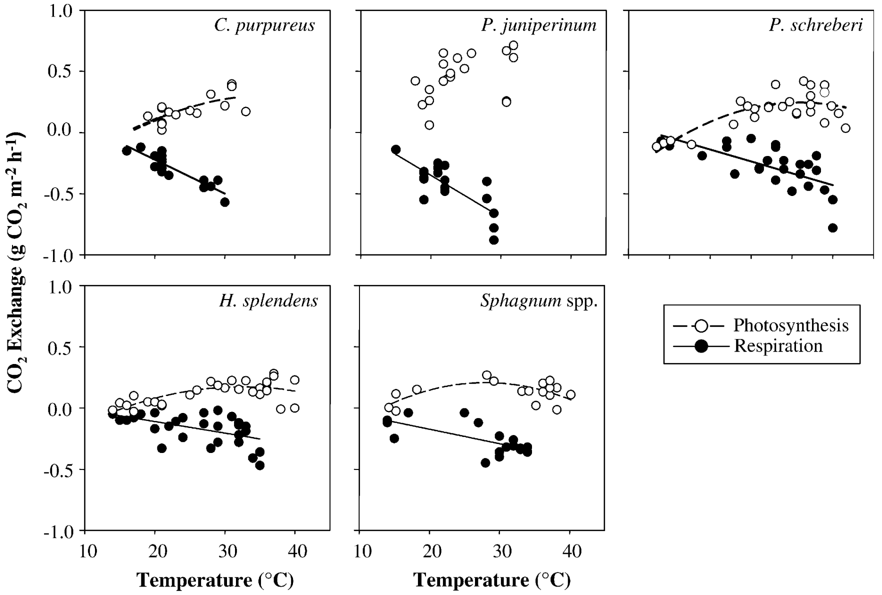


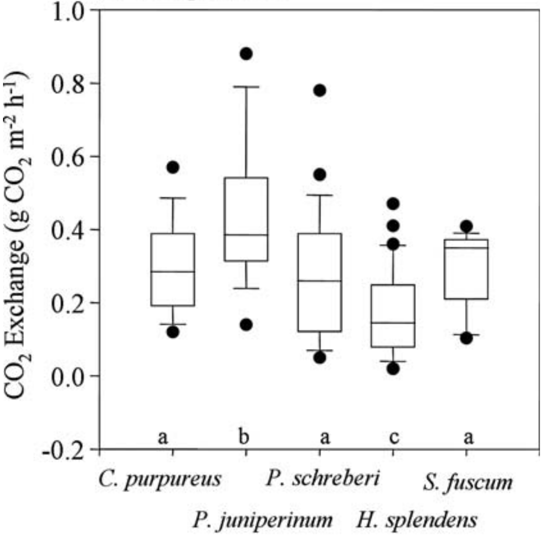
Figure 1. Net photosynthesis and respiration in five boreal moss species. Respiration data were fit with a linear regression model. Photosynthesis data were fit with a second-order polynomial regression model. Equations and parameters are provided in Table 3.

Table 3. Equations and statistics for linear regressions of respiration (g CO_2 m^{-2} h^{-1}) and photosynthesis (g CO_2 m^{-2} h^{-1}) as a function of temperature (Figure 1).

Species	Respiration				Photosynthesis			
	Equation	p	R^2(adj. R^2)	Standard error	Equation	p	R^2 (adj. R^2)	Standard error
C. purpureus	$y = -0.0277x + 0.3331$	<0.0001	0.81(0.79)	0.0585	$y = -0.6748 + 0.0535x - 0.0007x^2$	0.02	0.48(0.39)	0.0828
P. juniperinum	$y = -0.0343x + 0.3354$	0.0002	0.60 (0.58)	0.1231	–	–	–	–
P. schreberi	$y = -0.0193x + 0.2460$	<0.0001	0.48 (0.46)	0.1287	$y = -0.8948 + 0.0661x - 0.001x^2$	<0.0001	0.58(0.55)	0.0956
H. splendens	$y = -0.0095x + 0.0788$	0.0021	0.29 (0.27)	0.1032	$y = -0.4546 + 0.0394x - 0.0006x^2$	0.0001	0.48 (0.44)	0.0670
Sphagnum spp.	$y = -0.0118x + 0.0614$	0.0031	0.45 (0.42)	0.0972	$y = -0.5281 + 0.0528x - 0.0009x^2$	0.03	0.38 (0.30)	0.0720

greatest sensitivity to changes in temperature. With the exception of *P. juniperinum*, photosynthesis in all species showed a parabolic relationship, with minima at both high and low temperatures (R^2 = 0.38 to 0.58). Maximum rates of net photosynthesis were obtained at air temperatures between 28 and 34 °C. Across the range of temperature and light conditions encountered in the field (14 °C to 41 °C and 0 to 1700 μmol m^{-2} s^{-1}), mean rates of respiration were greatest in samples of *P. juniperinum* ($0.43 \pm 0.19_{\text{s.d}}$ g CO_2 m^{-2} h^{-1}) and lowest in *H. splendens* ($0.17 \pm 0.12_{\text{s.d.}}$ g CO_2 m^{-2} h^{-1}); differences in mean rates of respiration in *C. purpureus*, *P. schreberi*, and *S. fuscum* were not statistically significant (Figure 2). Similar patterns were observed in measurements of photosynthesis, with highest photosynthetic rates in *P. juniperinum* ($0.45 \pm 0.19_{\text{s.d.}}$ g CO_2 m^{-2} h^{-1}) and the lowest rates in the*Sphagnum* spp. ($0.12 \pm 0.09_{\text{s.d.}}$ g CO_2 m^{-2} h^{-1}).

(a) Respiration



(b) Photosynthesis

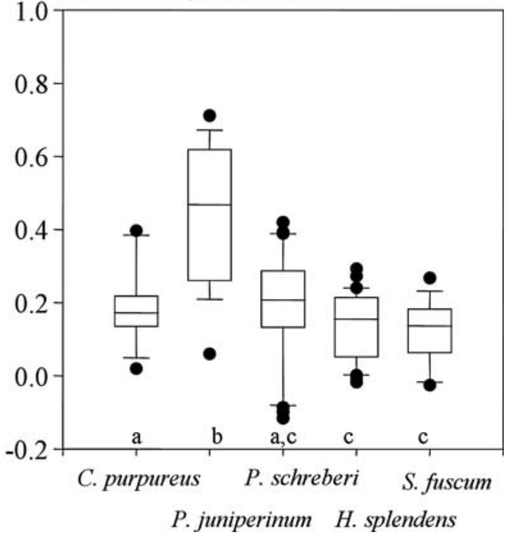


Figure 2. Box plots of photosynthesis and respiration in five moss species. The length of the box represents the interquartile range (IQR); the box is divided at the median. Vertical lines extend to the largest observation within 1.5 IQR's of the box. Observations beyond those limits are plotted individually. Species marked by the same letter were not significantly different ($p < 0.05$).

Incubation of humic materials

Rates of CO_2 flux from soil incubations were significantly greater in the recently burned soils across all combinations of temperature and moisture (Figure 3). Mean rates of CO_2 flux in control humic materials ranged over an order of magnitude from $0.20 \pm 0.11_{\mathrm{s.d.}}$ μmol CO_2 g C^{-1} h^{-1} (0 °C, 25% WHC) to $2.06 \pm 0.15_{\mathrm{s.d.}}$ μmol CO_2 g C^{-1} h^{-1} (22 °C, 90% WHC). Emissions from burned materials were 1.0 to 2.7 times greater than those from control samples and ranged between $0.43 \pm 0.05_{\mathrm{s.d.}}$ μmol CO_2 g C^{-1} h^{-1} (4 °C, 25% WHC) and $2.47 \pm 0.11_{\mathrm{s.d.}}$ μmol CO_2 g C^{-1} h^{1} (22 °C, 90% WHC).

Linear regressions of CO_2 flux on temperature were significant for all moisture-treatment combinations and explained 85 to 99% of the variability in the data (Figure 3). Despite the fact that the magnitude of emissions was greater from burned material, Q_{10} rates were higher in control material over all moisture ranges indicating a greater sensitivity to temperature perturbations. The control soil had highest Q_{10} values at a moisture content of 50% WHC; burned soils had highest Q_{10} functions at 50% WHC and 90% WHC.

The relative effect of post-fire changes in respiration that could not be explained by either temperature or moisture, ΔR, was estimated as:

$$\Delta R = (\mathrm{B}_{(\mathrm{M,T})} - \mathrm{C}_{\mathrm{O}(\mathrm{M,T})})/\mathrm{C}_{\mathrm{O}(\mathrm{M,T})} \tag{7}$$

where B represents CO_2 flux from burned humic material and C_O represents flux from control material for the same combination of moisture (M) and temperature (T); a ΔR value of 1 indicates a 100% increase in CO_2 flux that can not be directly attributed to differences in moisture or temperature (Figure 4). Across all

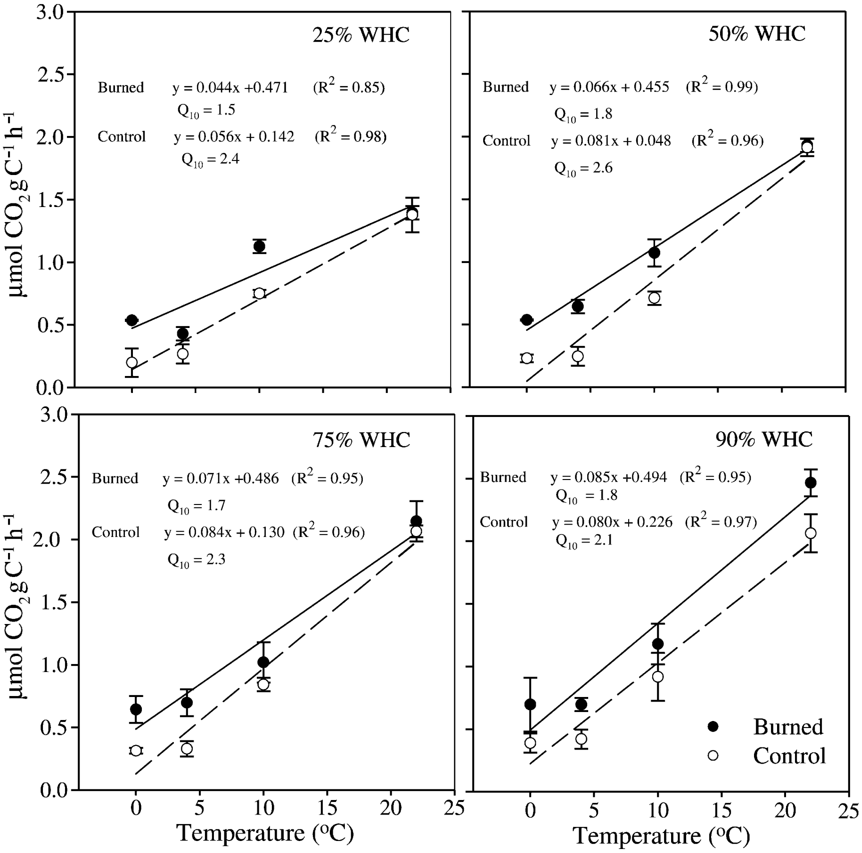


Figure 3. Temperature response curves for burned and control humic materials incubated at four moisture contents. Symbols represent the mean ± 1 s.d. of three replicate samples.

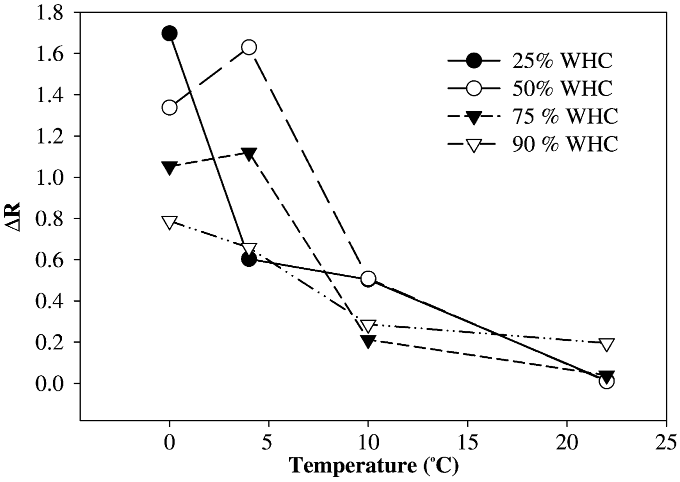


Figure 4. The relative effect of post-fire changes in respiration that could not be explained by either temperature or moisture (ΔR). ΔR was estimated as the ratio of the difference in CO_2 emissions between burned and control samples to emissions from control samples.

Table 4. Chemical characteristics of burned and control humic materials used in incubation analysis.

Analyte	Control	Burned
pH (water)	6.5 ± 0.07	6.5 ± 0.08
pH (0.01 M $CaCl^2$)	5.3 ± 0.01	5.3 ± 0.03
C (%)*	13.08 ± 0.94	18.65 ± 0.87
N (%)	0.41 ± 0.07	0.53 ± 0.04
Ca (cmolc (+) kg^{-1})*	28.29 ± 0.50	43.02 ± 0.42
Mg (cmolc (+) kg^{-1})*	13.06 ± 0.13	8.16 ± 0.58
K (cmolc (+) kg^{-1})*	0.40 ± 0.01	0.74 ± 0.01
Extract. P ($\mu g\ g^{-1}$)*	14.48 ± 0.34	70.87 ± 4.59

Values represent the mean ± 1 s.d. of three replicate samples. Items marked by an asterisk were significantly different ($p < 0.05$).

temperature–moisture combinations, ΔR values ranged between 0.1 and 1.7. For a given moisture content, ΔR was proportionately greater at lower temperatures and decreased as a function of temperature. Chemical analysis of samples indicated that burned soils had significantly higher concentrations of Ca, K and extractable P (Table 4), suggesting that changes in substrate chemistry may partially explain differences in flux rates between burned and control samples.

Components of surface CO_2 flux: decomposition, moss, and residual sources

Models suggest that decomposition from humic and char materials (HD) may account for between one-fifth and all of total soil CO_2 flux in burned stands as compared to only 11 to 17% in control stands (Table 5). Despite the smaller thickness of humic material contributing to CO_2 flux in burned stands, the combination of warmer soil temperatures and higher decomposition coefficients resulted in modeled contributions from HD that were 3.0 to 4.0 times those estimated for control stands in the first 7 years after fire. In the 10-year-old burn, the greatly reduced thickness of humic material compared to other chronosequence sites resulted in estimated contributions from HD that were 60% of those in the control stand.

Under saturated moisture conditions, moss respiration (MR) is estimated to contribute between one-tenth and one-half of total surface CO_2 flux (Table 6). Despite the much greater ground cover of mosses in mature black spruce stands ($72.5 \pm 21.3_{\text{s.e.}}$% in the 140-year-old stand), the potential contribution of mosses to soil CO_2 flux was relatively low in these stands due to the lower respiration rates associated with

Table 5. Modeled heterotrophic respiration in humic soil horizons as a function of soil temperature and humic layer thickness. Model assumes a bulk density of 0.365 g cm^{-3}.

Stand age		Modeled thickness of humic material (cm)	Average model temperature (°C)	Field CO_2 flux g CO_2 m^{-2} h^{-1}	Modeled HD (g CO_2 m^{-2} h^{-1})	Model: Field[b]	Decomposition enhancement[c]
1	Burn	14	7.6 ± 2.7	0.38 ± 0.12	0.40 ± 0.04	105.3	4.00
	Control	17	1.8 ± 1.4	0.63 ± 0.13	0.10 ± 0.03	15.9	
3	Burn	6	16.4 ± 1.9	0.40 ± 0.12	0.27 ± 0.02	67.5	3.00
	Control	12	3.0 ± 1.7	0.79 ± 0.20	0.09 ± 0.03	11.4	
7	Burn	7	13.7 ± 2.5	0.55 ± 0.19	0.28 ± 0.05	50.9	3.50
	Control	12	2.4 ± 1.3	0.69 ± 0.15	0.08 ± 0.02	11.6	
10	Burn	2	15.9 ± 3.7	0.47 ± 0.17	0.09 ± 0.01	19.1	0.64
	Control	8	8.5 ± 2.7	0.83 ± 0.25	0.14 ± 0.03	16.9	
80	Control	12	2.4 ± 1.3	0.69 ± 0.15	0.08 ± 0.02	11.6	N/A
140	Control	15	2.6 ± 1.1	0.97 ± 0.21	0.11 ± 0.02	11.3	N/A

Values represent the mean ± s.d. of weekly estimates for microbial respiration in the soil profile (June–August). The control for the 7-year-old burn is the same as the 80-year-old stand.

[a] Reflects the mean CO_2 flux measured during those weeks for which soil temperatures were also collected; flux values may differ from those presented in Table 1.

[b] Calculated as (modeled CO_2 flux/field CO_2 flux)*100.

[c] Calculated as (modeled burn/modeled control).

Table 6. Estimated contribution of moss, microbial, and root respiration to total soil CO_2 efflux along a chronosequence of burned black spruce stands (mean ± 1 s.d.).

Stand age (years)	Total CO_2 flux (F_T)[a] (g CO_2 m^{-2} h^{-1})	Modeled contributions from					
		Moss (MR)		Humic decomposition (HD)		Residual (RR)	
		g CO_2 m^{-2} h^{-1}	% of Total	g CO_2 m^{-2} h^{-1}	% of Total	g CO_2 m^{-2} h^{-1}	% of Total
1	0.38 ± 0.12	0	0%	0.40 ± 0.04	105.3%	− 0.02 ± 0.13	− 5.3%
3	0.40 ± 0.12	0.22 ± 0.06	55.0%	0.27 ± 0.02	67.5%	− 0.09 ± 0.14	− 22.5%
7	0.55 ± 0.19	0.08 ± 0.04	14.5%	0.28 ± 0.05	50.9%	0.19 ± 0.20	34.5%
10	0.47 ± 0.17	0.14 ± 0.07	29.8%	0.09 ± 0.04	19.1%	0.24 ± 0.19	51.1%
80	0.69 ± 0.15	0.07 ± 0.04	10.1%	0.08 ± 0.02	11.6%	0.54 ± 0.16	78.3%
140	0.97 ± 0.21	0.13 ± 0.04	13.4%	0.11 ± 0.02	11.3%	0.73 ± 0.21	75.3%

[a] Reflects the mean CO_2 flux during time period modeled; flux values may differ from those presented in Table 1.

late-successional moss species. Contributions from mosses to total soil flux were greatest in the 3-year-old stand ($0.22 \pm 0.06_{s.d.}$g CO_2 m^{-2} h^{-1}) and relatively constant over the remainder of the chronosequence, with estimated flux rates ranging between $0.07 \pm 0.04_{s.d}$ and $0.14 \pm 0.07_{s.d}$ in stands older than 3 years.

In recently burned stands (<3-year-old), estimates of contributions from residual sources of respiration were negative, reflecting that modeled estimates of HD and MR could more than account for all CO_2 production (Table 6). In mature stands, estimated contributions from RR increased to 75–78% of total CO_2 flux.

Sensitivity analysis

Modeled HD was sensitive to changes in soil moisture content, with increased moisture corresponding to increased HD across all sites evaluated (Table 7). An increase or decrease in the baseline moisture content of 25% resulted in an 8–22% change in HD for burned soils and an 8–33% change in control soils. Because temperature-moisture functions were defined on a per g dry soil basis, the effects of bulk density on HD were linear (i.e. a 10% increase in bulk density corresponded to a 10% increase in estimated HD).

The bulk density of organic materials can have a high degree of spatial variability in the field, and accurate measurement of organic bulk density is complicated by the high moisture content and compactability of the samples. Previous studies in this region have indicated that the bulk density of unburned humic materials may be less than half that of burned humic materials (0.21 ± 0.09 g cm^{-3} in control vs. 0.48 ± 0.18 g cm^{-3} burned; O'Neill et al. 2003). Incorporation of this potential difference in bulk density along the chronosequence increased estimates of decomposition enhancement in burned humic materials from a factor of 0.6–4.0 (Table 5; assuming constant bulk density) to 3.9–8.8 times greater than decomposition in control soils in the first 10 years after fire.

Estimates were more sensitive to assumptions about FD in the youngest stand (Table 7). Increasing FD from 0 to 50–100% of HR increased contributions to total organic profile decomposition (HD + FD) by 4–20%. The model was most sensitive to assumptions about FD in the 1-year-old stand and generally declined in older stands. Under a maximum case scenario that FD is twice as large as HD, our model underestimated decomposition by 40% in the 1-year-old stand and by 16–24% in all other stands.

Discussion

Soil temperature, moisture content, and the depth of thaw exert strong controls on soil CO_2 flux in northern latitudes (Flanagan and Veum 1974; Christensen et al. 1998; Gulledge and Schimel 2000). In

Table 7. Sensitivity of HD model to assumptions of soil moisture content.

	Moisture content (%)	Equation	% change in estimated HD relative to initial model assumptions					
			Stand age (y)					
			1	3	7	10	80	140
Burned	25	$y = 0.0878 + 0.0083x$	– 15.0%	– 21.4%	– 20.0%	– 21.9%	–	–
	50	$y = 0.0848 + 0.0122x$	–	–	–	–	–	–
	75	$y = 0.0907 + 0.0133x$	8.0%	8.4%	8.3%	8.4%	–	–
	90	$y = 0.0922 + 0.0159x$	20.0%	23.9%	23.1%	24.2%	–	–
Control	25	$y = 0.0186 + 0.0074x$	– 12.6%	– 17.2%	– 15.1%	– 25.9%	– 15.1%	– 16.5%
	50	$y = 0.0063 + 0.0106x$	– 29.4%	– 23.5%	– 26.2%	– 12.4%	– 26.2%	– 24.4%
	75	$y = 0.0165 + 0.011x$	–	–	–	–	–	–
	90	$y = 0.0296 + 0.0105x$	32.6%	24.1%	28.1%	8.0%	28.1%	25.4%
			% change in estimated contributions to decomposition (HD + FD)					
Modeled contributions from fibric decomposition as a percentage of HD								
	50		10.1%	6.0%	4.8%	4.8%	4.0%	5.6%
	100		20.2%	11.9%	9.6%	9.6%	8.0%	11.3%
	200		40.3%	23.9%	19.3%	19.2%	16.1%	22.5%

Equations were determined from incubation analysis (Figures 1 and 2) with regression expressed in g CO_2 m^{-2} h^{-1}. Based on field measurements, initial model run assumed a 50% moisture content in burned soils and a 75% moisture content in control soils.

The control for the 7-year-old stand is also the 80-year-old chronosequence stand.

black spruce systems underlain by permafrost, fire reduces canopy shading, removes insulating moss layers, and darkens soil surfaces, raising soil temperatures and increasing the thickness of the soil active layer. These changes correspond to increased decomposition in the months to years following disturbance (Richter et al. 2000; O'Neill et al. 2003). Because decomposition rates in mature stands are small relative to autotrophic sources of respiration, even a relatively large increase in decomposition may easily be masked by the loss of root and moss activity immediately after fire, as reflected in lower total CO_2 flux from the surface in recently burned stands (O'Neill et al. 2003; Table 1). For this reason, additional experimentation and models were needed to assess changes in CO_2 contributions from decomposition, roots, and mosses in the decades following disturbance.

Contributions from bryophytes (MR)

The sequence of bryophyte succession following fire supports findings from studies in boreal Canada (Maikawa and Kershaw 1976; Black and Bliss 1980; Foster 1985). Initial colonization is by mosses that are adapted to withstand the large diurnal fluctuations in summer temperature, high light levels, and low boundary layer humidity typical of recently burned soils (e.g., *P. juniperinum* and *C. purpureus*). Weft-forming moss species, such as *P. schreberi* and *H. splendens*, are susceptible to desiccation and cannot become established until an overstory has developed (approximately 30–40 years) (Longton 1988). The hummock-forming *Sphagnum* mosses are particularly sensitive to desiccation and can only become established if the time since the most recent fire is sufficient to allow for canopy closure (Clymo and Hayward 1982).

Because of their low biomass and diminutive stature, the role of early successional mosses in ecosystem C exchange may often be overlooked in favor of the more prominent feathermoss and *Sphagnum* species. However, results from C exchange studies suggest that under optimal moisture conditions, this 1- to 2-mm tall moss layer has the potential to contribute 10–55% of surface CO_2 flux (Table 6). Accounting for the activity of early successional mosses is critical for assessing point measurements of C fluxes from the forest floor. However, the length of time that these mosses are respiring at full capacity and the potential implications for C source-sink dynamics over longer time scales is still unknown.

Decomposition of humic materials (HB)

Carbon dating studies of soils from Alaskan black spruce forests indicates that humic materials are often more than 1000 years old (Mann et al. 1995). Because of these long turnover times, many biogeochemical models consider humic soil to be nearly inert (Goulden et al. 1998). However, results from incubation studies indicate that the low decomposition rates typically measured in boreal systems are primarily limited by environmental factors (e.g., low temperature and high moisture content); even in control samples, humic materials did not appear to be chemically recalcitrant. As a result, increased soil temperatures and decreased soil moisture following burning (O'Neill et al. 2002, 2003) have the potential to increase decomposition of stored C materials. However, care needs to be taken in extrapolating decomposition rates from laboratory incubations to the field due to the potential for disturbance effects that increase decomposition relative to *in situ* measurements.

Differences in CO_2 fluxes in burned and control samples not attributed to moisture or temperature (ΔR; Figure 4) may be partially explained by changes in substrate chemistry induced by combustion and ash deposition (Table 4). These findings support the work of Pietikäinen and Fritze (1996) in which CO_2 evolution from recently burned organic soils was found to be 12 times greater than that from unburned controls. Similarly, Burke et al. (1997) attributed increased CO_2 emissions in recently burned boreal stands to a short-term stimulation of microbial activity by input of labile substrates following fire. Although short-term heat shocks in the upper soil may reduce soil microbial biomass and soil respiration following fire (Fritze et al. 1993; Pietikäinen et al. 2000), the deposition of ash on the soil surface may counteract some of these effects by increasing soil pH and introducing a pulse of exchangeable nutrients and labile substrates to the soil surface (Bååth and Arnebrant 1994; Pietikäinen and Fritze 1996).

Models of HD may underestimate microbial contributions to soil respiration because they include only contributions from humic materials. Humic materials were selected as a basis for comparison for three reasons: (1) the fire consumed fibric and moss layers on the burned sites making humic materials the only basis for direct comparison, (2) humic material accounts for nearly 70% of the C in organic profiles of black spruce stands in the Alaskan interior (Kasischke et al. 2000), and (3) previous studies have indicated that humic materials may have respiration rates as much as four times greater than fibric organics (Van Cleve and Sprague 1971). Sensitivity analyses indicate that, despite the greater thickness of fibric materials in control stands, the effects of this assumption are more pronounced in burned stands. Additional measurements of decomposition in fibric materials are needed to further constrain C dynamics as burned stands recover from disturbance.

Residual respiration (RR)

Little is known about the contribution of root respiration and turnover to post-fire C dynamics because of the difficulty in distinguishing them from other fractions of SOM with short turnover times. This study evaluated changes in root activity indirectly, as the difference between total soil respiration, moss respiration, and decomposition. This analysis is further complicated by the fact that residual sources of CO_2 vary between burned and control stands. In control stands, the presence of frozen soil at the base of the organic profile minimizes CO_2 fluxes from mineral soils (O'Neill et al. 2002) and surface CO_2 fluxes arise primarily from processes within the organic soil profile. In burned soils, combustion largely removed fibric soil horizons while elevating soil temperature, resulting in permafrost thaw and increased biological activity in mineral soils (O'Neill et al. 2002). As a result of these differences, RR is comprised of different sources of CO_2 in burned and control stands. In control stands, RR consists of root activity and fibric soils. In burned soils, dominant contributions come from roots and mineral soils. As a burned stand recovers from disturbance, the contribution from minerals soils gradually decreases while the contribution from fibric horizons increases.

Because RR is indirectly estimated as the difference between two estimates, error terms are relatively large and difficult to quantify. However, proportionalities between HD and RR in mature stands are consistent with estimates of Schlentner and Van Cleve (1985) in which 80 to 90% of CO_2 emissions from the organic profile of mature black spruce stands were attributed to root activity. This, combined with the patterns of increasing RR as a function of stand age, suggests that our RR component may be largely dominated by root activity. Additional research using quantitative techniques (e.g., stable isotope fractionation) is needed to discriminate heterotrophic and autotrophic sources of $CO_{2.}$

Net ecosystem production (NEP)

O'Neill et al. (2003) estimated NEP and C source-sink dynamics for these stands using a modified mass-balance model of C storage that allowed both decomposition and NPP to vary over the fire cycle. Total inputs to the soil system (NPP) were estimated to increase from 0.0 to 0.8–1.5 Mg C ha^{-1} during the first 100 years after fire. The difference between modeled NPP and decomposition suggested that these soils were a net C source for 7 to 14.5 years after burning and a net sink of 0.3–0.6 Mg C ha^{-1} yr^{-1} over the remaining years of the simulation (t_{final} = 140 years). These trends are generally consistent with those of Bond-Lamberty et al. (2004) for a black spruce fire chronosequence in Manitoba, Canada in which NEP showed a small post-fire net C loss followed by a long period of positive accumulation with a maximum NEP of 1.1 Mg C ha^{-1} year^{-1} (71 years post-fire). The transition between net source to net sink was estimated at 11–19 years (Litvak et al. 2003). Similarly, modeling studies derived from satellite-based NPP estimates for the North American boreal forest suggest that NEP shifted from a net C source during the first 8 years after fire to a net sink that continued for many decades afterward (Hicke et al. 2003). Landscape analyses in Canada (Rapalee et al. 1998) and application of the CENTURY model to forest inventory data in Alaska (Yarie and Billings 2002) both placed the C compensation point at approximately 30 years after wildfire.

Evidence for succession-driven changes in components of soil respiration

Moss communities, decomposition, and root respiration respond in different ways to fire and the proportion of CO_2 flux contributed by each component changes as a stand recovers from disturbance. The results of these studies illustrate the complexity of interactions between moss cover, soil microclimate, decomposition, and C sequestration (Figures 5 and 6). In the first year following fire, field measurements indicate that total surface CO_2 fluxes were reduced by approximately 60% relative to a mature stand (140-year-old). Models indicate that nearly all of these fluxes could be accounted for by the decomposition of humic materials alone. As the time since fire increases, contributions from moss and residual sources of CO_2 increase steadily, reflecting the reestablishment of a moss cover on the forest floor and increased activity by vascular plant roots (Figure 5). During this same time, the relative contributions from decomposing humic materials declined by a factor of four, accounting for just 11% of total CO_2 fluxes from the mature stand.

These patterns of post-fire CO_2 exchange parallel the larger ecological shifts that black spruce stands undergo as they recover from disturbance (Figure 6). Following ground fires, moss communities are partially to completely removed, contributing to warmer soil temperatures (Figure 6a and b; O'Neill et al. 2003). The combination of these warmer temperatures, increased thickness of the soil active layer, and the potential for changes in substrate chemistry (Tables 1 and 4) increases decomposition and results in a net loss of C from the soil (O'Neill et al. 2003). Early successional moss species help to create a more favorable environment for vascular plants by moderating soil temperature and increasing moisture retention at the soil surface (Foster 1985). Understory vegetation and young trees begin to shade the surface within 30–40 years, reducing incoming solar radiation and moderating humidity sufficiently to allow for the reestablishment of weft-forming feathermosses (Longton 1988; Table 2; Figure 6a). Organic matter derived from these mosses has high moisture and heat capacities, making them effective insulators (Viereck 1975; Skre and Oechel 1981) that further reduce soil temperatures (Table 1; Figure 6b) and decomposition in

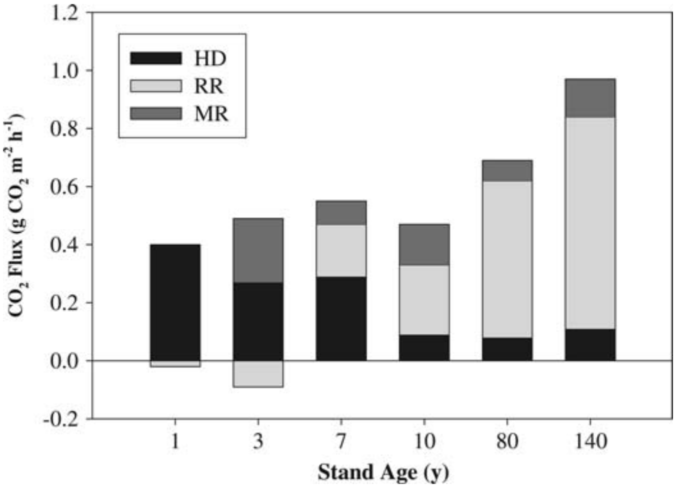
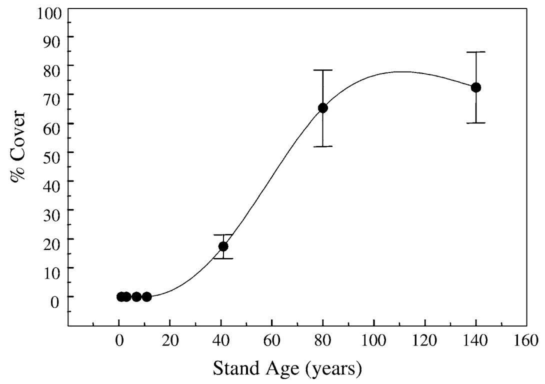
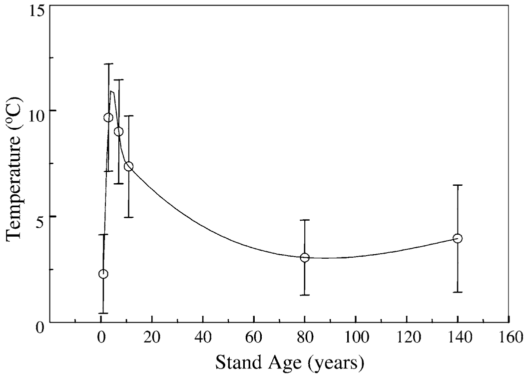


Figure 5. Modeled contributions of moss respiration (MR), humic decomposition (HD), and residual respiration (RR; fibric horizon, mineral soil, and roots) to total soil CO_2 flux along a chronosequence of burned black spruce stands.

(a) %Cover of Feathermoss and Sphagnum



(b) Soil temperature (20 cm)



(c) Carbon accumulation

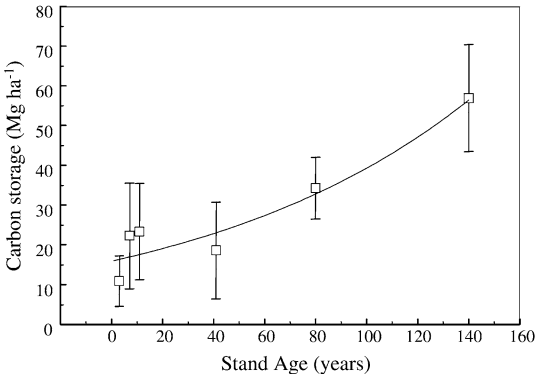


Figure 6. Changes in the percent cover of bryophyte species, soil temperature, and C accumulation in black spruce ecosystems. Data for (a) are presented in Table 3; data for (b) and (c) are presented in Table 1. As late-successional moss species (a) begin to reoccupy black spruce forests, soil temperature declines (b) and decomposition is reduced, resulting in an increase in soil C storage (c).

humic materials (Figure 3). Over time, the combination of increased C inputs from mosses and lower decomposition results in the accumulation of soil organic matter (Harden et al. 1997; Figure 6c). As the thickness of organic matter increases, it traps heat, moisture, and nutrients near the surface reducing plant productivity and rates of nutrient cycling (MacLean et al. 1983), until another fire disturbance restarts the cycle.

Conclusions

Together, field measurements, laboratory experiments, and models provide strong evidence that interactions between plant succession and soil microclimate largely regulate C source-sink dynamics from black spruce systems in the first century following fire disturbance. Bryophyte species exhibited a distinct successional sequence in the first five decades after fire disturbance, which corresponded to decreases in soil temperature and increased C accumulation as these systems recovered from disturbance. Under optimal moisture conditions, mosses contributed between 10 and 55% of total soil respiration, with highest contributions from early successional moss species (*C. purpureus* and *P. juniperinum)*. Incubation of burned and control humic materials indicated that post-fire changes in soil temperature and substrate quality have the potential to increase CO_2 losses from humic decomposition by a factor of 3.0 to 4.0 in the first 7 years following fire. Residual sources of CO_2 (those not attributed to moss respiration or humic decomposition) increased as a function of stand age, reflecting increased contributions from roots as the stand recovered from disturbance.

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