Environmental controls on soil CO_2 flux following fire in black spruce, white spruce, and aspen stands of interior Alaska

Katherine P. O'Neill, Eric S. Kasischke, and Daniel D. Richter

Abstract: Boreal forests contain large amounts of stored soil carbon and are susceptible to periodic disturbance by wildfire. This study evaluates the relationship between post-fire changes in soil temperature, moisture, and CO_2 exchange in paired burned and control stands of three Alaskan forest systems: *Picea mariana* (Mill.) BSP, *Picea glauca* (Moench) Voss, and *Populus tremuloides* Michx. In these systems, the environmental factor that most directly controlled rates of carbon exchange varied depending upon burn status and soil drainage. In mature unburned stands, CO_2 flux was highly correlated with seasonal patterns of soil temperature. Following fire, these soils became significantly warmer, and carbon exchange became more sensitive to fluctuations in surface moisture conditions. The effect of fire on soil climate was most pronounced in the *P. mariana* stands, which experienced a mean seasonal temperature increase of 5–8°C in the upper 1 m of the soil profile, a 200% increase in the rate of active layer thaw, and a reduction in mean surface moisture potential. Evidence from soil CO_2 profiles suggests that these environmental changes may have resulted in enhanced decomposition of carbon previously immobilized by permafrost, potentially transforming a landscape that was once a net sink for carbon into a carbon source.

Résumé : Les forêts boréales dont le sol recèle de grandes quantités de carbone sont périodiquement perturbées par le feu. Cette étude évalue la relation entre les perturbations qui surviennent après feu dans la température et l'humidité du sol et les échanges de CO_2 dans des peuplements témoins et des brûlis jumelés appartenant à trois écosystèmes forestiers en Alaska : *Picea mariana* (Mill.) BSP, *Picea glauca* (Moench) Voss et *Populus tremuloides* Michx. Dans ces trois écosystèmes, le facteur environnemental qui contrôle le plus directement le taux d'échange de carbone varie selon le drainage et le fait qu'il y ait eu ou non un feu. Dans les peuplements matures non brûlés, le flux de CO_2 est étroitement corrélé aux patrons saisonniers de température du sol. Après un feu, la température de ces sols s'élève et les échanges de carbone deviennent plus sensibles aux fluctuations du taux d'humidité en surface. L'effet du feu sur le climat du sol est le plus prononcé dans les peuplements de *P. mariana* qui subissent une augmentation de la température moyenne saisonnière de 5 à 8 °C dans le premier mètre du profil de sol, une augmentation de 200 % dans le taux de dégel de l'horizon actif et une diminution du potentiel hydrique moyen en surface. Des indices provenant des profils de CO_2 du sol indiquent que ces changements environnementaux ont pu entraîner une augmentation de la décomposition du carbone qui était immobilisé dans le pergélisol, transformant possiblement un paysage qui était jadis un puits de carbone en source de carbone.

[Traduit par la Rédaction]

Introduction

The soils of boreal forest ecosystems have one of the highest carbon densities in the world and are estimated to contain between one-quarter and one-third of all soil carbon (200–500 Gt C) (Gorham 1991; Dixon et al. 1994). On an ecosystem level, one of the primary regulators of carbon uptake and emission in northern landscapes is wildfire (Kasischke et al. 1995, 2000; Kasischke 2000). In addition to the immediate release of stored soil carbon during combustion and the subsequent reduction in carbon inputs from primary production, fire also has the capacity to alter several soil physical and biogeochemical properties (e.g., soil temperature, moisture, substrate quality) that regulate carbon exchange over longer time scales. Quantifying the relationship between environmental factors and soil carbon emissions is critical for developing models of ecosystem response to climate-driven changes in fire frequency and severity.

Soil temperature, moisture content, and the depth of thaw exert strong controls on decomposition rates in soils of northern latitudes (Flanagan and Veum 1974; Heal and Block 1987; Christensen et al. 1998). Unlike almost any other form of disturbance, fire has the capacity to alter soil thermal and moisture regimes for years to decades following burning (Richter et al. 2000; Kasischke et al. 1995; Dyrness

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et al. 1986; MacLean et al. 1983). Following fire, loss of canopy shading, removal of insulating moss layers, and darkened soil surface raise soil temperatures and cause a thickening or deepening of the permafrost active layer (O'Neill et al. 2003; Zhuang et al. 2003). In soils underlain by permafrost, these alterations in the soil energy and moisture budgets may result in enhanced decomposition and a net loss of stored carbon from the system.

Functional relationships between soil temperature, moisture, and respiration have been described for soils in mature, upland boreal forests (Bunnell and Tait 1974; Schlentner and Van Cleve 1985, Savage et al. 1997; Moosavi and Crill 1997). However, in organic-rich black spruce soils, these relationships are more complex and not well understood. In addition, little is known about the ways that the underlying relationships between soil CO_2 flux and environmental variables might change in response to fire disturbance. This study addresses these sources of variability by examining soils from three different forest ecosystems that all burned in the same fire under similar climatic conditions.

Seasonal patterns of soil temperature, moisture potential, and CO_2 exchange were measured in burned and control stands of three dominant forest species in the Alaskan interior: black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), and trembling aspen (*Populus tremuloides* Michx.). These stands represent a moisture gradient between well-drained, warm soils (aspen) and saturated, permafrost soils (black spruce). The objectives of this study were to (*i*) characterize seasonal patterns of CO_2 flux; (*ii*) examine the roles of soil temperature and moisture in determining the exchange of CO_2 with the atmosphere; and (*iii*) assess the extent to which fire disturbance changes both environmental variables and rates of soil carbon exchange.

Site description

Sample plots were established in paired burned and control aspen, white spruce, and black spruce stands located within 10-km of the town of Tok Junction, Alaska (Fig. 1). These stands burned during a series of wildfires that spread across 40 000 ha of the Tanana River outwash plain and adjacent uplands in July and August of 1990. Prior to the fire, this region was a mosaic of differently aged stands of black spruce, white spruce, and aspen, providing a unique opportunity to isolate the effect of fire disturbance on different forested systems that were all located on similar soils and landscape positions (Kasischke et al. 1995; French et al. 1996*a*, 1996*b*). In addition, all of the sampling sites burned during an extremely intense ground and crown fire in early July 1990 (Kasischke et al. 2000) such that fire severity is comparable among stands. Unburned controls for the white spruce and aspen stands were located immediately adjacent to the burned stands. However, because of the large size of the fire, no unburned black spruce stands remained within areas of the fire scar representative of typically burned stands, and the control stand was established within several kilometres of the burn site.

Soils consisted of nearly level, well-drained silt loams over gravel or sand located on outwash plains or terraces (coarse-silty, mixed, non-acid Pergelic Cryaquepts and Cryaquents). The primary difference between soils associated with different forest types was the thickness of the silt cap overlying the coarse gravel of the alluvial deposits beneath. In general, black spruce stands were located on portions of the landscape with a thicker silt cap, resulting in poorer drainage and the formation of permafrost within the upper 1 m of the soil profile. Soils in mature black and white spruce stands were characterized by thick organic profiles overlying the mineral soil. However, humic horizons were well developed in mature black spruce stands and minimal to absent in white spruce. In contrast, aspen stands had a forest floor characterized by a 1- to 2-cm layer of leaf litter overlying a more decomposed O_e horizon. Sites were located in the zone of discontinuous permafrost and soils underlying mature black spruce stands remained frozen within the upper 1 m throughout the entire growing season. Physical and chemical characteristics of soil profiles are provided in Table 1. The low relief of these soils (0–5% slope) suggests little horizontal percolation of water and minimal loss of carbon through erosion or runoff (Richter et al. 2000).

The lower Tanana River valley experiences a strong continental climate characterized by moderate temperatures and precipitation during the summer months (May–August) and exceedingly cold and dry conditions during the winter. Comparison of the 45-year mean temperature and precipitation with that observed during the 1997 and 1998 sampling seasons indicate that mean temperatures during this study were typical of the region (within one standard deviation of the long-term mean) (Table 2). However, the 1997 sampling season was much wetter than usual with more than 80% of mean annual precipitation (19 cm) falling during the growing season, compared with ~40% on average. The majority of this rainfall (10.9 cm) occurred over a 2-week period in late July making this the rainiest month on record for Tok Junction. Rainfall events of this magnitude (>7.5 cm in any 5-day period) accounted for less than 2% of rainfall events between 1954 and 1999 (National Weather Service 2000).

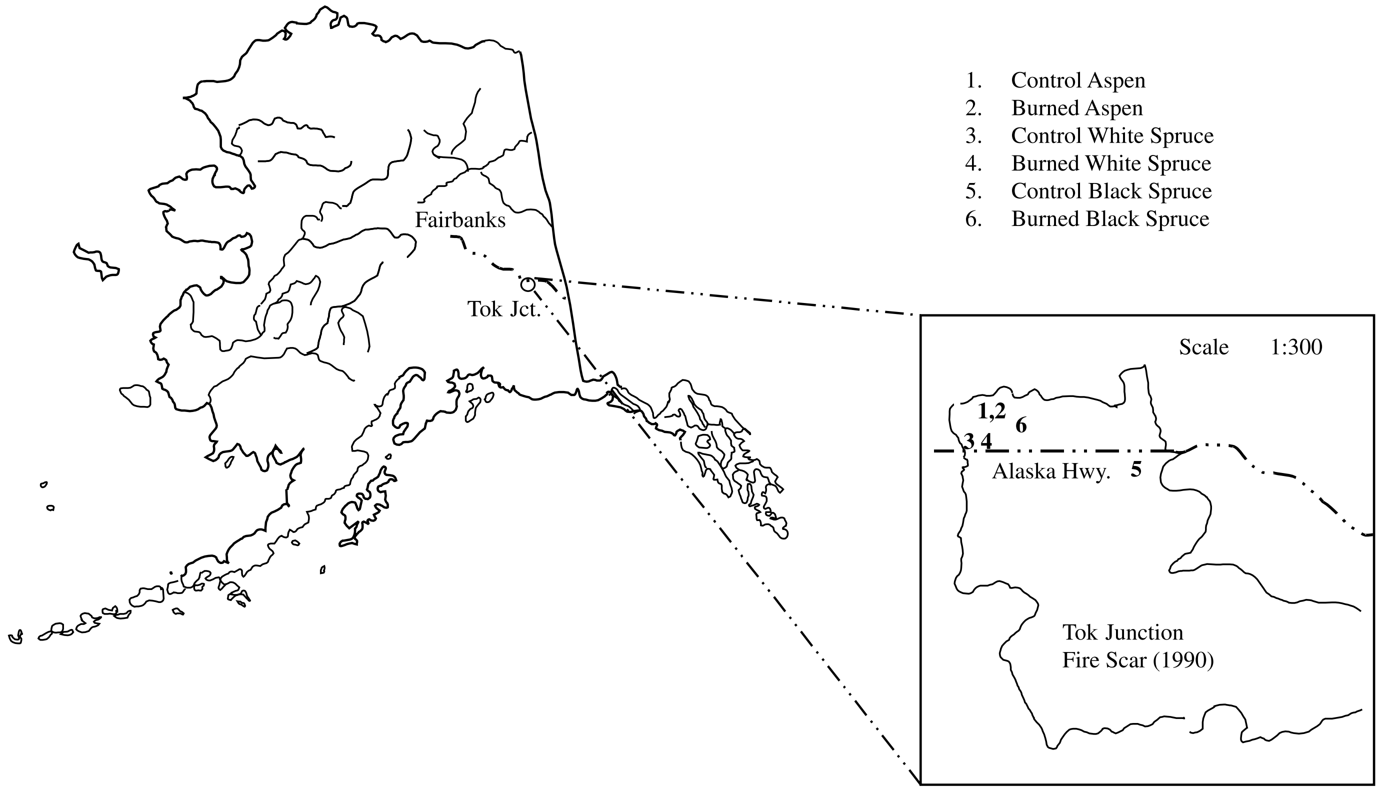
Methods

Soil carbon storage

At each burned and control site, three soil pits were excavated to a depth of 1 m or to the top of the seasonally frozen active layer (control black spruce). Soils were described and characterized following the Canadian Soil Classification System (Agriculture Canada Expert Committee on Soil Survey 1987). Within each genetic horizon, mineral soil samples were collected volumetrically using a 10.5-cm bulk density core. The high gravel content of the lower white spruce and aspen soil profiles prevented collection of representative bulk density samples; for these depths, a mean density of 1.5 $g \cdot cm^{-3}$ was assumed for the <2 mm fraction (Brady and Weil 1996).

To address the greater variability in carbon storage in organic profiles, carbon storage was measured at 20 randomly located points within each stand. At each measurement point, a 40-cm^2 soil core was excavated using a shovel and (or) saw and subdivided into genetic horizons (moss, fibric, and humic). Two cubes were cut from the centre of each horizon using an electric knife with two reciprocating blades; this method minimized the potential of compaction. Cube di-

Fig. 1. Site location map. Inset maps show boundaries of the Tok burn scar.



mensions were measured to the nearest 0.1 cm and the samples weighed, dried in a 65°C oven for 48 h and then reweighed to determine volumetric moisture content and bulk density. Ovendry samples were ground in a Wiley Mill until all material was able to pass through a 60-mesh sieve. Fine roots were not removed prior to grinding.

For both mineral and organic samples, total percent carbon and nitrogen were measured by combustion on a Perkins-Elmer model 2400 series II CHNS/O analyzer. Storage in the upper 80 cm of the soil profile ($g\cdot cm^{-2}$) was then estimated by multiplying the mean carbon concentration (%) and mean bulk density ($g\cdot cm^{-3}$) by the mean thickness (cm) for each horizon. Variance terms were calculated following the product of variance equation presented by Schumacher and Chapman (1954).

Soil CO_2 flux

Within each burned and control stand, 10 sampling points were located in two parallel rows spaced 10 m apart along 50 × 30 m grids. At each sampling point, CO_2 emissions from the surface of the forest floor were measured with a dynamic closed gas exchange system consisting of a nondispersive infrared gas analyzer (IRGA: EGM-1 environmental gas monitor, PP Systems) coupled with an opaque sampling chamber (SRC-1). A detailed description of this system and its operation may be found in Parkinson (1981). CO_2 concentration (ppmv) within the chamber was measured at 8-s intervals over a maximum 2-min period, and the rate of increase used to calculate flux ($g\ CO_2\cdot m^{-2}\cdot h^{-1}$). Care was taken to ensure that initial CO_2 concentration was at or below atmospheric levels (≈360 ppmv). Living moss and vegetation were not removed prior to measurement to limit site disturbance and the subsequent potential for enhanced decomposition and disturbance of root biomass; thus, respiration from living mosses is included as a part of soil flux. Measurements were made weekly during the growing season from May to mid-September 1997.

Environmental variables

Concurrent with each CO_2 measurement, soil temperature was measured adjacent to each flux measurement point at depths of 10 and 20 cm below the surface of the forest floor with digital thermometers. Soil temperatures were also measured weekly throughout the upper 1 m of the soil profile with Type K constantin–copper thermocouples that were installed at six depths (10, 20, 40, 60, 80, and 100 cm) in three soil pits within the aspen and white spruce pairs and in the burned black spruce stand. Because of the presence of permafrost in the control black spruce stand, we were unable to install thermocouples below the organic horizons without disrupting the soil thermal profile. For this reason, we assumed that mean seasonal soil temperature was 0°C for depths at which the soil was frozen for the entire summer. Depths that did not remain frozen were not included in further analysis.

Soil moisture potential was measured using a granular matrix sensor (GMS) (Watermark Irrometer, Riverside, Calif.) placed in the organic horizon immediately above the mineral soil boundary. Calibration of the GMS to soil water potential followed Thompson and Armstrong (1987). Measurements were made weekly from May to August 1997 immediately following the flux measurement.

Concentrations of CO_2 in the soil profile

Except where limited by permafrost, soil gas reservoirs were installed within two soil pits at each site at depths of

Table 1. Chemical and physical characteristics of soil profiles in control white spruce, black spruce, and aspen stands.

Stand and depth (cm)	pH ($CaCl_2$)	C (%)	N (%)	C/N	K ($mmol_c \cdot kg^{-1}$)	Na ($mmol_c \cdot kg^{-1}$)	Ca ($mmol_c \cdot kg^{-1}$)
White spruce							
0–10	6.41	47.16	1.89	25.0	96.51	0.82	600.61
10–20	4.88	1.34	0.09	15.4	4.73	0.47	41.60
20–36	5.24	0.71	0.04	16.9	4.57	0.31	42.37
36–61	5.32	0.32	0.02	13.9	2.22	0.23	16.12
61–86	5.46	2.19	0.13	16.8	2.06	0.43	18.44
Aspen							
0–3	6.33	29.50	1.10	26.8	28.69	1.00	425.17
3–15	5.44	5.85	0.29	20.2	7.27	0.69	109.13
15–50	5.68	1.18	0.09	13.8	2.52	0.89	65.12
50–60	6.14	0.75	0.05	14.9	5.26	1.84	98.95
60–80	6.28	0.10	0.01	11.0	1.97	0.59	36.97
80–100	6.36	0.22	0.01	15.5	2.82	0.77	63.83
Black spruce							
0–8	4.16	26.42	0.74	35.6	11.00	5.10	192.76
8–15	5.80	14.63	0.70	21.0	4.61	5.49	363.32
15–30	6.18	1.02	0.06	16.7	6.91	6.19	167.06
30–56	6.61	0.77	0.04	17.4	9.08	6.18	180.95
56–69	7.89	0.56	0.03	21.4	8.54	5.04	189.70
69–74	7.70	0.68	0.03	21.0	16.10	6.44	288.70
74–83	7.64	0.72	0.03	20.7	12.31	6.71	286.80

Note: Cations, effective cation exchange capacity (ECEC), and cation exchange capacity (CEC) were determined by buffered NH_4Oac. Total carbon and
[a]The sample was dominantly organic, and no texture analysis was done.

10, 20, 40, 60, 80, and 100 cm below the surface of the mineral soil. At the black spruce control site, the soil profile remained frozen into the organic horizons in both 1996 and 1997, which prevented excavation of the soil without altering the thermal properties of the profile. Gas reservoirs consisted of 15-cm segments of PVC pipe perforated with 12.5-cm holes at one end. At each site, a 1-m soil pit was excavated, with care taken to leave one face free of compaction. The perforated end of the reservoir was placed horizontally 10–15 cm into the undisturbed face of the soil pit and the other end sealed with a neoprene stopper and silicon sealant. Two pieces of 0.6-cm insulated copper tubing extended through the stopper to the surface and were sealed at the top with Tygon vacuum tubing and neoprene hose clamps. The pit was then back-filled by horizon and recovered with the original, intact, organic soil profile. Reservoirs were installed in July of 1996 and had 2 years to equilibrate prior to sampling in the summer of 1998. CO_2 concentrations in the reservoirs were measured at 1- to 2-week intervals throughout the summer of 1998 using an EGM-2 IRGA (PP Systems) with a range of 0 – 50 000 ppmv (5%) CO_2.

Statistical analyses

Multiple comparison procedures were performed with the software package AXUM (Math Soft, Cambridge, Mass.) to test for statistically significant differences in temperature, moisture potential, and CO_2 flux among sites. Each data group was tested for normality (Kolmogorov–Smirnov test) and equal variance (Levene median test). 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, then a Tukey (T method) all pairwise multiple comparisons procedure was performed to identify specific differences between groups. Probability and significance levels were set to 0.05.

For trend analysis, data from replicate samples within each stand were averaged to provide a mean value for the plot for a given sampling period. Seasonal patterns of temperature and CO_2 efflux were then analyzed by simple linear regression using date as the independent variable and the mean of the 10 replicate samples collected within the stand at each time period as the dependent variable, such that *n* is the number of sampling dates (Axum 6, Math Soft). When data for a given measurement appeared to depart from the linear model and there was ecological justification, nonlinear curve fitting was used to describe the shape of the relationship. Nonlinear analysis was performed using the Gauss–Newton method of least squares estimation procedure (Axum 6, Math Soft). The level of significance for all analyses was $p < 0.05$.

Results

Carbon storage

Mature black spruce soils contained the largest amount of carbon in the upper 80 cm of the profile, followed by the aspen and the white spruce (Fig. 2). More than 70% of the carbon in the black spruce profile (158.3 $Mg \cdot ha^{-1}$) was stored in the organic horizons, with 111.1 $Mg \cdot ha^{-1}$ in the humic horizon alone. In contrast, the majority of carbon in the aspen (92%) and white spruce (82%) profiles was in the mineral

Mg (mmol$_c$·kg^{-1})	ECEC (mmol$_c$·kg^{-1})	CEC (mmol$_c$·kg^{-1})	BS (%)	Particle size distribution (%) Clay	Silt	Sand	Texture class
79.15	785.80	1521.60	51.1	—[a]	—	—	—
15.21	71.70	256.20	24.2	16.7	65.6	17.7	Silt loam
13.65	63.00	171.40	35.5	8.7	22	69.3	Gravelly sandy loam
4.24	24.20	54.70	41.7	4.4	9.3	86.3	Gravelly loamy sand
4.86	26.40	39.20	65.8	1.6	7.1	91.3	Gravelly sand
92.49	547.40	977.70	56.0	—	—	—	—
27.28	146.00	349.30	41.3	21.4	71.5	8.1	Silt loam
22.52	91.10	184.90	49.2	19.5	72.2	8.3	Silt loam
35.98	142.00	204.40	69.5	15.8	62	22.2	Silt loam
11.94	51.50	77.20	66.7	3.2	2.3	94.5	Gravelly sand
21.40	88.80	125.50	70.8	6.2	36.7	57.1	Gravelly sandy loam
87.12	313.00	1149.00	25.8	—	—	—	—
103.67	478.20	919.90	51.9	—	—	—	—
75.06	255.20	323.80	78.8	27.4	69.0	3.6	Silt loam
84.19	280.40	327.10	85.7	31.6	66.6	1.8	Silty clay loam
62.80	266.10	310.80	85.7	25.9	64.8	9.3	Silt loam
69.93	381.20	416.90	91.4	30.6	68.3	1.1	Silty clay loam
77.53	383.40	411.60	93.1	26.2	68.3	5.6	Silt loam

nitrogen were determined by dry combustion. CEC was measured at pH 8.2. BS, base saturation.

soil. Although some of this carbon may have been derived from carbonates in the parent material (Marion and Oechel 1993), the relatively low pH (5.2–6.4) of these soils indicates that the majority of the carbon in the white spruce and aspen profiles was organic.

Soil temperature

Over the entire growing season (May–August 1997), mean temperatures at both 10 and 20 cm below the surface of the forest floor were significantly warmer in burned than in control stands (Table 3; $p < 0.001$). At 10 cm, mean temperatures were 3.0°C (aspen) to 3.6°C (black spruce) warmer than those in control stands. This temperature difference increased slightly at 20 cm for aspen (from 3.0 to 3.3°C) and white spruce (from 3.6 to 3.8°C). However, in black spruce stands, the temperature difference between burned and control stands nearly doubled from 3.6°C at 10 cm to 6.3°C at 20 cm.

The effect of fire on mineral-soil temperature was most strongly pronounced in the black spruce stands with temperatures in the burned profiles that were 4.8–7.6°C warmer than those in the control (Table 3). The magnitude of this difference was greatest at 40 cm (using the top of the mineral soil profile as a baseline) and declined with increasing depth. Significant temperature increases ($P < 0.001$) were also observed in aspen profiles, with burned soils averaging 2.8–3.3°C warmer than unburned controls. In white spruce stands, temperature differences between burned and control soil profiles ranged between 0.4 and 2.5°C. However, these differences were not statistically significant at depths below 10 cm ($P > 0.05$). With the exception of the control black spruce stand, exponential regression of seasonal mean temperature against depths was highly significant for all soil profiles (P values ranged from <0.005 in the aspen and white spruce stands to 0.002 in the burned black spruce) and explained 94–99% of the variability in the data (Table 3).

Soil temperatures in all stands at 10 and 20 cm below the forest floor surface followed a strong seasonal pattern with maximum temperatures occurring in late July and August (Fig. 3). Second-order polynomial regressions of mean temperature at 10 and 20 cm against Julian date were highly significant ($P < 0.001$) for all stands. In control stands, mean temperatures at 10 cm were close to 0°C in late May, whereas temperatures in burned stands were 3–4°C warmer. In all three systems, a difference in mean temperature between burned and control stands persisted throughout the entire growing season. However, in the aspen and white spruce systems, the ratio of temperatures (10 cm) between burned and control stands decreased linearly throughout the summer (Fig. 4) whereas this relationship was nonlinear for the black spruce pair. Temperatures in mineral soil profiles followed similar seasonal patterns. For all soils at all depths, a second-order polynomial regression of temperature against date was highly significant ($P < 0.0001$) and explained between 84 and 99% of the variability in the data. In general, the strength of this correlation was weakest at 10 cm and increased with depth.

Active layer thaw

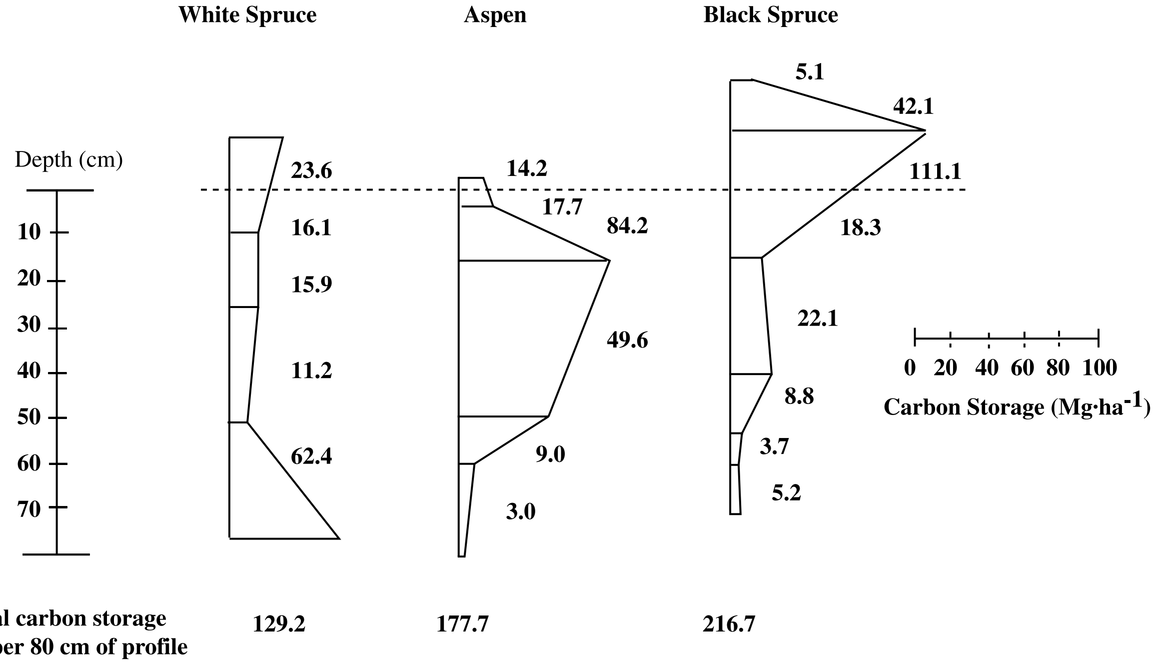
In the burned black spruce stand, warmer soil temperatures corresponded to an increase in the thickness of the active layer (Fig. 5). The control stand remained frozen above

Table 2. A comparison of temperature and precipitation at Tok Junction during study years to the long term means (1954–1999).

	March	April	May	June	July	August	September	October	Annual
Precipitation (cm)									
Mean	0.41±0.46	0.41±0.48	1.40±1.42	5.1±2.5	5.00±2.72	3.15±2.57	1.68±1.42	1.42±1.47	23.42±7.52
1997	0.66	0.25	0.94	4.52	10.85	3.43	1.57	0.74	27.15
1998	0.25	0.08	nd	4.22	4.80	1.27	1.57	1.27	19.35
Temperature (°C)									
Mean	–12.49±3.98	–1.31±2.48	7.07±1.71	12.68±1.51	14.46±1.69	11.90±1.68	5.29±1.59	–5.77±2.49	–4.66±1.43
1997	–15.60	–0.76	8.07	13.97	17.21	11.92	6.44	–10.58	–3.96
1998	–9.92	2.09	nd	13.72	15.61	11.44	5.93	–7.72	–4.84

Note: Data are from National Weather Service, Alaska Region (http://www.wrcc.dri.edu/summary/climsmak.html). nd, no data.

Fig. 2. Carbon storage as a function of depth in aspen, white spruce, and black spruce soil profiles. The broken line represents the top of the mineral soil; all horizons above the broken line are in the organic profile. Values are the estimated carbon storage in each horizon ($Mg \cdot ha^{-1}$). Estimates for organic horizons were determined as the product of the mean thickness of the organic profile at each site and the mean carbon concentration for each organic horizon.



the mineral soil interface until the third week of June (Julian date 172) with a maximum depth of thaw 28 cm at the end of August (Julian date 229). In contrast, the burned soils had already thawed to a depth of 25 cm by mid-May (Julian date 139) and the upper 1 m of the soil profile was completely thawed within another month (Julian date 172).

Soil moisture potential

The high midseason precipitation in the Tanana River valley during the summer of 1997 was reflected in measurements of soil moisture potential (Table 2, Fig. 3). In the aspen and white spruce pairs and the burned black spruce stand, moisture potential declined throughout the first part of the growing season until late July, when heavy rains returned the upper soil profile to near-saturation levels. In contrast, soil moisture in the control black spruce stand remained at or near saturation levels throughout the entire growing season, and there was no noticeable response to the high levels of precipitation in late July. In both the aspen and white spruce pairs, the ratio of moisture potentials in burned to control stands followed a linear pattern throughout the growing season (Fig. 4). However, the opposite direction of the slopes in these two relationships indicates differences in root activity and hydrology.

The response of soil moisture to burning varied depending on the pre-burn drainage characteristics of the system. In the well-drained aspen and white spruce stands, seasonal moisture potentials in the burned stands were significantly higher than in the unburned controls (two-sample Student's *t* test; $P < 0.0001$ for both). The opposite pattern was observed in the more poorly drained black spruce soils in which seasonal mean moisture potentials in the burned stands were approximately significantly lower than in the control ($P < 0.001$).

CO_2 flux

All burned and control stands showed a strong seasonal pattern of CO_2 emissions with maximum rates in late July to mid-August. Second-order polynomial regressions of CO_2

Table 3. Mean summer temperature (May–August 1997) in burned and control stands of aspen, white spruce, and black spruce.

Stand and system	Organic soil temperature (°C)		Mineral soil temperature (°C)					
	10 cm	20 cm	10 cm	20 cm	40 cm	60 cm	80 cm	100 cm
Aspen								
Control	7.7±3.2 (110)	6.3±2.8 (84)	7.6±3.6 (24)	6.4±3.5 (24)	4.8±3.4 (24)	3.8±3.1 (24)	2.5±2.5 (24)	2.0±2.4 (24)
Burned	10.7±3.0 (109)	9.6±2.4 (88)	10.4±3.1 (23)	9.1±3.3 (23)	7.9±3.4 (23)	6.6±3.8 (23)	5.7±3.6 (23)	5.3±3.5 (23)
	3.0***[a]	3.3***	2.8*	2.7*	3.1*	2.8*	3.2*	3.3*
White spruce								
Control	7.8±3.1 (110)	6.3±2.4 (100)	9.3±2.7 (18)	8.5±2.7 (18)	7.0±2.7 (18)	6.0±2.8 (18)	5.4±2.8 (18)	5.0±2.8 (18)
Burned	11.4±3.1 (110)	10.1±2.4 (79)	11.8±2.9 (16)	10.2±3.0 (16)	8.7±2.8 (16)	7.6±2.8 (16)	6.3±2.8 (16)	5.4±2.8 (16)
	3.6***	3.8***	2.5*	1.7	1.7	1.6	0.9	0.4
Black spruce								
Control	6.8±3.2 (110)	2.7±1.7 (121)	—[b]	—	0.0[c]	0.0[c]	0.0[c]	0.0[c]
Burned	10.6±3.1 (110)	9.2±2.7 (120)	13.0±3.8 (22)	10.7±2.9 (22)	7.6±3.2 (22)	5.6±3.0 (22)	5.1±2.6 (22)	4.8±2.6 (22)
	3.6***	6.5***	—	—	7.6*	5.6*	5.1*	4.8*

Note: Depths in organic horizons were measured relative to the surface of the forest floor. Depths in mineral horizons were measured relative to the top of the mineral soil. Values for control and burned stands are means ± SDs of all measurements collected; the number of samples (n) is provided in parentheses. Because of permafrost in the control black spruce stand, no thermocouples were installed in the mineral soil. For depths at which the soil remained frozen all winter, mean temperature was assumed to be 0°C.

[a]Values are the mean differences between the control and burned stands. Asterisks indicate that the differences were significantly different from 0: *, $P < 0.05$; ***, $P < 0.001$.

[b]No temperature measurements were collected.

[c]Soil was frozen throughout the entire summer season; mean temperature was assumed to be 0°C.

flux against Julian date were significant ($p < 0.05$) for all stands (Fig. 3) and explained most of the variation in the control white spruce and aspen stands ($R^2 = 0.85$ and 0.80, respectively). With the exception of the control black spruce stand, all stands experienced a sharp peak in respiration during the third week of July (Julian dates 208 and 209) that corresponded temporally to record high levels of precipitation (Table 2; National Weather Service 2000).

Within each forest system, mean soil CO_2 flux from the burned stand was significantly lower than from its control ($p < 0.05$) (Fig. 3). For both aspen and white spruce stands, the ratio of emissions from burned to control stands was greatest in the early part of the growing season and then decreased at a linear rate throughout the summer (Fig. 4). The rate of decrease was greatest in the aspen stands in which CO_2 emissions from burned and control stands were nearly equal at the start of the growing season in May (ratio = 0.85) and decreased to approximately one-third (36%) of emissions from the control stand by late August. In contrast, for black spruce stands, the ratio of emissions between burned and control stands did not follow a linear pattern throughout the growing season.

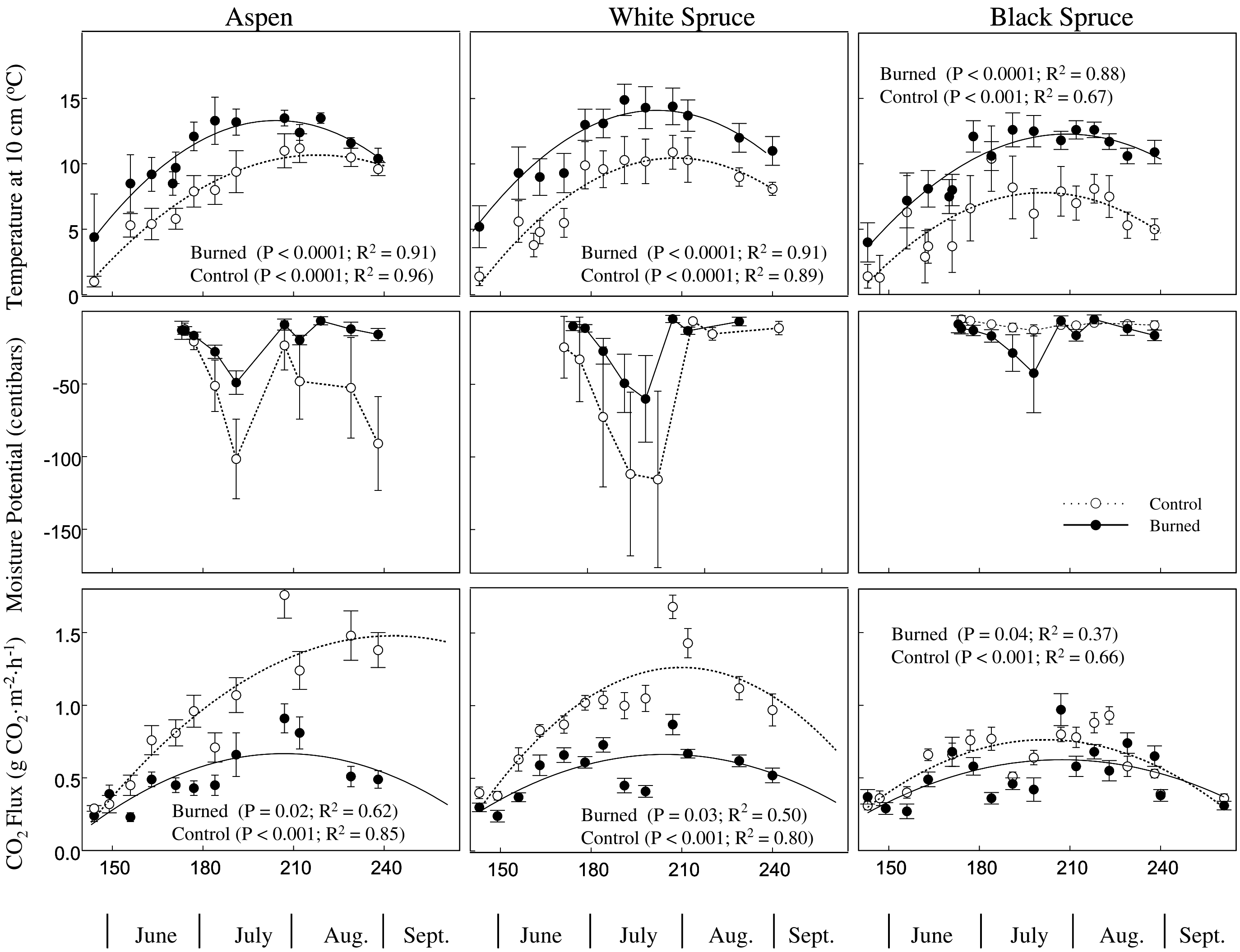
Environmental controls on soil respiration

The environmental factor most strongly correlated with CO_2 flux differed in control and burned stands. Linear regressions of mean respiration on mean temperature at 10 cm were statistically significant ($p < 0.05$) for all of the control stands as well as for the burned aspen stand (Fig. 6). In the control aspen stand, the relationship between CO_2 flux and temperature was slightly stronger at 20 cm ($R^2 = 0.83$ at 20 cm compared with $R^2 = 0.80$ at 10 cm; $P < 0.001$ for both). Surface CO_2 emissions were also highly correlated with temperature in the mineral soil profile in both the control and burned aspen stands ($R^2 = 0.76$–0.82 and 0.65–0.78, respectively) and the control white spruce stand ($R^2 = 0.57$–0.78) (Table 4). In general, the strength of this correlation decreased with depth. As with temperatures in the upper profile, relationships between CO_2 flux and mineral soil temperature were not statistically significant for either the burned white or black spruce stands.

An exponential regression of each CO_2 measurement against the corresponding soil temperature at 10 cm was highly significant for all stands ($p < 0.001$); this relationship was used to determine Q_{10} values at 10 cm (Table 5). For all forest systems, Q_{10} values were lower in burned stands than in unburned controls. In the aspen pair, Q_{10} values in the burned stand were 31% lower than in the control, compared with a 37% reduction in the white spruce stand. Although the regression of CO_2 flux against soil temperature was statistically significant ($P < 0.001$) in the burned black spruce stand, the strength of this relationship was very low ($R^2 = 0.06$) and this relationship is not meaningful for predicting temperature response in this stand.

In the burned white and black spruce stands, carbon emissions were most strongly correlated with soil moisture potential (Fig. 6). A linear regression of mean weekly CO_2 flux on mean soil moisture potential was significant for both of these stands ($R^2 = 0.63$ and 0.40, $P = 0.02$ and 0.05, respectively). Although the period of peak decline in surface soil moisture potential in burned stands appears to be temporally

Fig. 3. Seasonal patterns of soil temperature (10 cm), soil moisture potential at the organic–mineral boundary, and soil CO_2 flux in soils of three forest systems (May to late August 1997). For temperature plots, values are means ± SDs of 10 measurements; for moisture and CO_2 flux measurements, values are means ± SEs of 10 measurements. For temperature and CO_2 flux, data were fit with second-order polynomial regression models using sampling date as the independent variable and the mean of the 10 replicate samples collected within the stand at each time period as the dependent variable. For moisture data, a value of 0 indicates that the soil is saturated. GMS sensors were placed in the humic horizon (black spruce), mesic horizon (white spruce), or A horizon (aspen).



correlated with decreased rates of soil respiration in all stands, a regression of soil respiration against water potential was not statistically significant for the burned aspen stand (P = 0.49) or any of the three control systems (P = 0.23, 0.44, and 0.39 for aspen, white spruce, and black spruce, respectively).

To isolate the effects of temperature and moisture on soil CO_2 flux, linear multiple regression analyses were conducted for each burned and control system with mean temperature and mean moisture as the independent variables and mean CO_2 flux as the dependent variable. Multiple regressions were statistically significant for the burned and control white spruce stands (R^2 = 0.69 and 0.74, P = 0.05 and 0.03, respectively) and the control aspen stand (R^2 = 0.91, P = 0.03) and improved the fit of the model. However, with the exception of the control white spruce stand, multiple regression did not change the fundamental relationships between temperature, moisture potential, and CO_2 flux in burned and control stands as shown in Fig. 6. For the control white spruce stand, partial regression on moisture potential with temperature (10 cm) held constant was statistically significant (P = 0.04), whereas the simple linear regression was not, potentially reflecting interactions between soil temperature and soil moisture in this system.

CO_2 concentrations in the soil profile

At all depths, CO_2 concentrations in soil profiles of unburned aspen and white spruce exhibited a distinct increase throughout the growing season (Fig. 7). The magnitude of seasonal increase was greater in the aspen stand (3200–5900 ppm) with a peak in CO_2 concentration at 40 cm corresponding to the primary rooting zone. In contrast, CO_2 concentrations in burned aspen and white spruce profiles declined at most depths throughout the growing season. In the burned aspen stand, CO_2 concentrations in the upper part of the profile (10–60 cm) declined between June and Au-

Fig. 4. Ratio of soil temperature (10 cm), soil moisture potential, and CO_2 flux from burned and control stands as a function of Julian date. Data were fit using a linear regression model through the ratio of mean values for each sampling date. ns, regression was not significant ($P > 0.05$).

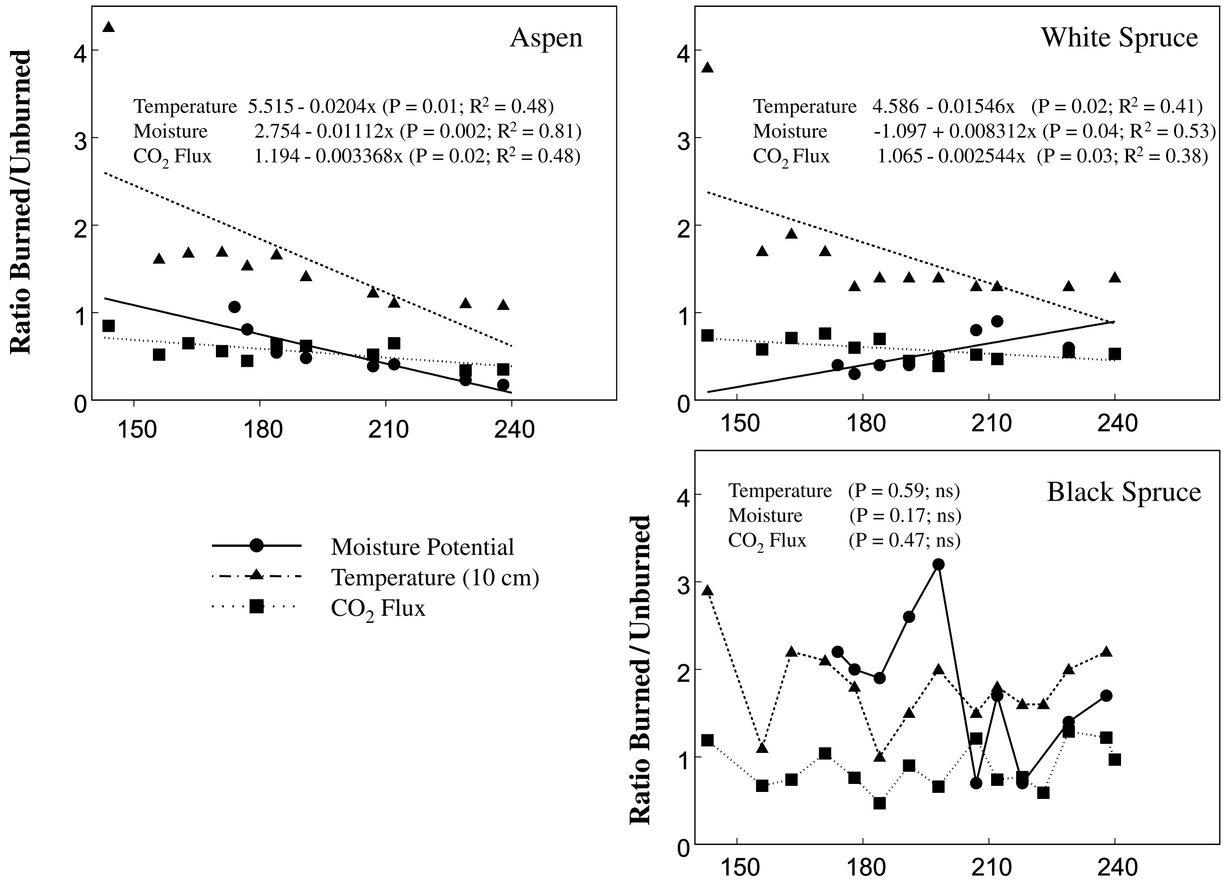


Fig. 5. Seasonal active layer thaw in a burned and mature black spruce stand (May to late August 1997). Values are means ± SDs of 10 measurements. Baseline is the top of the mineral soil. Depths > 0 indicate organic soils; depths < 0 indicate mineral soil. Data were fit using a linear regression model through the mean value for each sampling date.

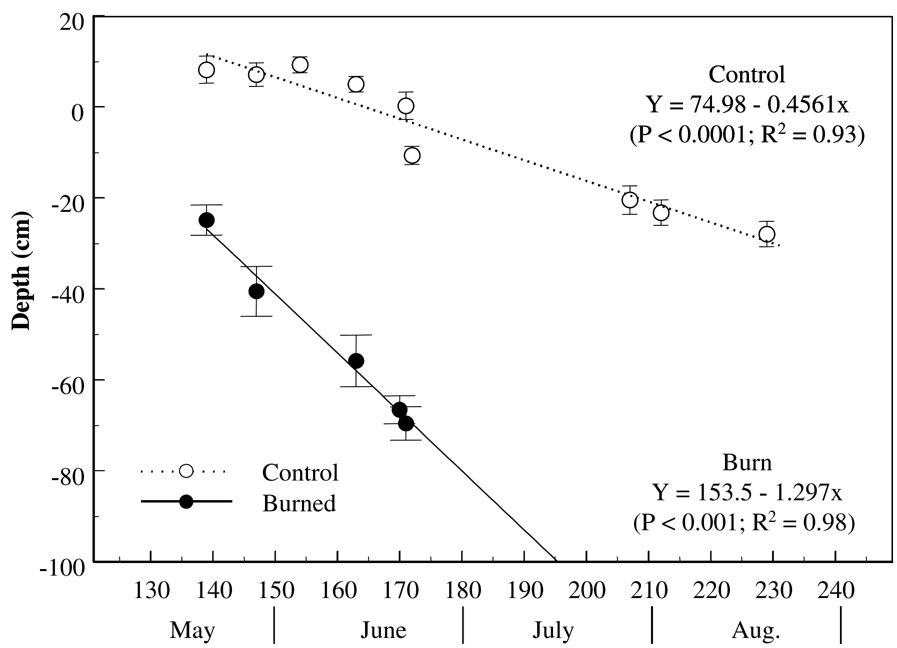
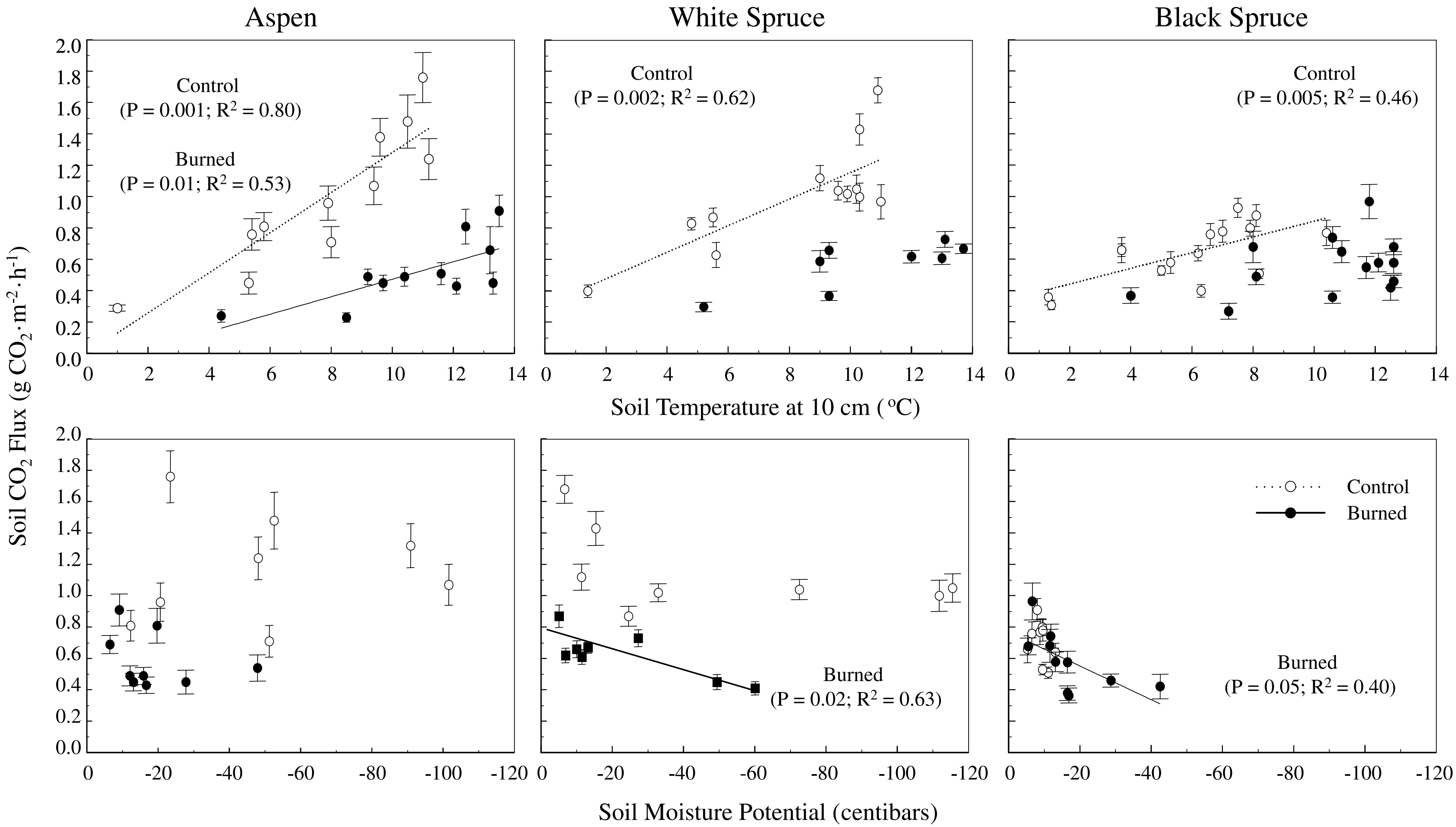


Fig. 6. Soil CO_2 flux as a function of temperature (10 cm) and moisture potential at the organic–mineral interface. Values are means ± SEs of 10 measurements. Data were fit with a linear regression model through the mean value for each sampling date. Only significant correlation coefficients are shown.



gust; below 60 cm, concentrations increased. In the white spruce profile, CO_2 concentrations were vertically homogenous in May and June. Concentrations in the upper part of the profile (0–20 cm) increased slightly in July and August, whereas CO_2 concentrations in the remainder of the profile declined by as much as 60%. Mean CO_2 concentrations in the burned black spruce stand followed the same pattern observed in the control aspen and white spruce stands with a steady increase throughout the growing season. The greatest increase in CO_2 production occurred near the base of the profile with a fourfold increase occurring over the growing season at depths between 40 and 100 cm.

Early in the growing season, CO_2 profiles in the two control stands (white spruce and aspen) were relatively homogenous with a mean gradient in the upper 1 m of 2.1 $ppm \cdot cm^{-1}$ (white spruce) and 8.2 $ppm \cdot cm^{-1}$ (aspen). By the middle of August, these gradients had increased to 9.6 $ppm \cdot cm^{-1}$ (white spruce) and 20.9 $ppm \cdot cm^{-1}$ (aspen). In contrast, concentration gradients in burned white spruce and aspen stands were negative in late May and had a shallower slope than the corresponding control late in the summer (0.52 $ppm \cdot cm^{-1}$ in the white spruce, 13.12 $ppm \cdot cm^{-1}$ in the aspen). Concentration gradients in the burned black spruce stands were steeper than in all other stands with a mean increase of 3.49 $ppm \cdot cm^{-1}$ in late May and 32.95 $ppm \cdot cm^{-1}$ in August.

Table 4. Equations and summary statistics for regressions of respiration on temperature at six depths in mineral soil profiles of white spruce and aspen.

Site and depth (cm)	Regression equation	P	R^2
Control aspen			
10	$0.2860\ e^{0.1425x}$	<0.0001	0.82
20	$0.3253\ e^{0.1461x}$	<0.0001	0.83
40	$0.4036\ e^{0.1499x}$	<0.001	0.84
60	$0.4508\ e^{0.1598x}$	<0.001	0.81
80	$0.5138\ e^{0.1874x}$	<0.001	0.73
100	$0.5643\ e^{0.1909x}$	0.001	0.76
Control white spruce			
10	$0.3135\ e^{0.1185x}$	<0.001	0.78
20	$0.3520\ e^{0.1155x}$	0.001	0.78
40	$0.4082\ e^{0.1196x}$	<0.0001	0.78
60	$0.4955\ e^{0.1068x}$	0.003	0.68
80	$0.5453\ e^{0.1009x}$	0.008	0.60
100	$0.5828\ e^{0.09597x}$	0.01	0.57
Burned aspen			
10	$0.1263\ e^{0.1293x}$	<0.001	0.78
20	$0.1529\ e^{0.1265x}$	<0.001	0.74
40	$0.1806\ e^{0.1246x}$	<0.001	0.73
60	$0.2229\ e^{0.1196x}$	0.001	0.71
80	$0.2480\ e^{0.1182x}$	0.002	0.65
100	$0.2574\ e^{0.1198x}$	0.002	0.64

Note: Depths were measured using the top of the mineral soil as the baseline.

Discussion

Soil CO_2 flux represents an integrated response to many biophysical processes in the soil, all of which respond differently to environmental parameters. In these three systems, the low thermal diffusivity and high water-holding capacity of moss-derived organic material resulted in significant differences in soil thermal and moisture characteristics between stands with well-developed organic profiles (black spruce) and those without (aspen and white spruce). Ultimately, these differences influenced the ways in which these soils responded to fire disturbance, the magnitude of post-fire CO_2 flux, and the ecological significance of these emissions.

Table 5. Q_{10} functions and equations for exponential regressions of soil respiration on soil temperature (10 cm) in burned and control stands of aspen, white spruce, and black spruce.

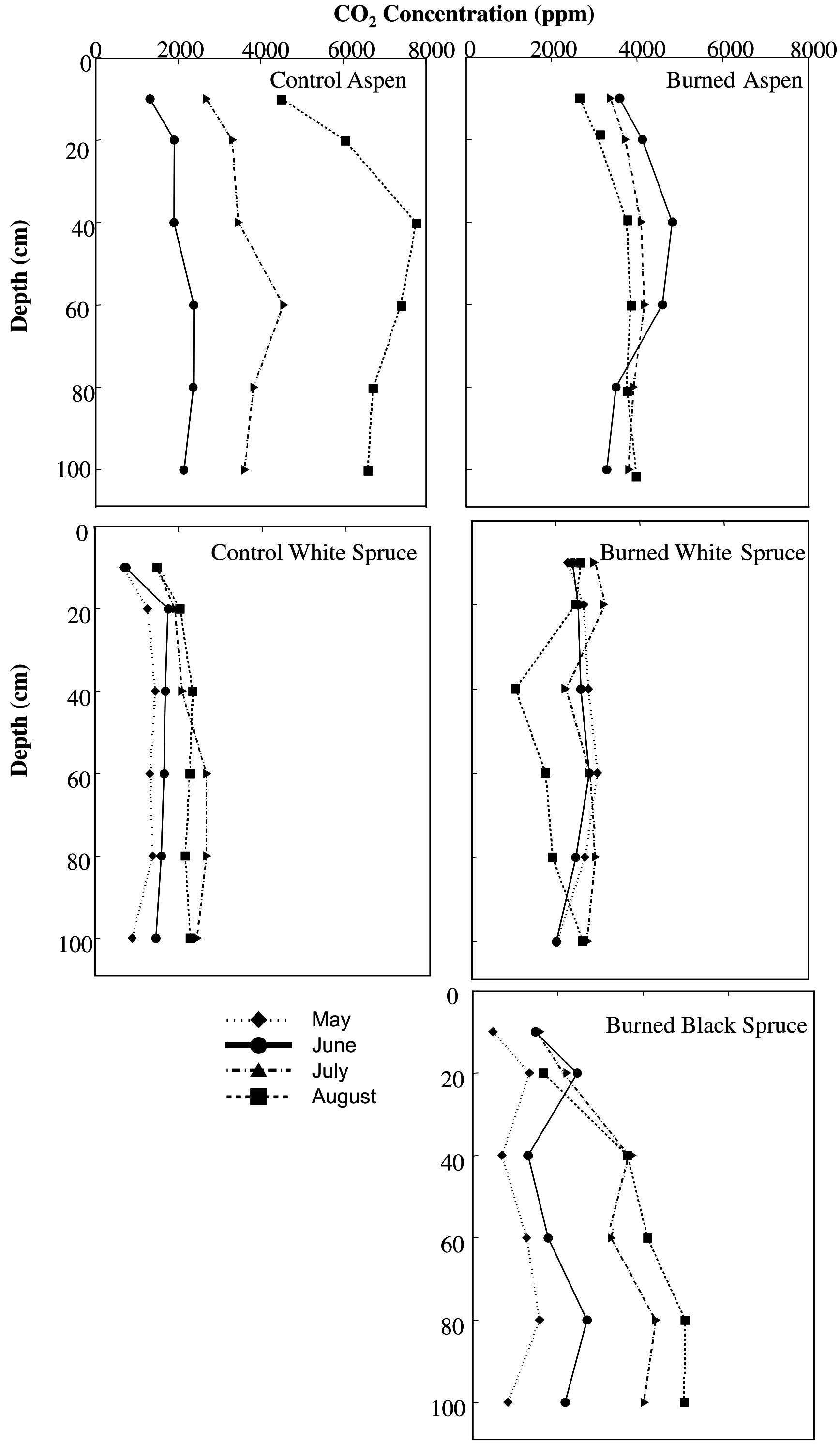
System and treatment	Q_{10} 10 cm	Regression equation	P	R^2
Aspen				
Control	4.71	$0.2474\ e^{0.155x}$	<0.0001	0.50
Burned	3.23	$0.1234\ e^{0.1171x}$	<0.0001	0.33
White spruce				
Control	2.73	$0.4071\ e^{0.1003x}$	<0.0001	0.41
Burned	1.71	$0.2775\ e^{0.05339x}$	<0.0001	0.21
Black spruce				
Control	2.39	$0.3438\ e^{0.08711x}$	<0.0001	0.24
Burned	1.40	$0.584\ e^{0.03399x}$	<0.001	0.06

Soil temperature and moisture

In mature black spruce stands, thick organic-rich profiles retain moisture near the surface and limit heat gain from the atmosphere, resulting in cooler and wetter conditions near the soil surface that promote the development of permafrost (Bonan 1992; Bonan and Van Cleve 1992; Fig. 3). In contrast, the less-developed organic profiles and lack of moisture-holding organic materials near the surface in mature aspen and white spruce stands facilitated a more rapid transfer of heat, moisture, and oxygen through the soil profile, resulting in warmer and drier subsoil conditions (Fig. 3). Following fire, darker soil surfaces, the elimination of canopy shading, and the loss of insulating organic materials allowed for greater penetration of heat into the soil profile and resulted in significant increases in soil temperatures throughout the upper 1 m of the profile in all forest types (Fig. 3). These findings are in general agreement with results from a number of studies in experimental (Viereck et al. 1979; Dyrness and Norum 1983) and naturally burned boreal systems (Viereck and Dyrness 1979; Dyrness 1982; Brown 1983; Mackay 1995; Swanson 1996) that have found increased soil temperature and active layer thickness resulting from changes in local energy balance in the months to years following fire.

The effect of fire on soil moisture differed depending on the pre-burn drainage characteristics of the forest system. In well-drained sites (aspen and white spruce stands), increased moisture in the upper profiles of burned stands was consistent with lower plant water demand resulting from removal of vegetation during combustion. In contrast, in the poorly drained black spruce soils, increased thaw depth and removal of moisture-retaining organic matter from the soil surface improved soil drainage and were correlated with significantly drier soils following fire ($P < 0.001$) (Fig. 3).

Fig. 7. Seasonal patterns of CO_2 concentrations as a function of depth (May–August 1998) in burned and control stands of aspen, white spruce, and black spruce. Values are the means of biweekly measurements in two soil pits.



The difference in the direction of the slopes for ratios of moisture potentials in aspen and white spruce pairs (Fig. 4) reflects differences in water demand and soil drainage in these two systems. In the control aspen stand, increased root activity during the second half of the summer resulted in greater moisture demand and a consistent reduction in soil moisture potential relative to its burned counterpart. Although root activity also increased in the control white spruce stand, the coarser soil texture limited the water-holding capacity of the burned stand and resulted in a slight increase in the ratio of soil moisture potentials during the summer. The lack of a linear relationship between moisture potentials in the black spruce pairs indicates a more complicated hydrology caused by active layer thaw and thick, moisture-retaining organic layers at the soil surface.

CO_2 flux

In boreal soils, CO_2 flux from the soil surface represents the net result of microbial decomposition, root respiration, and moss respiration (e.g., Schlentner and Van Cleve 1985; Bonan 1992; Richter et al. 2000; O'Neill et al. 2003). One of the complications in interpreting the ecological significance of surface flux data is the difficulty in distinguishing between CO_2 contributions from autotrophic (root) and heterotrophic (microbial) sources, since only the latter represents a loss of stored carbon from the system. In this study, the seasonal patterns of CO_2 flux (Figs. 3 and 4) (Rayment and Jarvis 2000), the response of flux rates to changes in temperature (Fig. 6), and the calculated Q_{10} values (Table 5) are all consistent with a reduction in root activity following fire. In particular, the declining ratio of emissions between burned and control aspen and white spruce stands throughout the growing season indicates greater levels of root activity in the control stands later in the summer season. The burned stands have fewer roots and hence a smaller increase in CO_2 during the growing season. Similarly, the lower Q_{10} values and the reduction in the slope of the temperature response curve in burned stands both provide support for this hypothesis of lowered root activity following fire. Although there is undoubtedly a reduction in root activity in the burned black spruce stand as well, the evidence for this is confounded by the increased volume of aerated soil contributing to CO_2 emissions as a result of soil warming and permafrost thaw. For example, on several dates, the ratio of emissions from burned and unburned stands is greater than 1 (Fig. 4), potentially indicating that metabolic activity in the burned profile was greater than that in the control despite the apparent reduction in root biomass. However, when these CO_2 fluxes were normalized by volume (i.e., soil flux divided by the thickness of unfrozen soil (Fig. 5)), emissions were 1.5–3.0 times larger in the control black spruce stand throughout the growing season and the burned to control ratio was less than 1. These results are in agreement with Rayment and Jarvis (2000) who found that seasonal variation in soil CO_2 flux rates was strongly correlated with the volume of biologically active soil.

Mean seasonal CO_2 emissions from control stands measured in this study were higher than those reported for other boreal systems (Table 6). This difference can be attributed to three factors. Firstly, the EGM-1 IRGA system used in this study was configured with an opaque chamber that precluded measurement of carbon uptake during moss photosynthesis. As a result, measurements may have overestimated soil respiration by an amount equal to the rate of moss activity. Secondly, all soil flux measurements in this study were collected mid-day, during the hours of peak CO_2 production, and would necessarily report higher values than studies that integrated measurements over a diurnal period. Finally, in control stands, the high porosity of moss creates some uncertainty in chamber volume and increases the risk of mass flow (Goulden and Crill 1997). Measurements of CO_2 exchange over moss surfaces are also sensitive to transient changes in moss physiology and moisture content. As a result of these types of uncertainties, CO_2 flux measured in moss-dominated boreal forests may vary in response to differences in chamber design and methodology (Norman et al. 1996; Goulden and Crill 1997).

Response of CO_2 flux to environmental parameters

In these three forest systems, soil respiration was responsive to either soil temperature or soil moisture, whichever was most limiting at the time of measurement. These results are in general agreement with findings from other studies of soil respiration in undisturbed temperate and upland boreal ecosystems (Ino and Monsi 1969; Bunnell and Tait 1974; Flanagan and Bunnell 1980; Flanagan and Veum 1974; Schlentner and Van Cleve 1985). However, temperature–moisture dynamics in these fire-disturbed systems differ in that the environmental factor limiting rates of soil respiration changed in response to fire.

In control stands, particularly of black spruce, soils were relatively cold and moist for the first half of the growing season (Fig. 3). These low temperatures represent a major limitation on soil activity (Flanagan and Veum 1974; Tryon and Chapin 1983; Bonan 1989, 1992; Bonan and Van Cleve 1992), and as a result, soils in these mature stands were highly responsive to changes in soil temperature but relatively insensitive to fluctuations in moisture potential in the early part of the growing season (Fig. 6). Similar results were reported by Rayment and Jarvis (2000) for a black spruce stand in Saskatchewan, Canada. During mid-summer, when soil temperatures were no longer limiting, soil carbon flux became increasingly sensitive to low precipitation and declining moisture potentials. In contrast, in burned black and white spruce systems, changes in the local energy balance result in increased soil temperatures that were no longer limiting for root and microbial activity, and as a result, soil respiration became increasingly responsive to changes in soil moisture. The lack of a similar moisture response in the burned aspen stand may be attributed to the rapid reestablishment of aspen seedlings following fire, which resulted in moisture and temperature responses that were more similar to those observed in control stands.

Despite the fact that relationships between mean moisture potential and mean CO_2 flux were not statistically significant in control stands, evidence from seasonal patterns of soil respiration suggests that these soils are not entirely unresponsive to changes in soil moisture conditions. Following the intense period of rainfall at the end of July (Julian date 207) during which 9.6 cm of rain fell in 1 week, soil CO_2 flux increased by a factor of two in all stands except the control black spruce (Fig. 3). The response of control soils to less dramatic changes in soil moisture may not have been fully reflected in our measurements because of the placement of GMS sensors in the upper soil profile above the zone of primary rooting. Future studies should address moisture conditions throughout the entire rooting zone of the mature forest.

In addition, the present analysis may not account for all of the effects of moisture deficit on CO_2 flux because of the potential for confounding effects from soil temperature. Because of the installation of GMS sensors after the initiation

Table 6. Comparison of soil flux rates measured in this study with data reported in the literature.

Respiration ($g\ CO_2 \cdot m^{-2} \cdot h^{-1}$)	Source	Location	Method
Aspen			
0.55–0.66	Schlentner and Van Cleve 1985	Fairbanks, Alaska	Soda lime
0.59–0.68	Russell and Voroney 1998	Canada	Li-COR (IRGA)
0.36±0.17[a]	Savage et al. 1997	Manitoba, Canada	Static chamber
0.9 1±0.56	This study	Tanana River valley, Alaska	IRGA
White spruce			
0.42±0.06	Billings et al. 1999	Fairbanks, Alaska	Static chamber
0.18	Gordon et al. 1987	Alaska	
0.63	Schlentner and Van Cleve 1985	Alaska	Soda lime
0.94±0.42	This study	Tanana River valley, Alaska	IRGA
Black spruce			
0.53	Schlentner and Van Cleve 1985	Fairbanks, Alaska	Soda lime
0.08±0.05	Savage et al. 1997	Manitoba, Canada	Static chamber
0.04 to 0.76	Moosavi and Crill 1997	Manitoba, Canada	Static chamber
0.46±0.15	Funk et al. 1994	Fairbanks, Alaska	Phytotron
0.15 to 0.76	Burke et al. 1997	Manitoba, Canada	Static chamber
2.22[b]	Rayment and Jarvis 2000	Saskatchewan, Canada	Open chamber gas exchange cuvette
0.56±0.25	This study	Tanana River valley, Alaska	IRGA

[a]Values are means ± SDs.
[b]Seasonal maximum value.

of the flux measurements, the number of sampling dates included in the multiple regression analysis was relatively small (n = 7–9) and measurements did not fully capture temperature–moisture dynamics at the beginning of the growing season. The potential impact of these interactions is most apparent in the control aspen and white spruce stands where soil flux at high moisture potentials was measured across a wide range of temperatures. These interactions might be less pronounced in burned stands, because soil temperatures increased more rapidly early in the growing season such that high moisture potentials were associated with a narrower range of soil temperatures.

Belowground CO_2 production

The structure of CO_2 profiles in the soil are indicative of the microbial and root processes active in different soil layers at any given time (De Jong and Schaeppert 1972; Zimov et al. 1993; Russell and Voroney 1998; Burton and Beauchamp 1994). Most soil profiles demonstrate a sharp increase in CO_2 concentration with depth, reflecting both the presence of CO_2 sources (root and microbial) and changes in diffusivity that cause unequal mixing throughout the profile. Both the seasonal and depth gradients in control aspen and white spruce stands reflect the dominant role that root respiration plays in these systems. As soils warmed (Fig. 3) and both root metabolism and microbial activity increased, CO_2 concentration profiles developed a steeper gradient with peak concentrations at 30–60 cm corresponding to the primary zone of rooting (Fig. 7). Following fire, burned aspen and white spruce stands both demonstrated a seasonal decline in CO_2 concentrations despite warming soil temperatures and a reduction in CO_2 concentration gradients, a combination which argues either for the absence of a significant CO_2 source or the presence of a strong CO_2 sink at depth.

The coarse texture and oxidized color of the subsoils in these stands make the presence of a large sink due to methanogenesis unlikely. However, the absence of a CO_2 source is consistent with a number of post-fire changes in soils conditions, including (*i*) a reduction in root biomass and root activity within the profile, (*ii*) low levels of microbial activity resulting from a limitation in available energy sources (e.g., root exudates), or (*iii*) increased diffusivity of the soil profile resulting from the loss of surface organic matter (Burton and Beauchamp 1994). The relatively high CO_2 concentrations measured at the beginning of the growing season (Fig. 7) may be a reflection of the production of labile forms of carbon by freeze–thaw action in the spring (Schimel and Clein 1996). In the absence of other CO_2 sources, once this labile carbon is depleted, CO_2 concentrations decline. Similar patterns of high spring carbon flux resulting from the release of stored decomposition products have been noted in both Canadian (Winston et al. 1997) and Siberian (Zimov et al. 1993) boreal forests.

In the burned black spruce stand, vertical and seasonal CO_2 gradients were more similar to those observed in the control aspen and white spruce stands than to the other burned stands. Throughout the 1998 measurement period, mean CO_2 concentrations increased sharply with depth at a gradient greater than that observed in the control stands (Fig. 7). These increased CO_2 concentrations occurred below the primary zone of rooting (10–20 cm) and were not associated with a change in soil texture or diffusivity (Table 1), suggesting that the source of this CO_2 might be attributed to the decomposition of carbon stored at depth. Incubations studies on Canadian (Goulden et al. 1998) and Alaskan (O'Neill 2000) black spruce soils suggest that decomposition of these deep organic materials is regulated more by temperature limitations than by chemical protection. Given the temperature increase of 5–8°C measured in this study combined with a source of soil carbon at depth (Table 1) and an expanded volume of aerobic soil, it is reasonable to expect that rates of decomposition might be increased following fire (e.g., Richter et al. 2000; O'Neill et al. 2003). For example, in a study of a black spruce system in boreal Canada, Goulden et al. (1998) attributed a release of 0.5–1.5 Mg C·ha^{-1}·year^{-1} to enhanced decomposition in recently thawed and warming black spruce soils. However, more detailed isotopic analysis is necessary to conclusively determine the source of the carbon in this study.

Conclusions

Many models of soil carbon dynamics use moisture and soil temperature in the upper part of the profile (typically 10 cm) to drive rates of soil respiration (e.g., Ino and Monsi 1969; Bunnell et al. 1977; Singh and Gupta 1977; Schlentner and Van Cleve 1985; Bonan 1989; Bonan and Van Cleve 1992; Thierron and Landelout 1996). Results from this study suggest that while these environmental variables can explain as much as 90% of the variability in mature, well-drained aspen and white spruce stands, these models may be less effective at predicting patterns of CO_2 flux in burned stands and in poorly drained black spruce systems.

In general, soil temperature at 10 cm was the best predictor of rates of carbon exchange in control stands, whereas burned soils were more sensitive to changes in soil moisture potential. In aspen and white spruce systems, seasonal changes in the ratio of burned control CO_2 fluxes and the patterns of belowground CO_2 production are consistent with a large reduction in root activity following fire. Although dynamics in black spruce systems appear to be more complicated, surface CO_2 measurements and CO_2 concentration profiles suggest that increases in soil temperature and improved drainage following fire may result in both a reduction in root activity and enhanced rates of decomposition of stored organic matter.

Under a global warming scenario, warmer surface temperatures and increased prospects for summer drought are expected to increase both the frequency and severity of wildfires in northern latitudes (Wotton and Flannigan 1993; Stocks et al. 2000). Recent evidence from chronosequence studies suggests that post-fire changes in soil temperature and CO_2 flux in black spruce systems may persist for as long as one to two decades after fire disturbance (O'Neill et al. 2003; Richter et al. 2000) resulting in a net loss of carbon from the system that is equal or greater than the amount of carbon released during combustion itself. Soil warming following fire can also extend the length of time that the soil remains unfrozen (Fig. 3), potentially providing a source for carbon emissions during the fall and even winter (Winston et al. 1997; Zimov et al. 1993). Given the extent of black spruce forests, the large amounts of carbon stored in these soils, and the sensitivity of these systems to changes in soil temperature and moisture, post-fire decomposition of subsoil organic materials represents an important loss of stored organic carbon to the atmosphere that needs to be incorporated into regional carbon models.

Acknowledgments

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