

Interactive Effects of Fire, Soil Climate, and Moss on CO₂ Fluxes in Black Spruce Ecosystems of Interior Alaska

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ABSTRACT

Fire is an important control on the carbon (e) balance of the boreal forest region. Here, we present findings from two complementary studies that examine how fire modifies soil organic matter properties, and how these modifications influence rates of decomposition and C exchange in black spruce (*Picea mariana*) ecosystems of interior Alaska. First, we used laboratory incubations to explore soil temperature, moisture, and vegetation effects on CO₂ and DOC production rates in burned and unburned soils from three study regions in interior Alaska. Second, at one of the study regions used in the incubation experiments, we conducted intensive field measurements of net ecosystem exchange (NEE) and ecosystem respiration (ER) across an unreplicated factorial design of burning (2 year post-fire versus unburned sites) and drainage class (upland forest versus peatland sites). Our laboratory study showed that burning

reduced the sensitivity of decomposition to increased temperature, most likely by inducing moisture or substrate quality limitations on decomposition rates. Burning also reduced the decomposability of *Sphagnum*-derived organic matter, increased the hydrophobicity of feather moss-derived organic matter, and increased the ratio of dissolved organic carbon (DOC) to total dissolved nitrogen (TDN) in both the upland and peatland sites. At the ecosystem scale, our field measurements indicate that the surface organic soil was generally wetter in burned than in unburned sites, whereas soil temperature was not different between the burned and unburned sites. Analysis of variance results showed that ER varied with soil drainage class but not by burn status, averaging 0.9 ± 0.1 and 1.4 ± 0.1 g C m⁻² d⁻¹ in the upland and peatland sites, respectively. However, a more complex general linear model showed that ER was controlled by an interaction between soil temperature, moisture, and burn status, and in general was less variable over time in the burned than in the unburned sites. Together, findings from these studies across different spatial scales suggest that although fire can create some soil climate conditions more conducive to rapid decomposition, rates of C release from soils may be constrained following fire by changes in

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moisture and/or substrate quality that impede rates of decomposition.

INTRODUCTION

The boreal forest region accounts for 16% of the Earth's terrestrial land mass but contains approximately 27% of the world's vegetation carbon (C) (McGuire and others 2002) and between 25 and 30% of the world's soil C (300–500 Pg C; Dixon and others 2002). The majority of soil C at northern latitudes is found in deep deposits of organic soil in peatlands and forests underlain by permafrost (Post and others 1982; Gorham 1991; Smith and others 2004),

which accumulates where CO₂ fixation through plant production is greater than C released through microbial decay, dissolved export, or disturbance losses such as fire. Due to this imbalance, soils in boreal regions have served as an important reservoir for terrestrial C since the end of the last ice age (12000–18000 y ago; Harden and others

1992). At high latitudes, permafrost degradation may expose deep soil C to warmer temperatures and enhanced decomposition (Goulden and others 1998; Turetsky 2004; Carrasco and others 2006). As a result, the sensitivity of decomposition to a changing climate may largely determine whether boreal ecosystems will continue to function as a net C sink or switch to a C source (Cox and others 2000).

Fire is a particularly important control on the C balance of the boreal forest (Kasischke and others 1995, 2000; Harden and others 2000). And fire return intervals and fire severity appear to have increased over the past several decades in North America (Kasischke and Turetsky 2006). In addition to the immediate release of stored C to the atmosphere through organic matter combustion, fire also modifies soil conditions, which may affect C exchange for decades following the burn (Richter and others 2000; O'Neill and others 2002,

2003). Fire has the capacity to alter controls on decomposition, through changes in soil temperature (Vioreck and others 1983), soil moisture (Imeson and others 1992; O'Neill and others

2002), microbial communities (Fritze and others 1994; Waldrop and others 2003, Hart and others 2005; Waldrop and Harden 2008), and/or organic matter content and quality (Johnson and Curtis 2001). For example, decreased albedo during the snow-free period immediately following fire (~1–2 years post-fire; Chambers and Chapin 2002; Liu and others 2005) lead to an increase in absorption

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of solar radiation and can increase soil temperature during the summer, and stimulate rates of decomposition. After a few years post-fire, albedo effects are likely reversed as vegetation recovers (Randerson and others 2006). Fire can increase soil moisture content (Klock and Helvey 1976; Moore and Keeley 2000) via reduced rates of evapotranspiration and interception (Moody and Martin 2001, but can also decrease soil moisture content (Imeson and others 1992; Harden and others 2006) due to changes in hydrophobicity, which can alter decomposition rates (Davidson and Janssens 2006). Fire also has been shown to alter the chemical composition of organic matter (Certini 2005; Neff and others 2005) and reduce microbial biomass (Fritze and others 1994; Hart and others 2005). Fire can also increase the availability of nitrogen (Smithwick and others

2005), which limits net primary productivity in terrestrial ecosystems in the boreal region (Van Cleve and others 1983), and is tightly linked to rates of C exchange (Gruber and Galloway 2008). The relative sensitivity of these physical and biological factors to fire will likely determine the rate of decomposition, and in turn, will determine the net ecosystem carbon budget (Chapin and others 2006) and long-term C stocks on the boreal landscape.

Given that the majority of soil C stocks in the boreal region are found in peatlands (Wieder and others 2006) and in forested systems underlain by permafrost (Harden and others 2003), soil drainage class also is an important control on the spatial distribution of carbon stocks in boreal regions (Turetsky and others 2005). In upland forests, the presence of permafrost restricts percolation of surface water into deeper soil horizons and confines soil water to shallow soil horizons (Woo 1996).

During the summer, thawing of seasonal ice increases percolation of soil water, which decreases surface moisture content and likely affects rates of decomposition (Goulden and others 1998). In peatlands, the predominance of a high water table position and saturated soils is thought to promote peat accumulation (Clymo 1984). However, the recalcitrant nature of *Sphagnum* mosses that dominate many peatlands (Turetsky 2003) and low rates of fire combustion in peatlands (Harden and others 2000) also have historically promoted soil carbon storage as peat.

Here, our primary research objectives were to explore the effects of fire on soil climate and substrate quality (susceptibility of organic material to decomposition), and in turn, to determine how these controls regulate decomposition in black spruce-dominated ecosystems in interior Alaska. To address these objectives, we conducted two studies: 1) we used a series of laboratory incubations to explore soil temperature, moisture, and vegetation effects on C flux rates in burned and unburned black spruce forest soils collected from three different study areas, 2) at one of the study areas used in the incubation experiments, we conducted intensive field measurements of net ecosystem exchange flux (NEE) and ecosystem respiration flux (ER) across an unreplicated factorial design of burning (burned versus unburned) and drainage class (upland forest versus peatland). Together, these approaches allowed us to examine the main mechanisms controlling decomposition and net C exchange in fire-prone black spruce dominated ecosystems in interior Alaska, and the role that fire plays in regulating C fluxes and accumulation in Alaska's boreal forest.

METHODS

Fire, Vegetation, and Soil Climate Controls on Potential Decomposition Rates

We used a series of laboratory incubation experiments to explore temperature, moisture, and vegetation controls on CO₂ and dissolved organic carbon (DOC) production rates. These incubations included surface organic horizons from forests in three separate study regions in interior Alaska. All three study regions were moderately well-drained sites dominated by black spruce and feather mosses (*Pleurozium schreberi*, *Hylocomium splendens*, *Aulacomnium palustre*), and were underlain by permafrost with active layer depths around 40 cm. Throughout the Pleistocene, these study regions were not glaciated, and the underlying mineral soils are dominated by wind-deposited loess, which consists mainly of silt and very fine sand. The three study regions included burned sites within 1) the Rex Bridge fire near Anderson, Alaska, which occurred in May 2003, 2) the Albert Creek fire near Central, Alaska, which occurred in June 2003, and 3) the Erickson Creek fire near Livengood, Alaska, which also occurred in June 2003 (Figure 1). These three fires ranged in size from 5.7 to 488 km² and were mapped as individual fire events (that is, not part of a larger

fire unit). The Albert Creek and Erickson Creek fires were lightning-initiated, whereas the Rex Bridge fire was initiated by human activity. Using aerial photography and overflight surveys, we selected unburned sites adjacent to each burned site (3 upland sites and 1 peatland site) with similar slope, aspect, ground layer, and canopy characteristics relative to each burned site. At the Rex Bridge sites, organic soil layer depth averaged 18.4 ± 1.6 cm in the unburned site and 12.9 ± 1.4 cm in the burned site (data are means $\pm$ one standard error, $n=10$ pedons). At the Albert Creek sites, organic soil layer depths averaged 24.5 ± 3.2 cm and 13.3 ± 1.0 cm in the unburned and burned sites, respectively. At the Erickson Creek sites, organic soil depth averaged 21.0 ± 7.0 cm and 13.1 ± 6.8 cm in the unburned and burned sites, respectively. These data suggest that the recent fire activity consumed approximately 5.5, 11.2, and 8 cm of surface organic soil at the Rex Bridge, Albert Creek, and Erickson Creek burned sites, respectively.

At the Erickson Creek study region, we also harvested soil from a nearby black spruce and Sphagnum-dominated peatland, located at the toeslope of a north-facing hillside. Active layer depths in the peatland ranges from 50- to 70 cm and the maximum depth of peat is greater than 2.5 meters.

In both the burned and unburned sites at each of the 3 study regions (Erickson Creek, Albert Creek, Rex Bridge), we sampled the fibric organic horizon to a maximum depth of 10 cm. All living moss parts (approximately the surface most 2 cm) were removed. Samples were collected at ten randomly selected locations in each of the 6 sites in September 2004. At all sampling locations, organic horizon samples were a mixture of dead moss (feather moss species in the upland sites and *Sphagnum* species in the lowland site) and fine roots. Burned samples included the surface char layer plus unburned fibric organic matter. Organic horizon samples were harvested by hand for accurate volume and bulk density measurements. At each of the 10 sampling locations, organic horizon samples were split in half, frozen immediately, and transported to the laboratory. Prior to incubation, samples were allowed to thaw at 2°C for 2 weeks. Roots larger than 2 mm were removed from samples, but otherwise the organic matter structure was left intact. Organic horizon samples were placed at field moisture within Nalgene filter units inside mason jars. Chambers of each filter unit were separated by Whatman GF-F glass fiber filters and glass wool following Neff and Hooper (2002).

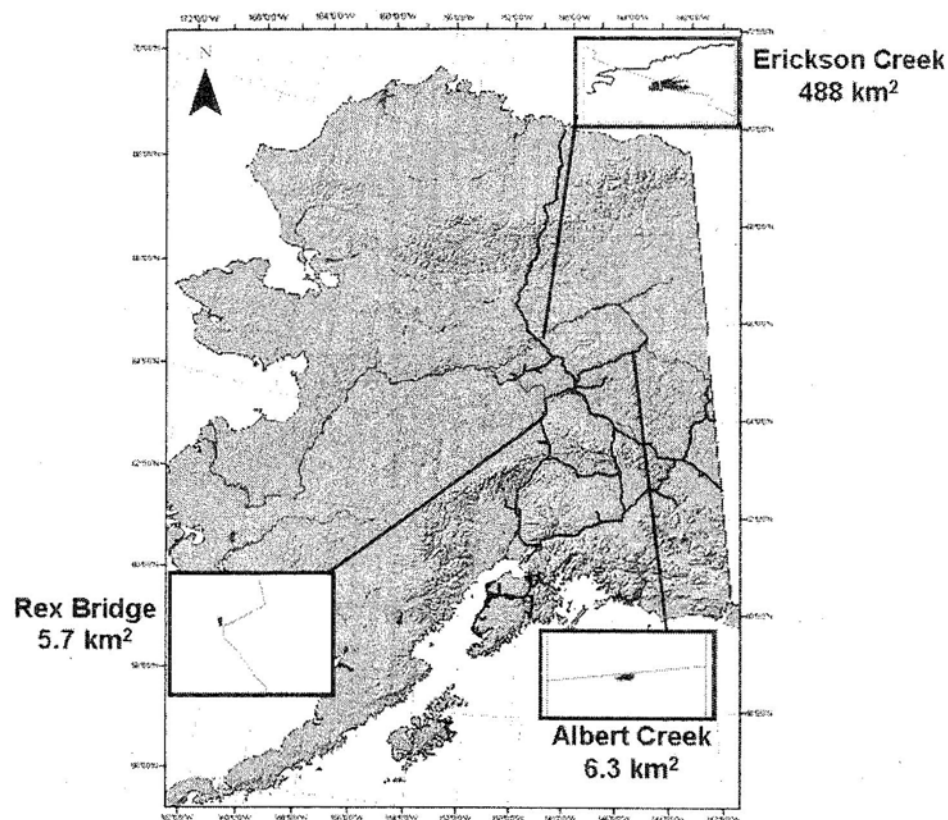


Figure 1. Map of study regions in interior Alaska. Inset figures show fire perimeters and area burned of three study sites during the summer of 2003 (U.S. Department of the Interior Bureau of Land Management, <http://agdc.usgs.gov/data/land/fire/index.html>).

One set of subsamples from each sampling location across the Erickson Creek, Albert Creek, and Rex Bridge study regions were incubated at 2°C, while the remaining samples were incubated at room temperature conditions (10°C). The 20°C temperature treatment is consistent with daily maximum temperature measurements recorded 5 cm below the ground surface at the Erickson Creek study sites during the summer (June through August). Every 4–5 days throughout the experiment, we measured CO₂ production rates over a 48-h sampling period. To quantify CO₂ production rates, jars were sealed with lids fitted with rubber septa for headspace sampling and 5 ml of headspace was removed with gas tight syringes 0, 4, 12, 24, and 48 h after jars were sealed. CO₂ concentrations were analyzed on a SRI gas chromatograph with a TCD detector and purified Helium as a carrier gas. External standards of CO₂ (Scott Gases, Plumsteadville, PA) were used for calibration. Multiple injections of external standards were used to determine instrument error, which consistently was less than 5% of standard means. After the sampling period, lids were removed and jars were covered with saran wrap to prevent water loss. Jars were gently shaken

approximately every 6–8 h to enhance mixing of the headspace gas with soil.

Organic horizon samples were kept at field collection moisture levels for the first five weeks of the incubation experiment, during which time we saw no decline in CO₂ production rates. After this initial sampling period, we leached organic horizon samples weekly with de-ionized water to remove DOC and total dissolved nitrogen (TDN) (Neff and Hooper 2002). Measurement of CO₂ production continued as described above. Thus, soils in both temperature treatments were maintained at field capacity (determined gravimetrically, and defined as the moisture content of organic horizon samples after excess moisture has drained away) for the remainder of the incubation period (8 weeks total). To leach the samples, we saturated each sample with 100 ml of water for 30 min before placing each sample under vacuum to retrieve 100 ml of leachate (Neff and Hooper 2002). DOC concentrations were measured by high temperature oxidation of DOC to CO₂ followed by detection with an infrared gas analyzer (Shimadzu Instruments, Columbia, Maryland, USA).

Following the incubation experiment, headspace volume within each jar was estimated from the

weight of water required to fill each jar to capacity. Samples were dried at 60°C to a constant mass for dry mass determinations. Production rates were calculated from the slopes of headspace (within mason jar) gas concentration regressed with time. The majority of slopes were linear; however, several non-linear slopes were rejected that appeared to be caused by headspace leaking.

Organic horizon subsamples from the Erickson Creek upland and peatland sites were used to examine the effect of fire on hydrophobicity. To measure hydrophobicity, we followed standard 'water drop test' methods (compare Watson and Letey 1970). Briefly, we weighed out triplicate 1 g subsamples of each sample used in the laboratory incubation described above. Each sample was oven-dried at 65°C for 24 h and then allowed to cool in a desiccator. We then place four drops of distilled water on each subsample, and measured the length of time for each drop to be absorbed. All water drop tests were performed simultaneously to minimize between-sample variation in hydrophobicity due to relative humidity (Doerr and others 2002).

Burning Effects on Vegetation, Soil Climate, and Ecosystem CO₂ Fluxes

We examined the effects of burning on soil climate, vegetation, and carbon exchange at the four Erickson Creek sites described above (burned and unburned upland, burned and unburned peatland). In 2005, at each of the 4 Erickson Creek sites (recently burned and unburned upland forest and peatland sites), we dug soil pits and described soil horizons following USDA-NRCS (Staff 1998) and Canadian (Committee 1998) methodologies. Common terms included lichen, live moss, dead moss (more moss than roots), fibric organics (more roots than moss), mesic (moderately decomposed organics), and humic (highly decomposed organics). Samples of each organic horizon type were collected by hand to preserve bulk density ($n = 5$ per site). Samples were ground, oven-dried for 48 h at 65°C, and subsamples were analyzed on a Carlo Erba NA 1.500 elemental analyzer for % C and N (sample precision standard error was <0.5 % for both C and N). We determined C and N stocks (in g m^{-2}) using C and N concentrations, oven-dried soil bulk density, and organic horizon thickness (Table 1).

Percent moss cover was quantified in 30 x 30 cm square vegetation subplots ($n = 10$ per site) using digital photographs and ESRI ArcMap and ArcCatalog software to digitize polygon boundaries of each dominant species and total moss cover using methods described in Harden and

others (unpublished manuscript). In addition, understory vascular plants within each 30 x 30 cm plot were harvested, dried at 65°C, and then weighed for aboveground biomass estimates. Throughout 2005, soil temperature was measured every hour in surface organic soil layers (5 cm below the moss surface) at all plots using HOBO Single-channel dataloggers (Onset Inc., Pocasset, Massachusetts, USA), which were calibrated at the USGS thermal calibration facility in Denver, CO, using methods described in Clow (2006). We also measured volumetric moisture content (VWC) of the upper organic horizons using an ECH₂O Dielectric Aquameter (Decagon Devices, Inc., Pullman, Washington, USA). We measured VWC of the mineral soil moisture using a Hydrosense Water Content Meter (Decagon Devices, Inc., Pullman, Washington, USA). At all soil pits ($n = 10$ per site), ECH₂O probes were inserted horizontally into the organic layer at a depth of 10 cm below the moss surface in early May. Probes were not moved during the growing season, so that the physical properties of the organic layer were not disturbed. VWC was measured once a week in the organic horizon, by connecting an ECH₂O-Check meter to the ECH₂O probe and recording the readout (in millivolts). VWC in the mineral soil was measured weekly by placing the Hydrosense probe vertically into the mineral soil. At the end of our study, we calibrated the ECH₂O probes by harvesting a block of the organic horizon encompassing each probe (approximately 1300 cm³) and transporting each block to the laboratory. Organic horizon blocks were saturated, allowed to drain to field capacity, and dried at room temperature, during which time we weighed each organic horizon block and measured soil moisture content using the ECH₂O-Check meter to generate a soil moisture standard curve for each individual soil block from each plot. In general, we observed strong linear relationships between measured organic VWC values and ECH₂O readings (mean $R^2 = 0.94$; range of R^2 values: 0.75-0.99).

We measured CO₂ fluxes at the soil-atmosphere interface every 7-10 days at each site from mid-May to mid-September 2005 at each of the four Erickson Creek sites. Five permanent plexiglass collars (30 x 30 cm) were installed at random locations within each site and inserted about 3 cm into the moss layer. NEE and ER were measured using a U-840 infrared gas analyzer (Licor Inc., Lincoln, Nebraska, USA) and a clear plexiglass chamber (26 x 26 x 26 cm). CO₂ fluxes were measured under ambient light conditions for NEE, and under dark conditions for ER using a two-layer

Table 1. Results from Laboratory Hydrophobicity Assay and Leachate Chemistry

Site	Hydrophobicity (absorption time in seconds)	DOC (mg C g soil ⁻¹)	TDN (mg N g soil ⁻¹)	Incubation DOC:TDN
Unburned feather moss	2.0 (0.9) ^a	2.42 (0.4) ^a	0.10 (0.02) ^a	21.7 (5.1) ^a
Burned feather moss	8.4 (3.0) ^b	2.22 (0.3) ^{ab}	0.05 (0.01) ^b	36.0 (8.5) ^a
Unburned <i>Sphagnum</i>	14.2 (3.4) ^{ab}	0.82 (0.1) ^{bc}	0.02 (0.002) ^b	21.6 (8.8) ^a
Burned <i>Sphagnum</i>	13.2 (5.3) ^{ab}	0.72 (0.1) ^c	0.03 (0.004) ^{ab}	18.3 (7.5) ^a

Note: Same letter superscripts denote non-significant differences determined from *post hoc* comparison of means tests.

cloth shroud with a reflective surface to exclude solar radiation for ER. For both NEE and ER measurements, CO₂ concentrations inside the chamber headspaces were logged every 1 s for a measurement period of about 90 s. CO₂ flux rates were calculated as the linear regression between CO₂ concentrations between 15 and 70 seconds time. The average chamber volume was estimated by injecting 2 ml of 100% CO₂ into the chamber headspace (closed from atmosphere) and recording the increase in CO₂ concentration after 90 seconds of diffusive mixing. We monitored internal chamber temperatures using a small electronic thermometer during each gas flux campaign. We also measured PAR using a handheld probe (Apogee Instruments, Inc., Logan, Utah, USA). Three replicate PAR measurements were taken at both the moss surface (Ground PAR) and 2 meters (Sub-canopy PAR) above each plot during the flux measurements. Thaw depth was measured every 7–10 days in conjunction with the C flux measurements by inserting a stainless steel depth probe into the soil and recording depth to ice. All environmental variables (soil temperature, soil moisture, PAR, thaw depth) were measured at the same time as CO₂ flux measurements.

Statistical Analyses

Data from the laboratory incubations were analyzed using a mixed effects model (PROC MIXED; SAS, Inc.) with CO₂ flux as the dependent variable, and burn status (burned versus unburned), moisture treatment (field moisture versus field capacity), and temperature treatment (2°C versus 20°C) as fixed effects. Site (Albert Creek, Erickson Creek, Rex Bridge) and sample ID (to account for repeated measurements per sample) were analyzed as random effects. The model also included all interactions among the fixed main effects. DOC and TDN concentrations, which were measured only at 20°C, were analyzed using general linear models with burning and sampling date as fixed effects, site

and sample ID as random effects, and interactions between burning x date.

Field measurements of soil temperature, soil moisture, thaw depth, moss cover, understory vascular biomass, and PAR were analyzed using general linear models with site and date as fixed effects as well as interactions between site x date (PROC GLM; SAS, Inc.). In situ CO₂ fluxes (NEE and ER) were analyzed using repeated measures analysis of variance (ANOVA; PROC MIXED; SAS, Inc.). Data were tested for normality and homogeneity of variance, although we note that ANOVA is fairly robust to violations of some of these assumptions. We used Tukeys multiple comparisons tests for *post hoc* comparison of means. General linear models (PROC GENMOD; SAS, Inc.) were used to evaluate the influence of both continuous variables (temperature, moisture, thaw depth, PAR) and categorical variables (burn status, drainage class) on in situ CO₂ fluxes. We tested interactions between all variables, but only report significant results here (where $P < 0.05$). All data are shown as means $\pm$ one standard error.

RESULTS

Fire, Vegetation, and Soil Climate Controls on Potential Decomposition Rates

Burning altered the effects of temperature and moisture treatments on potential decomposition of organic horizon samples. Incubation CO₂ production rates from the three upland forest study regions (Erickson Creek, Albert Creek, Rex Bridge; Figure 1) showed a significant interaction between burn status (burned versus unburned sites), temperature (2°C versus 20°C treatments), and moisture treatment (field moisture versus field capacity; Figure 2A; $df = 94$, $F = 63.23$, $P < 0.0001$). The unburned sites corresponded to incubation CO₂ production rates that were 8-fold faster at the higher temperature treatment under field weight

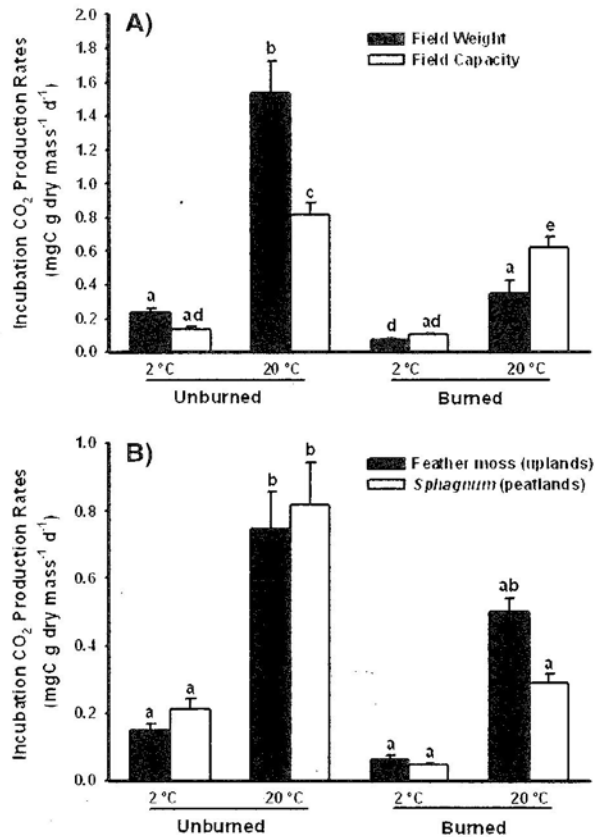


Figure 2. Results from laboratory incubations examining the effects of fire, temperature, moisture, and vegetation on decomposition rates in upland black spruce forests and peatlands located in interior Alaska. (A) Across three black spruce forest study regions, CO₂ production rates varied by a temperature treatment $\times$ moisture treatment $\times$ burn status interaction, (B) At the Erickson Creek study sites, CO₂ production rates varied by an interaction between temperature treatment and burn status. Same letter superscripts denote non-significant differences among means determined from *post hoc* comparison of means tests.

conditions, and 6-fold faster at the higher temperature treatment under field capacity conditions (Figure 2A). The burned sites corresponded to incubation CO₂ production rates that were 6-fold faster at the higher temperature treatment under both field weight and field capacity conditions. Incubation CO₂ production rates in the unburned sites decreased by approximately 50 % with greater moisture content at the 20°C treatment, but showed no change with greater moisture content at the 2°C treatment. However, incubation CO₂ production rates in the burned sites increased 2-fold with greater moisture content in the 20°C treatment, but showed no change with greater moisture content at the 2°C treatment (Figure 2A).

Dissolved organic C concentrations in leachate collected during the incubation experiment varied by a burn status $\times$ leaching event interaction ($df = 28$, $F = 3.40$, $P = 0.016$; Figure 3A). Concentrations of DOC were lower in leachate from burned samples than from unburned samples during the first leaching event, but did not vary between burned and unburned samples during the second and third leaching events. Ratios of DOC:TDN concentrations in leachate also varied by a burn status $\times$ leaching event interaction ($df = 28$, $F = 5.81$, $P = 0.0008$), with greater ratios in leachate from burned samples than from unburned samples during the second and third leaching events (Figure 3B). Cumulative CO₂ production over the 8-week incubation period was a significant predictor of average DOC concentration in leachate from organic horizons across all study regions and leaching events (Figure 4).

Results from the Erickson Creek study sites (which included four sites representing a factorial combination of burned and unburned sites in both upland forest and peatland) showed that incubation CO₂ production rates varied by a burn status $\times$ temperature $\times$ moss type interaction ($df = 63$, $F = 28.40$, $P < 0.0001$; moss type is confounded with drainage class). Incubation CO₂ production rates were three times greater in unburned *Sphagnum* samples than in burned *Sphagnum* samples at the 20°C treatment, but were not different at the 2°C treatment (Figure 2B). Incubation CO₂ production rates did not vary between burned or unburned feather moss at either temperature treatment. On average, DOC concentrations from leachates were three times greater in feather moss samples than in *Sphagnum*, but did not vary with burn status ($df = 42$, $F = 7.35$; $P = 0.0005$; Table 1).

Hydrophobicity of organic horizon samples from the Erickson Creek study region varied by an interaction between burn status and moss type ($df = 41$, $F = 4.59$, $P = 0.0073$). Across burn status, hydrophobicity was nearly five times greater in *Sphagnum*-derived organic matter than in feather moss-derived organic matter (Table 1). Although there was no change in hydrophobicity with burning in the *Sphagnum* samples, hydrophobicity was more than four times greater in burned feather moss-organic matter than in unburned feather moss.

Fire Effects on Vegetation and Soil Climate

At the Erickson Creek study region, organic matter combustion during fire significantly reduced moss

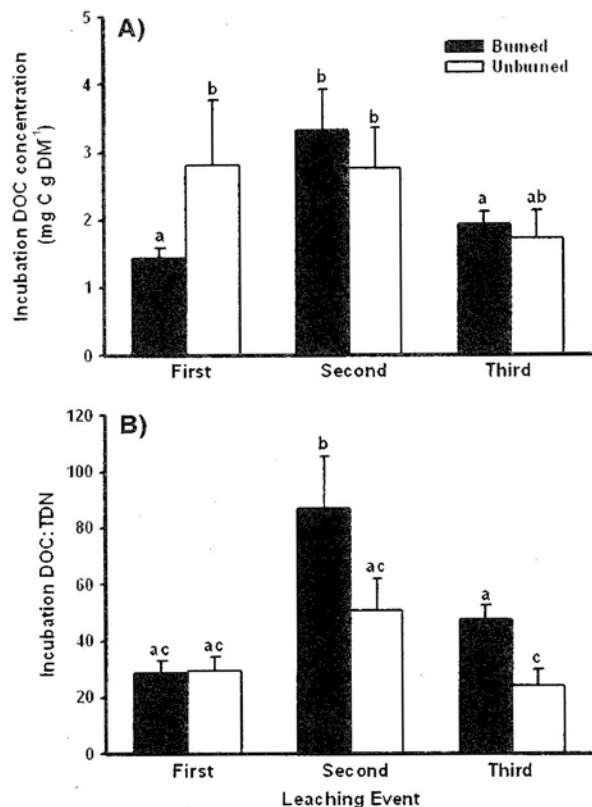


Figure 3. Results from laboratory incubations examining the effects of burn status and leaching date on leachate chemistry. (A) DOC concentration varied by an interaction between burn status and leaching event. (B) DOC:TDN ratios varied by an interaction between burn status and leaching event. Same letter superscripts denote non-significant differences among means determined from *post hoc* comparison of means tests.

cover and vascular plant biomass at both the upland and peatland sites (Table 2). Groundcover at the unburned upland site was dominated by lichens and feather mosses, whereas more than 90% of groundcover at the burned upland site was charred soil or woody debris. The unburned peatland site was dominated by *Tomenthypnum nitens* and *Sphagnum* species, whereas nearly 80% of groundcover in the burned peatland site was charred soil and woody debris. We observed significant colonization of the moss species, *Ceratodon purpureus*, in burned sites during our 3-year study, particularly in the peatland.

Soil organic horizons at the Erickson Creek study region were thinner in burned sites than in unburned sites (Table 2). In the upland sites, organic horizon thickness averaged 17 ± 2 cm in the unburned site, and 13 ± 2 cm in the burned site. Organic horizon thickness exceeded 2.3 meters in

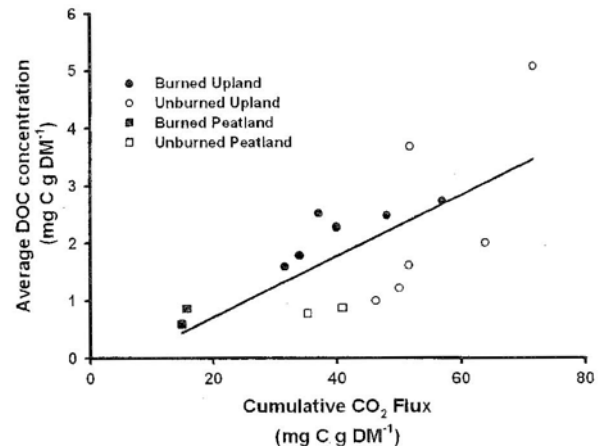


Figure 4. Relationship between mean DOC concentration in leachate and cumulative CO₂ flux over the 8-week incubation, including results of a linear regression using all data points ($R^2 = 0.34$, $P = 0.02$, $df = 13$, $F = 6.77$).

depth in the unburned peatland and 18 ± 1 cm at the burned peatland. Organic matter stocks also varied across sites (Table 2). C stocks averaged 42 ± 1 kg C m⁻² in the unburned peatland, which was nearly (our times greater than the C stocks measured in the burned peatland and eight times greater than the C stocks measured in both upland sites. Organic matter storage increased with depth at all sites (Table 2), owing largely to increases in bulk density in deeper soils.

Soil temperature at 5 cm below the moss surface varied by both site ($df = 3$, $F = 31.79$, $P < 0.0001$; Figure 4) and date ($df = 4$, $F = 172.2$, $P < 0.0001$; Figure 5A) with no significant interaction among these main effects. There was no difference between burned and unburned upland sites in mean daily surface soil temperatures. However, the burned peatland site had cooler surface soil temperatures than the burned peatland site (Figure 5B). In general, the unburned peatland site was warmer than all of the other sites. At all sites, growing season surface soil temperatures were warmest during June and July and coolest in September. VWC of the organic soil at 10 cm below the moss surface varied by a significant interaction between site and date ($df = 12$; $F = 2.64$; $P = 0.002$). Across our sampling dates in the upland forest, VWC was greater in the burned than in the unburned site (Figure 5C). On average, VWC was also greater in the burned peatland relative to the unburned peatland (Figure 5D). Mineral soil was frozen through the first week of June at all four sites. Between mid-June and September,

Table 2. Soil Climate and Vegetation Parameters at Erickson Creek Study Region

Site	Active layer depth (cm)	Organic horizon depth (cm)	Mineral soil moisture (%)	Moss cover (%)	Vascular biomass (g m ⁻²)	Subcanopy PAR (μmol m ⁻² s ⁻¹)	Ground PAR (μmol m ⁻² s ⁻¹)
Burned upland	67 (3) ^a	13 (2)	59.0 (1) ^a	0.02 (0.03) ^a	7.8 (1.9) ^a	548 (33) ^a	457 (29) ^a
Unburned upland	53 (2) ^b	17 (2)	59.4 (1) ^a	0.45 (0.23) ^b	14.3 (2.8) ^b	464 (22) ^a	347 (18) ^b
Burned peatland	68 (2) ^a	28 (5)	—	0.14 (0.05) ^c	4.3 (2.0) ^a	675 (38) ^b	587 (37) ^c
Unburned peatland	72 (3) ^c	>250*	—	0.80 (0.20) ^d	12.3 (1.7) ^b	557 (38) ^{ab}	454 (34) ^{ab}

*We drilled to 2.5 meters at 3 locations in the burned peatland and did not reach mineral soil.

Note: Same letter superscripts denote non-significant differences determined from post hoc comparison of means tests.

Table 3. Soil C and N Stocks at the Erickson Creek Study Region

Site	Field horizon	Horizon thickness (cm)	C stock (g m ⁻²)	N stock (g m ⁻²)
Unburned upland	Live moss	2 (0)	104	2
	Lichen	3 (1)	437 (158)	8 (5)
	Dead moss	2 (1)	303	6
	Fibric	8 (1)	1787 (544)	31 (10)
	Mesic	3 (1)	1503 (227)	46 (8)
	Humic	3 (0)	1774	55
	Cumulative		5936 (1870)	133 (40)
Burned upland	Burned fibric	1 (0)	460 (57)	10 (2)
	Dead moss	3 (1)	464 (243)	8 (4)
	Fibric	5 (1)	862 (164)	16 (3)
	Mesic	5 (1)	3168 (486)	77 (12)
	Cumulative		4860 (1080)	117 (27)
Unburned peatland	Live moss	2 (0)	104	2
	Dead moss	3 (1)	623 (176)	11 (3)
	Fibric	7 (1)	1353 (35)	27 (4)
	Mesic	9 (1)	39620 (3017)	1527 (226)
	Cumulative*		41648 (990)	1566 (187)
Burned peatland	Burned fibric	2 (1)	552 (216)	10 (2)
	Fibric	7 (2)	2063 (662)	8 (4)
	Mesic	6 (1)	3498 (706)	77 (12)
	Humic	6 (1)	3923 (890)	16 (3)
	Cumulative		11238 (4023)	588 (202)

*Does not include C and N stocks between from 1.11 and 2.5 meters.

mineral VWC was not different between sites ($df = 1.36$, $F = 0.24$, $P = 0.52$), or dates ($df = 9$, $F = 1.459$, $P = 0.16$), with no significant interaction between site and date (data not shown). At the peatland site, the mineral soil was either frozen or inundated throughout the entire growing season.

Thaw depth varied by a significant interaction between site and date ($df = 12$, $F = 4.60$, $P < 0.0001$). In general, thaw depth was deeper in peatland sites than upland sites, with active layer depths (for example, maximum thaw depth) of 55 and 68 cm in the unburned and burned uplands, respectively, and 72 and 67 cm in the unburned and burned peatlands, respectively (Table 2).

In Situ Studies: Fire Effects on Ecosystem Carbon Fluxes

NEE varied by a significant interaction between site and date (Repeated measures ANOVA; $df = 29$, $F = 1.79$, $P = 0.0123$). Averaged across dates, mean NEE showed greater rates of CO₂ uptake (negative values denote uptake) in the unburned peatland site than in the burned peatland (Figure 5F), averaging -1.51 ± 0.17 and 0.16 ± 0.21 g C m⁻² d⁻¹, respectively. However, NEE rates were not significantly different in the two upland forest sites, averaging 0.0005 ± 0.09 g C m⁻² d⁻¹ across the sites (Figure 5E).

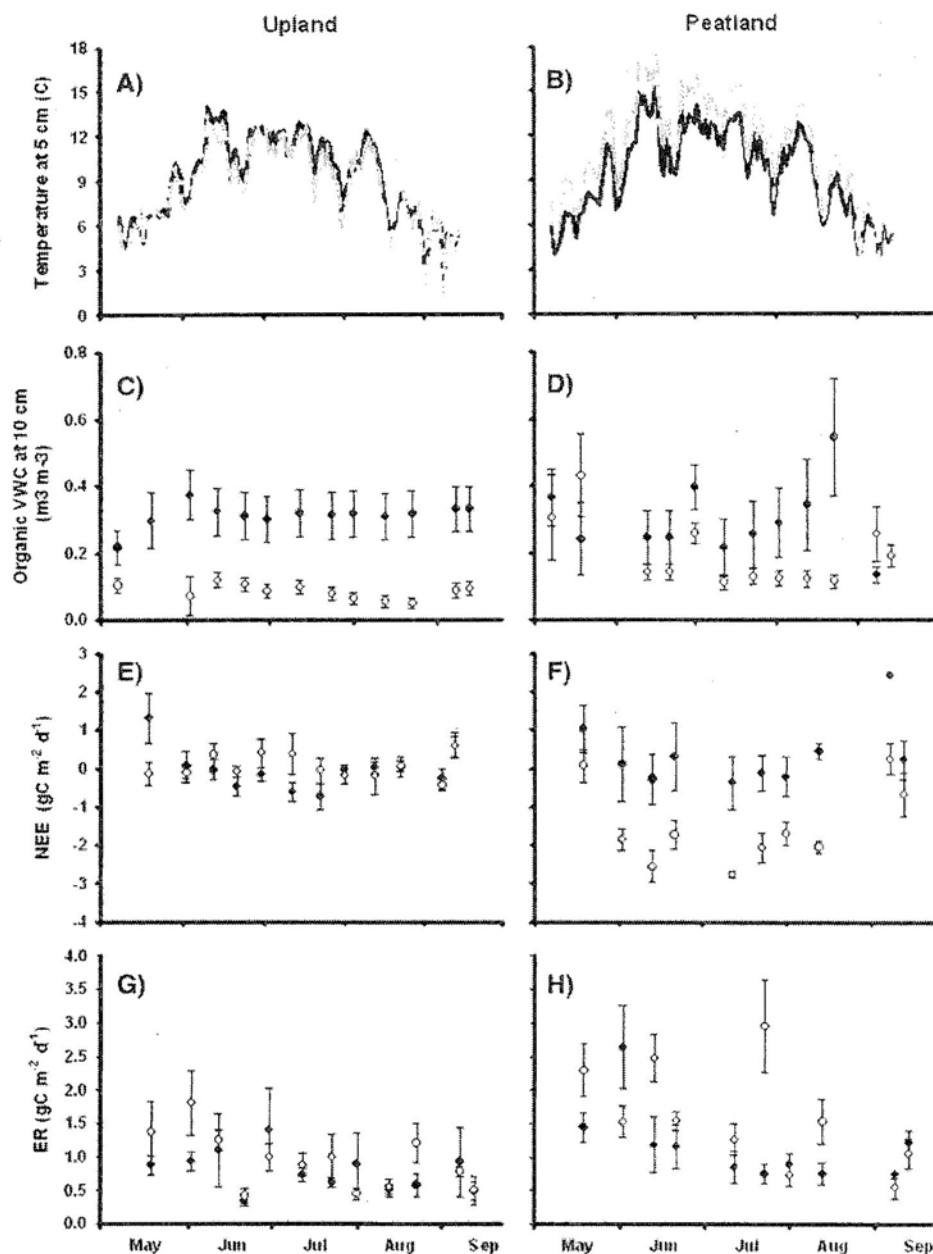


Figure 5. Seasonal variation in soil climate and in situ C fluxes at the four Erickson Creek study sites. Data from unburned sites are depicted by gray lines or open circles, whereas data from burned sites are depicted by black lines or closed circles. Surface soil temperatures (5 cm beneath the moss surface) did not vary between burned and unburned upland sites (A; $P > 0.05$), but did vary between burned and unburned peatland (B; $P = 0.0003$, $df = 3$, $F = 16.42$). Volumetric moisture content in surface organic soils varied between burned and unburned sites in both uplands (C; $P = 0.000008$, $df = 3$, $F = 31.38$) and peatland (D; $P = 0.00007$, $df = 3$, $F = 31.38$). Net ecosystem exchange did not vary between burned and unburned sites in black spruce (E; $P > 0.05$) but did vary with burn status in the peatlands (F; $P = 0.000008$, $df = 3$, $F = 28.32$). Similarly, ecosystem respiration did not vary between burned and unburned sites in black spruce sites (G; $P > 0.05$) but did vary with burn status in the peatlands (H; $P = 0.006$, $df = 3$, $F = 9.87$).

ER varied by a significant interaction between site and date ($df = 43$, $F = 3.66$, $P < 0.0001$). Averaged across dates, ER fluxes in the uplands were not significantly different between burned and un-

burned sites, averaging $0.86 \pm 0.09 \text{ g C m}^{-2} \text{ d}^{-1}$ across the two sites (Figure 5G). In the peatland sites, ER fluxes were greater in the unburned site than the burned site, averaging 1.59 ± 0.14 and

Table 4. Results from General Linear Model Evaluating Controls on in situ C Fluxes

Dependent variable	Independent variable	Parameter estimate	Estimate SE	Chi-square	P
NEE (g C m ⁻² d ⁻¹)	Soil temperature × VWC	0.075	0.038	3.97	0.05
	Burn status	0.389	0.188	4.29	0.04
	Landscape position	-0.943	0.187	25.36	<0.0001
ER (g C m ⁻² d ⁻¹)	VWC	-1.220	0.551	4.93	0.03
	Soil temperature × VWC	0.100	0.047	4.50	0.03
	Soil temperature × VWC × Burn status	0.360	0.057	40.28	<0.0001
	Thaw depth	-0.008	0.004	4.12	0.04
	Landscape position	-0.290	0.137	4.64	0.03

Note: General linear model was used to evaluate surface soil temperature, thaw depth, organic soil volumetric moisture content, burn status (burned vs. unburned sites), and landscape position (upland black spruce forest vs. peatland) as controls on net ecosystem exchange and ecosystem respiration at the Erickson Creek study sites. Burn status and landscape position were included in the general linear model as categorical variables, whereas soil temperature, volumetric water content, and thaw depth were included as continuous variables. The model included all interactions among main effects. Only significant results are reported.

1.21 ± 0.13 g C m⁻² d⁻¹, respectively (Figure 5H). Rates of ER fluxes were generally greater in the peatland sites than in the upland forest sites.

Results from our general linear model suggest that a temperature × VWC interaction, burn status, and landscape position (upland versus peatland; Table 4) were significant predictors of NEE. Volumetric water content, thaw depth, landscape position, and an interaction between temperature × VWC × burn status were significant predictors of ER (Table 4). To evaluate the fit of each model, we compared the full model to the null model using the log likelihood ratio test, which follows a chi-square distribution. For both NEE and ER, we accepted the full model over the null model (NEE: critical value = 136.31, *df* = 3, *P* < 0.0001; ER: critical value = 156.80, *df* = 5, *P* < 0.0001).

To evaluate the sensitivity of ER fluxes to seasonal variations in temperature and moisture, we calculated the coefficient of variation (CV) for every flux plot over time, and then averaged these CV percentages for each site. ER fluxes were less variable over time in the burned upland site (CV = 49 %) than the unburned upland (60 %; *t*-test, *df* = 8, *t* = -2.45, *P* = 0.039). However, variability in ER fluxes was not significantly different between the burned and unburned peatland sites (*P* = 0.98), where the CV averaged 53 % across the sites.

DISCUSSION

Effects of the Post-Fire Environment on Decomposition

The fire disturbance regime of the North American boreal forest has undergone dramatic changes over the last 40–50 years (Goetz 2005; Kasischke and Turetsky 2006), both the annual area burned and the frequency of larger fires (> 1000 km²) have

doubled (Kasischke and Turetsky 2006). Although these recent shifts in the fire regime have resulted in significant loss of C via combustion (Bond-Lamberty and others 2007; Kasischke and others 1995; Balshi and others 2007), the post-fire changes in soil thermal conditions, organic matter quality, and ER are less clear (O'Neill and others 2003), owing largely to the complex interactions among burning, soil temperature, soil moisture, organic matter quality, and soil microbial communities.

Findings from our laboratory incubations suggest that burning decreased the sensitivity of decomposition to warmer soil conditions, as measured by incubation CO₂ production rates (Figure 2A). This effect was consistent in both feather moss samples from the upland forest sites and *Sphagnum* samples from the peatland sites. However, it is not clear from these incubation results whether fire altered the chemical composition of organic matter, the biological properties of the soils, or both (Davidson and Janssens 2006). In a prior study, the decomposability of organic matter substrates was reduced by fire through the selective burning of labile compounds (Neff and others 2005) and the production of charred material (for example, "black carbon"; Kuhlbusch and Crutzen 1995), which has high residence times in post-burn soils (Forbes and others 2006; Preston and Schmidt 2006; DeLuca and Aplet 2008). Other studies have reported a reduction in microbial biomass in near-surface soils (Certini 2005; Hart and others 2005; Waldrop and Harden 2008), which can greatly reduce the response of microbial respiration to increased temperature. In the field, fire-induced effects on the chemical and microbial composition of organic soils can be coupled with changes in soil temperature and moisture, both of which strongly influence rates of decomposition (O'Neill and others 2002).

Our incubation results also showed that increased moisture content reduced incubation CO_2 production rates in the unburned sites and enhanced CO_2 production rates in the burned sites. However, these effects were only observed at the warmer temperature treatment (20°C; Figure 2A). These findings suggest that decomposition of organic matter in burned sites is moisture limited, an effect that may be exacerbated by post-fire increases in soil hydrophobicity (Table 1). Burning can increase the hydrophobicity of surface organic horizons (DeBano and Krammes 1996; DeBano

2000), as we observed on feather moss-derived organic matter (Table 1). Fire-induced hydrophobicity can persist for a few months to a few years, depending on the severity of the burn (DeBano 2000). In the boreal forest, the effects of fire on soil hydrophobicity and its influence on carbon fluxes are not well understood. However, based on our measurements, fire has the capacity to increase the hydrophobicity of soils of black spruce sites with a feather moss-dominated forest floor, which may indirectly control rates of decomposition by reducing soil moisture infiltration and increasing surface runoff.

Substrate quality, as reflected by different types of moss litter used in this study, may also play an important role in landscape-scale variations in decomposition, particularly during early succession in burned sites. Bryophyte litter is generally more resistant to decomposition than vascular litter (Aerts and others 1999; Hobbie 2000; Turetsky 2000).

In particular, species in the genus *Sphagnum* tend to decay more slowly than other moss species across a range of microhabitat conditions in boreal wetlands (Rocheffort and others 1990; Johnson and Damman 1991; Belyea 1996; Turetsky 2003). Our incubation results showed that burning further reduces the decomposability of *Sphagnum*, which may be due, in part, to the production of black carbon during combustion, which is highly resistant to decomposition (Preston and Schmidt 2006; DeLuca and Aplet 2008). By contrast, however, we measured no effect of burning on the decomposition of feather moss-derived organic matter, despite a strong increase in hydrophobicity in our feather moss samples following fire (Figure 2B, Table 1). Based on these incubations, we might predict lower rates of heterotrophic respiration (per gram C) in landscapes dominated by *Sphagnum* than by feather mosses, and that this effect might be enhanced in recently burned sites.

Whereas incubation CO_2 fluxes were highly sensitive to burning, incubation DOC concentration was less variable between burned and un-

burned samples (Figure 3A; Table 1). However, the ratio of DOC:TDN was generally greater in leachate from burned samples (Figure B), suggesting a shift in the chemical composition of dissolved organic matter following fire. This shift in DOC:TDN ratio may have been caused by higher volatilization of nitrogen relative to carbon during fire, or perhaps elevated sorption of ammonium to burned organic surfaces (Certini 2005). However, in a 2000 burn near Delta Junction, Alaska, the opposite effect was observed in soils with persistent, high nitrate losses detected in the field (Neff and Harden, *unpublished data*). We also observed a significant positive relationship between incubation CO_2 fluxes and incubation DOC concentrations across all burned and unburned treatments (Figure 4), an effect that suggests DOC production may be linked to soil organic matter quality (Neff and Hooper 2002).

Effects of Fire on Soil Temperature and Moisture

Although the combustion and regrowth of northern forested ecosystems following fire can have large effects on soil temperature and moisture conditions (Dyrness 1982; Burn 1998, O'Neill and others 2002; Kasischke and Johnstone 2000; Harden and others 2006, we did not detect warmer summer soil temperatures in the second year following fire when compared with unburned sites (Figure 5A and B). Surprisingly, mean daily surface soil temperatures were cooler in the burned peatland site compared to the unburned peatland site (Figure 5B). This trend was likely driven by a quick recovery of vegetation to a canopy with higher albedo than the unburned site and/or post-fire changes. Although fire typically reduces canopy shading for at least 1–3 years post-fire (Yoshikawa and others 2003), recovery can then lead to increased albedo and potentially cooler soils (Randerson and others 2006). In addition to the effect of albedo, the role of soil moisture is also important in governing soil temperature trends following fire. In this study, organic soils at the Erickson Creek burned sites (2 years post-fire) were generally wetter than the unburned sites (Figure 6C and D). In the unburned peatland site, a thick organic layer (>2 m) with a shallow water table likely dampened interannual and diurnal fluctuations in soil temperature relative to the burned site (Lachenbruch 1959; Romanovsky and Osterkamp 1995). At a burned site near Fairbanks, Alaska, Yoshikawa and others (2003) also observed cooler conditions at the surface of the burned site during the

summer, but warmer temperatures deeper in the active layer, reflecting moisture-driven changes in thermal conductivity.

Effects of Fire on Ecosystem CO₂ Fluxes

Net ecosystem exchange integrates both ER and gross primary production, and indicates whether an ecosystem functions as a CO₂ source or sink. In general, plots at all four sites at Erickson Creek functioned as a net CO₂ sink from June through August and a net source of CO₂ in May and September. Because our measurements were confined to the forest floor, we attribute CO₂ uptake primarily to mosses, which dominate aboveground biomass in late successional Alaskan black spruce sites (Barney and Van Cleve, 1973). In the uplands, we did not observe a difference in NEE between the burned and unburned upland sites, suggesting that dry conditions in the unburned site were limiting moss productivity (Busby and Whitfield 1978; Bonan and Shugart 1989) or that recolonizing vegetation in the burned site had high CO₂ uptake rates. However, NEE was greater (higher uptake) in the unburned peatland site than the burned peatland site, reflecting a reduction of moss cover from 80 to 14%, post-fire (Table 2).

Following fire, ER (which includes heterotrophic respiration primarily as microbial decomposition and autotrophic respiration as both root and moss respiration), typically decreases (Burke and others 1997, O'Neill and others 2002). This trend often is attributed to a decrease in autotrophic respiration following the death of vegetation (Sawamoto and others 2000; Richter and others 2000; Wang and others 2003). In the present study, we also observed lower ER in the burned peatland relative to the unburned peatland (Figure 5G and H), due in part to post-fire reductions in autotrophic respiration. However, this difference in ER between peatland sites may also be due to differences in heterotrophic respiration, owing to large differences in organic horizon thickness (Table 2), C stocks (Table 3), and reduced decomposability of *Sphagnum* in burned sites, as reflected in the laboratory incubations (Figure 2B). In the uplands, we did not observe a difference in ER between the burned and unburned sites, despite the presumed decreased in autotrophic respiration. Burke and others (1997) also reported no effect of fire on soil respiration in a Canadian boreal forest for the first 2 years post-fire, followed by a decrease in soil respiration and then a recovery of rates to pre-burn levels after 7 years.

Although our field measurements of ER at the Erickson Creek study region were not replicated and

may not reflect larger trends across the boreal region, they do provide a good opportunity to further explore patterns observed in our incubation studies under more natural field conditions. In black spruce forests of interior Alaska, ER generally is sensitive to seasonal fluctuations in soil temperature and moisture (Schlentner and Van Cleve 1985; O'Neill and others 2002; Vogel and others 2005). However, in our field study, we observed a weak relationship between ER and soil temperature (Table 3), which differs from our incubation findings (Figure 2). At the Erickson Creek upland sites, the weak relationship between ER and temperature was likely due to the lack of climatic variation during the study period, a time when warm temperatures and low precipitation were anomalously constant (Alaska Climate Research Center; <http://climate.gi.alaska.edu/>). Although low soil moisture content was an important factor affecting temperature sensitivity in the upland sites (Wickland and Neff 2007), inundation from seasonal runoff was probably a dominant control in the peatlands, potentially slowing the diffusion of oxygen to microbes (that is, Davidson and Janssens 2006) and lowering the temperature sensitivity of ER.

To address confounding effects of temperature and moisture, we constructed a general linear model to examine the interaction between temperature and moisture as a predictor of ER (Table 4). Our model results showed that the influence of temperature alone on ER rates was negligible, most likely due to the extreme moisture conditions (drought and inundation) that occurred throughout the duration of this study. A three-way interaction between temperature, moisture, and burn status (Table 3) was a significant predictor of ER, suggesting that the sensitivity of ER rates to this temperature and moisture interaction varied between burned and unburned sites. Variation in ER rates over time, as estimated by CV (%), was lower in the upland burned site than the upland unburned site. This is consistent with ER rates in the upland burned sites being less sensitive to climatic fluctuations than in the upland unburned site, which is also consistent with findings from our laboratory incubation.

CONCLUSIONS

Together, the findings from our laboratory and field studies indicate that fire can reduce the sensitivity of organic matter decomposition to variation in soil climate. Incubation CO₂ production rates increased seven to eight times with increased incubation

temperatures in unburned soils, but increased only by three to five times in burned soils. Increased moisture content reduced incubation CO_2 production rates in the unburned sites and enhanced CO_2 production rates in the burned sites. These incubation findings were consistent with our in situ measurements of ER, which appeared to be controlled by a complex interaction among soil temperature, moisture, and burn status. In the upland black spruce sites, ER was less variable over time in the burned site than in unburned site, which is consistent with decreased sensitivity of C fluxes to fluctuations in soil climate following fire. Burning also reduced the decomposability of *Sphagnum* biomass and caused a shift in DOC leachate toward higher C:N ratios, which suggests a shift in the quality of substrate available to microbial decomposers post-fire. By modifying soil climate conditions, fire appears to reduce the temporal variability of organic matter decomposition in burned sites while increasing the spatial variability of CO_2 fluxes at larger scales that include both burned and unburned stands.

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