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Experimental warming and burn severity alter soil CO_2 flux and soil functional groups in a recently burned boreal forest

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Abstract

Global warming is projected to be greatest in northern regions, where forest fires are also increasing in frequency. Thus, interactions between fire and temperature on soil respiration at high latitudes should be considered in determining feedbacks to climate. We tested the hypothesis that experimental warming will augment soil CO_2 flux in a recently burned boreal forest by promoting microbial and root growth, but that this increase will be less apparent in more severely burned areas. We used open-top chambers to raise temperatures 0.4–0.9 °C across two levels of burn severity in a fire scar in Alaskan black spruce forest. After 3 consecutive years of warming, soil respiration was measured through a portable gas exchange system. Abundance of active microbes was determined by using Biolog EcoPlates™ for bacteria and ergosterol analysis for fungi. Elevated temperatures increased soil CO_2 flux by 20% and reduced root biomass, but had no effect on bacterial or fungal abundance or soil organic matter (SOM) content. Soil respiration, fungal abundance, SOM, and root biomass decreased with increasing burn severity. There were no significant interactions between temperature and burn severity with respect to any measurement. Higher soil respiration rates in the warmed plots may be because of higher metabolic activity of microbes or roots. All together, we found that postfire soils are a greater source of CO_2 to the atmosphere under elevated temperatures even in severely burned areas, suggesting that global warming may produce a positive feedback to atmospheric CO_2, even in young boreal ecosystems.

Keywords: bacteria, carbon, fungi, microbe, respiration, root, soil, storage, temperature, warming

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Introduction

Northern boreal forests represent about 30% of the world's forested area (Conard *et al*., 2002) in which the soil carbon pool is approximately 90–290 Pg (Kasischke & Stocks, 2000), or 12–42% of the global soil carbon pool (Post *et al*., 1982; Batjes, 1996). Estimates of soil carbon flux in the boreal region are variable, ranging from a net source of 0.2 Pg to a sink of 1 Pg (Chapin *et al*., 2000). Northern forests were thought to be net carbon sinks in the past because of relatively cool temperatures that limit decomposition rates (Gorham, 1991). However, observations from recent studies suggest that these ecosystems are current carbon sources (Burke *et al*., 1997; Savage *et al*., 1997; Goulden *et al*., 1998; Lindroth *et al*., 1998; Rayment & Jarvis, 2000; Swanson & Flanagan, 2001). A switch from carbon sink to carbon source may be caused by recent increases in average surface air temperatures, which have warmed 0.3 ± 0.03 °C per decade during the 20th century in the high latitudes of western North America (Keyser *et al*., 2000) and Eurasia (Kasischke & Stocks, 2000). This trend is consistent with projections of climate change in this region because of altered greenhouse forcing (McGuire *et al*., 2000; Serreze *et al*., 2000).

Well-established empirical and theoretical work regarding the effects of temperature on soil respiration

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indicates that elevated temperatures increase decomposition and soil respiration in many biomes (e.g. Lloyd & Taylor, 1994; Kirschbaum, 1995). In a metaanalysis covering a wide range of habitats, Rustad *et al*. (2001) report that experimental warming significantly increased soil respiration by an average of 20%. In addition, across the globe, soil respiration rates are well predicted by mean annual temperature (Raich & Schlesinger, 1992), and these two variables are most strongly correlated in the boreal region (Kirschbaum, 1995). This response, coupled with large C stocks in boreal soil, may produce a positive feedback in the global C cycle by raising atmospheric CO_2 levels (Raich & Schlesinger, 1992; Kirschbaum, 1995; Amundson, 2001).

Global climate change is expected to elicit additional disturbances in boreal regions, including widespread forest fires (Kasischke & Stocks, 2000). Fire is the most pervasive disturbance in the boreal forest (Payette, 1993) and it represents a major factor controlling the long-term dynamics of soil carbon (Harden *et al*., 2000; Kasischke & Stocks, 2000). In North America (Kasischke & Stocks, 2000) and Siberia (Conard *et al*., 2002), fire activity has increased over the past half century, and fires are returning more quickly, potentially because of increasing temperatures, decreasing precipitation rates, and melting permafrost associated with climate change (Harden *et al*., 2000; Kasischke & Stocks, 2000). In addition, the growing season is predicted to lengthen in boreal forests under global warming, so late-season forest fires are likely to become more common (Kasischke *et al*., 2000). Fire severity tends to increase as the summer progresses, because of thawing of frozen soil. Variations in fire severity affect the availability of soil carbon following a burn (Kasischke *et al*., 2000).

Burn severity could interact with warmer temperatures to influence soil respiration. Fires remove soil organic material (SOM) and vegetation biomass, negatively affecting plants and microbes alike. As a result, soil respiration typically declines for the first several years following fires (Burke *et al*., 1997; Savage *et al*., 1997; O'Neill *et al*., 2002). As fire severity increases, this response should become more marked because of greater losses of soil carbon and vegetation biomass. Warmer conditions may alleviate the temperature limitation of microbial activity, but without readily available organic material, microbes could become substrate-limited instead. As such, increasing burn severity may counteract warming effects to some extent. We tested the hypothesis that experimental warming will raise soil CO_2 flux in a recently burned boreal forest by promoting microbial growth and activity, but that this increase will be less apparent in more severely burned areas.

Methods

Field site

Our research site was located in east-central Alaska near Delta Junction, Alaska, 63°55′N 145°44′W. We selected an area of boreal forest that burned by wildfire in 1999. The regional climate is cold and dry. Mean monthly temperatures range from −20 °C in January to 16 °C in July. July is the wettest month, with an average of 690 mm rain. Winter months are driest, with averages of 80 mm precipitation per month, mostly as snow (http://weather.noaa.gov/). The growing season lasts from mid-May to early September. Soils are well drained, alluvial gravels overlaid by silt. Permafrost is discontinuous in this region, and no permafrost occurs under our sites.

Picea mariana (black spruce) dominated the site prior to the fire. In the summer of 1999, a high intensity crown-fire removed on average 65% of SOM from the top 10 cm of soil (Treseder *et al*., 2004). The ground remained essentially bare until the 2000 growing season, when grasses, sedges, and some mosses began to recolonize. In addition, some herbs and shrubs resprouted from underground roots. By the end of the 2002 growing season, vegetation cover in lightly burned areas averaged 30% for both vascular plants and mosses, while cover in severely burned areas averaged 10% and 75% for the two groups, respectively (Johnstone, 2003). Vascular cover was dominated by the grass *Festuca altaica* and mosses were predominantly *Ceratadon purpureus*.

Experimental design

We tested our hypotheses by establishing 24 circular, 1.77 m^2 plots in which temperature was manipulated within two levels of burn severity. Specifically, temperature treatments consisted of warming and ambient plots, crossed factorially with two levels of burn severity, with six replicates per treatment. The experiment used natural, small-scale variations in burn severity, caused by differential smoldering of the organic layer (Miyanishi & Johnson, 2002) as burn severity treatments. Residual patches of lightly burned organic mat indicated the area had relatively homogeneous soil conditions prior to burning, with an 8–10 cm thick organic layer that was covered by lichens (*Cladonia* spp. and *Cladina* spp.) and feather moss (*Pleurozium shreberi* and *Hylocomium splendens*). Plots were systematically placed in patches to achieve an even replication of severe and lightly burned plots. Organic layer depths averaged 7.5 ± 0.7 cm (mean ± SE) in the lightly burned plots and 2.1 ± 0.1 cm in the severely burned

plots (Johnstone, 2003). Warming and control treatments were then randomly assigned to the plots.

The warming treatment used 1.77 m^2 open-top greenhouse chambers (OTCs), constructed with transparent 0.15 mm plastic sheeting covering a plastic tubing and wood frame. Greenhouses of similar design have been previously used to increase mean air temperatures by 1–3 °C in tundra environments (Marion *et al.*, 1997). Twelve control plots designed to control for greenhouse treatment effects were placed in the field at the same time that the 12 OTC and 12 control plots were positioned. These OTC–control plots were constructed with 5 cm mesh chicken-wire fence instead of plastic. We found no differences between the OTC–control and control plots in vegetation or soil parameters during the 2000–2001 seasons, so we excluded the OTC–control plots from further analyses. OTCs were removed during the winter months and then replaced in the same location at the beginning of each growing season. Hereafter, we will refer to the temperature treatments as 'ambient' vs. 'warming', and to the burn severity treatments as 'light' vs. 'severe'. The experiment was initiated in June 2000 and ran for three growing seasons.

Temperature and soil moisture

Air and soil temperatures were monitored for the duration of the growing seasons. Temperatures reported are from June 3 to July 17 of 2001 and 2002, the period during which temperature measurements were best replicated. Thermocouples (108 Temperature Probe, Campbell Scientific, Logan, UT, USA) were installed in the soil at 5 cm depth, in one plot per treatment (four total). An additional set was placed aboveground at a height of 10 cm (two to three per warming and burn severity treatment: 11 total in 2001 and eight total in 2002). In some places, two to three thermocouples were placed in a given plot and then averaged to provide a single reading. Temperatures were recorded every 15 min throughout both field seasons. Soil moisture was measured volumetrically ($cm^3\,cm^{-3}$) in the organic layer of soil core samples collected in all plots on July 11 and July 17, 2002.

Soil respiration

We measured soil respiration as CO_2 flux in all plots on each of four dates in July 2002, during the seasonal peak in plant biomass. We used a portable gas exchange system with a LiCor 6252 CO_2 analyzer (LiCor Instruments, Lincoln, NE, USA) in a dynamic, closed-chamber technique (Vourlitis *et al.*, 1993; Rochette *et al.*, 1997; Swanson & Flanagan, 2001). A 0.25 m^2 PVC collar was placed into the soil to a depth of 2 cm in each plot. We waited 10 min before commencing to allow the soil community to acclimate. A fitted plastic cover was placed over the PVC collar to create a sealed chamber, which was connected to the CO_2 analyzer via 0.33 cm diameter plastic tubing. Air from inside the chamber was circulated through an IRGA inside the LiCor 6252 and then returned to the chamber. A CR10X datalogger (Campbell Scientific) instantaneously recorded CO_2 levels every 5 s over a 3 min interval. From these data, we selected the 2 min interval in which the rate of increase in CO_2 concentrations was most constant. CO_2 flux was estimated by calculating the best-fit slope of the line denoting CO_2 vs. time. We adjusted this CO_2 flux rate according to the volume of the chamber to calculate mg $CO_2\,m^{-2}\,h^{-1}$.

Soil sampling

After soil respiration measurements were completed, soil samples were collected within the boundaries of the PVC collar of the CO_2 chamber. Two 10 cm deep × 4 cm diameter soil cores were removed from each plot and packed in ice. One was subsequently stored at 4 °C for analyses of SOM and bacterial abundance. Fungal biomass (as ergosterol) was determined on the other, which was immediately fixed with 90% isopropyl alcohol after field collection, frozen within 2 h, and then freeze-dried within 2 weeks. This approach minimizes ergosterol losses from field-collected samples (Newell, 1995).

SOM

SOM was measured by mass loss of soil after incineration at 360 °C (Storer, 1984). The organic horizon of each core was removed and dried at 100 °C for 24 h. Two plots were excluded as insufficient organic soil was present. (We required 5 g for the analysis.) Two replicate subsamples of dried soil (2.5 g each) were weighed and then incinerated in an ashing oven (Isotemp, Fisher Scientific, Hampton, NH, USA). After incineration, soils were dried again at 100 °C for 4 h before weighing.

Microbial abundance

We used Biolog EcoPlates™ (Catalog #1506, Biolog Inc., Hayward, CA, USA) as an index of abundance of eubacteria and archaea (Garland & Mills, 1991; Garland, 1997). Each Biolog plate consists of three replicates of 32 wells. Thirty-one wells contain different carbon substrates (one substrate/well) and one well serves as a control. The carbon substrates are a rough

representation of the carbon substrates that eubacteria and archaea are likely to use in their natural environment. Microbial activity is detected by tetrazolium dye in each well, which turns purple once reduced. Samples with greater density of active microbes will turn color faster (Garland, 1997).

All samples were processed under sterile conditions within 48 h of collection from the field. Ten milliliters of 0.87% sodium chloride was added to 1 g of soil from each plot and diluted 1 : 10 000. We then added 150 μL of the soil dilution into each of the 32 wells on the plate and incubated the plates at 22 °C for 6 days. Absorbance of the well color at 529 μm was determined every 24 h using a microplate reader (EL800, Biotek Instruments, Winooski, VT, USA).

We measured fungal abundance by extracting ergosterol, a compound found within the cell membranes of living fungi only (Nylund & Wallander, 1992). To 1 g of each soil sample, 4 mL of 10% potassium hydroxide and 1 mL cyclohexane were combined in a 15 mL culture tube and vortexed. Samples were sonicated for 15 min, and then heated at 70 °C for 90 min. An additional 2 mL cyclohexane plus 1 mL deionized water were added, and the mixture was mixed thoroughly. The top phase, which was cyclohexane, contained the ergosterol. This fraction was isolated. Two milliliters of cyclohexane was added again to the soil solution, mixed, and top phase (cyclohexane) was collected. The two cyclohexane phases were combined and evaporated under nitrogen gas at 40 °C. The extracted ergosterol was diluted to 3 mL with methanol, heated in a water bath at 40 °C for 15 min, and passed through a 0.2 μm PTFE filter. The extract was stored in a refrigerator in the dark until processing on a high-performance liquid chromatography device (Polaris System, Varian Inc., Woburn, MA, USA) equipped with a C18 reverse-phase column (Chrompack Microsorb 300-5, $250 \times 4.6\,mm^2$; Varian Inc.). Methanol was used as an eluent, and the ergosterol peak appeared at 7.5–8 min. Ergosterol concentrations were calculated by comparing peak area with an ergosterol standard (ICN Biomedicals, Aurora, OH, USA).

Root biomass

Roots were extracted from soil cores after all other measurements were completed. Soil was removed from the roots using 1 mm sieves. Roots were rinsed thoroughly, dried at 60 °C for 48 h, and then weighed.

Statistics

All statistical analyses were performed with JMP IN statistical software (v. 4, SAS Institute, Cary, NC, USA). We analyzed all response variables except CO_2 flux by applying a two-way analysis of variance (ANOVA) with warming and burn severity as treatment factors. We used repeated measures ANOVAs to analyze air temperature, soil temperature, and CO_2 flux from multiple measurement dates. Carbon dioxide flux, root biomass, and SOM data were log transformed in order to maintain statistical assumptions of normality. Differences were considered significant when $P < 0.05$.

Results

Temperature and soil moisture

Air temperatures at 10 cm height were marginally significantly higher in the warming plots than in ambient plots, with an average increase of 0.4 °C during both 2001 and 2002 (Tables 1 and 2). Burn severity had no discernable effect on air temperature (Tables 1 and 2), and there was no interaction between warming and burn treatments. Soil temperatures were measured in only one plot per treatment, so our ability to distinguish treatment effects statistically was limited. In plots

Table 1 Mean daily temperatures and soil moisture June 3–July 17 of 2001 and 2002

Temperature treatment	Burn severity	Year	Air temperature (°C)*	Soil temperature (°C)	Soil moisture (%)†
Ambient	Light	2001	15.79 ± 0.33 (3)	17.16 (1)	nd
		2002	14.83 ± 0.07 (2)	16.73 (1)	11.22 ± 1.36 (6)
Warming	Light	2001	16.16 ± 0.17 (3)	18.12 (1)	nd
		2002	15.26 ± 0.29 (2)	18.10 (1)	10.73 ± 0.90 (6)
Ambient	Severe	2001	15.83 ± 0.21 (3)	17.46 (1)	nd
		2002	15.17 ± 0.25 (2)	16.48 (1)	10.24 ± 0.53 (6)
Warming	Severe	2001	16.37 ± 0.23 (2)	18.10 (1)	nd
		2002	15.62 ± 0.38 (2)	17.06 (1)	13.18 ± 2.27 (6)

*Mean ± SE (*n*).
†Volumetric measurements on July 11 and 17, 2002.
nd, not determined.

Table 2 Statistical results of warming and burn severity treatments

	Warming		Burn severity		Warming × burn severity interaction		Date*	
	F-ratio	*P*-value	*F*-ratio	*P*-value	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Air temperature	5.20	**0.09**‡	1.45	0.30	0.02	0.90	261.97	**0.001**
Soil temperature†	5.71	**0.08**	0.08	0.80	0.27	0.63	21.51	**0.01**
Soil CO_2 flux	4.61	**0.04**	5.37	**0.03**	0.11	0.75	144.26	**0.001**
Soil organic matter content	1.56	0.23	14.64	**0.002**	1.33	0.27	nd	nd
Bacterial abundance	0.14	0.72	0.14	0.72	0.02	0.88	nd	nd
Fungal abundance	0.04	0.84	50.49	**0.0001**	0.04	0.84	nd	nd
Root biomass	4.55	**0.05**	16.46	**0.0006**	0.06	0.81	nd	nd

*Temperature, between years; CO_2 flux, among sampling dates in July 2002.
†Includes estimates based on air temperature (Fig. 1).
nd, not determined.
‡Significant *P*-values in bold.

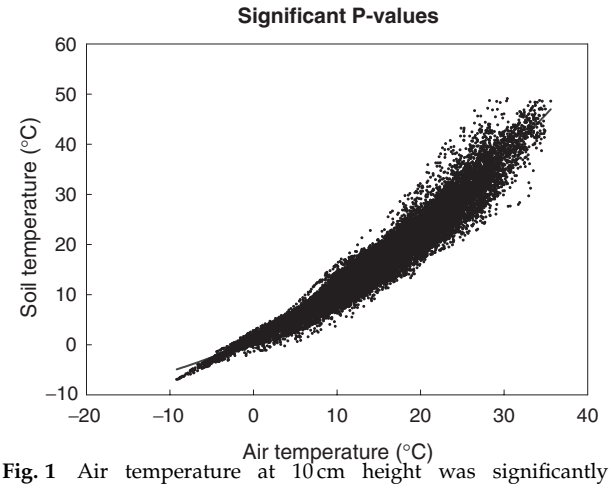

Fig. 1 Air temperature at 10 cm height was significantly correlated with soil temperature at 5 cm depth. Symbols represent average instantaneous temperatures across all treatments at 15 min intervals throughout the growing seasons of 2000, 2001, and 2002. Line is best fit linear regression: soil temperature = 0.014 (air temperature)^2 + 0.8 (air temperature) + 1.1 ($r^2 = 0.94$).

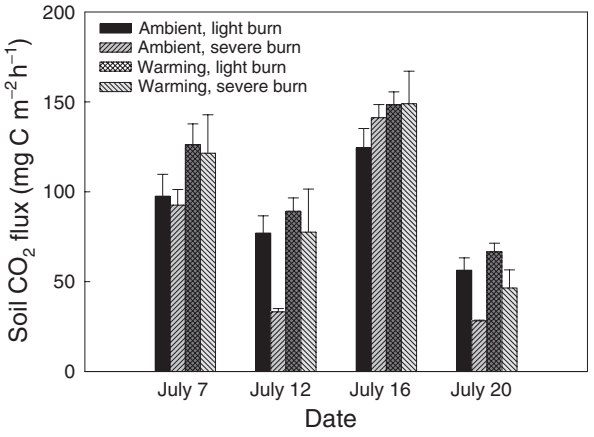

Fig. 2 Warming significantly increased soil CO_2 flux across all measurement dates in 2002. Symbols represent means (± SE) of six plots.

where air temperature and soil temperatures were measured simultaneously, average air temperatures across treatments were significantly correlated with average soil temperatures (Fig. 1; Pearson's correlation, $r = 0.965$, $n = 24426$, $P < 0.01$) across the entire experimental period (i.e. growing seasons of 2000–2003). We used a best-fit linear regression of this relationship (Fig. 1) to estimate soil temperatures in an additional four plots where direct soil temperature measurements were not available. Actual soil temperatures were consistently greater in the warming treatment than in the ambient treatment (Table 1). When estimated soil temperatures were included, a repeated measures ANOVA indicated that OTCs warmed soil temperatures by 0.9 °C during both years, and that this effect was marginally significant (Table 2). We found no indications of burn severity effects on soil temperature, and neither warming nor burn severity treatments significantly affected soil moisture (Tables 1 and 2).

Soil respiration

Soil CO_2 flux was 20% higher in warmed plots than in ambient plots across all measurement dates; this difference was significant (Table 2, Fig. 2; warming: 103.1 ± 7.1 mg C m^{-2} h^{-1}; ambient: 82.8 ± 6.3 mg C m^{-2} h^{-1}). Soil CO_2 flux was significantly reduced by 11% in severely burned plots compared with lightly burned plots (Table 2, Fig. 2; severe burn: 87.64 ± 9.08 mg C m^{-2} h^{-1}; light burn: 98.23 ± 5.85 mg C m^{-2} h^{-1}), but there were no significant warming × burn severity

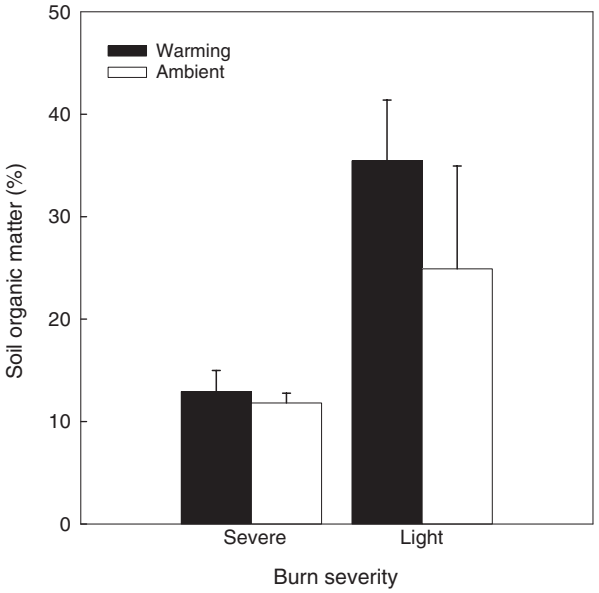

Fig. 3 Warming did not significantly affect soil organic matter (SOM) content; however, severely burned plots had significantly less %SOM than the control burn. Bars represent means (± SE) of six plots.

interactions (Table 2). Measurement date significantly affected soil CO_2 flux, but a consistent trend of increased flux was maintained in the warmed plots across all dates (Table 2, Fig. 2).

SOM

Percent SOM did not change in response to warming. Severely burned areas, however, had 60% less SOM than lightly burned plots (Table 2, Fig. 3). This pattern is consistent with the $\sim 60\%$ reduction in organic layer depth in the severely burned plots (see Methods).

Microbial abundance

Biolog EcoPlate™ analysis indicated that the abundance of active eubacteria and archaea was not affected by either elevated temperatures or burn severity (Table 2, Fig. 4a). Active fungal biomass, as ergosterol, was not changed by elevated temperatures (Table 2, Fig. 4b). However, ergosterol was not detectable in the severe-burn plots, indicating that severe burns effectively eliminated fungi.

Root biomass

Root biomass was strongly affected by both experimental treatments. Specifically, root biomass declined significantly in response to warming (warming: $3.4 \pm 1.0\,mg\,cm^{-3}$ soil; ambient: $5.1 \pm 0.8\,mg\,cm^{-3}$ soil)

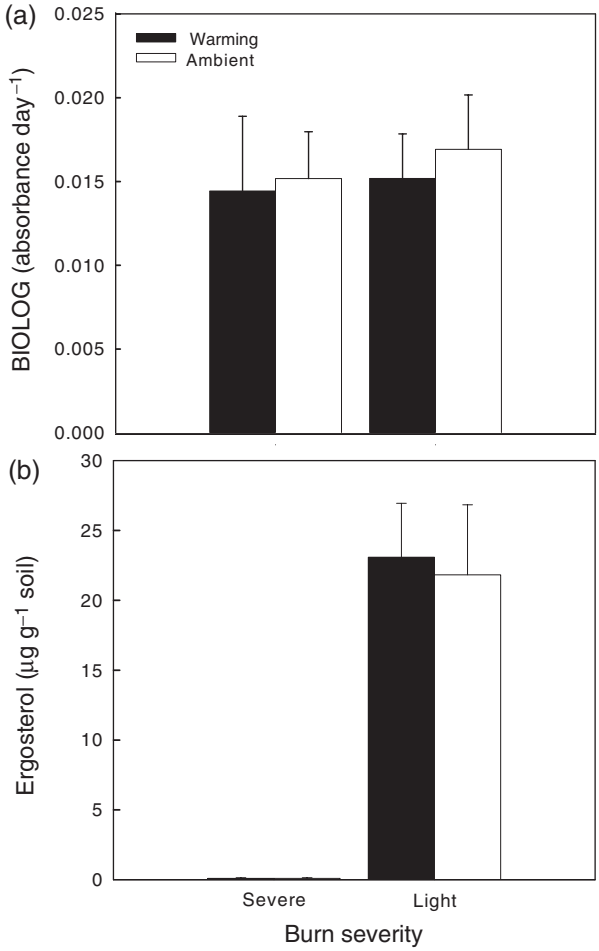

Fig. 4 Burn severity had no effect on (a) bacterial abundance but it significantly decreased (b) fungal abundance in soil. Proxy for bacterial abundance was rate of color development of Biolog EcoPlates™. Ergosterol content was used as an index of live fungal biomass. Bars represent means (± SE) of six plots.

and burn severity (severe: $2.6 \pm 0.6\,mg\,cm^{-3}$ soil; light: $6.0 \pm 1.2\,mg\,cm^{-3}$ soil; Table 2, Fig. 5).

Discussion

Our data support the hypothesis that soil respiration should increase under warming. Variations in burn severity influenced respiration levels, but did not affect the magnitude or direction of the warming response. This study is the first to document the effect of global warming on soil carbon flux in postfire soils of the boreal region. The level of experimental warming used here (0.4–0.9 °C) is consistent with the magnitude of temperature increases observed over the past century (Keyser *et al.*, 2000), indicating that carbon fluxes in boreal soils are already likely to be responding to observed changes in climate.

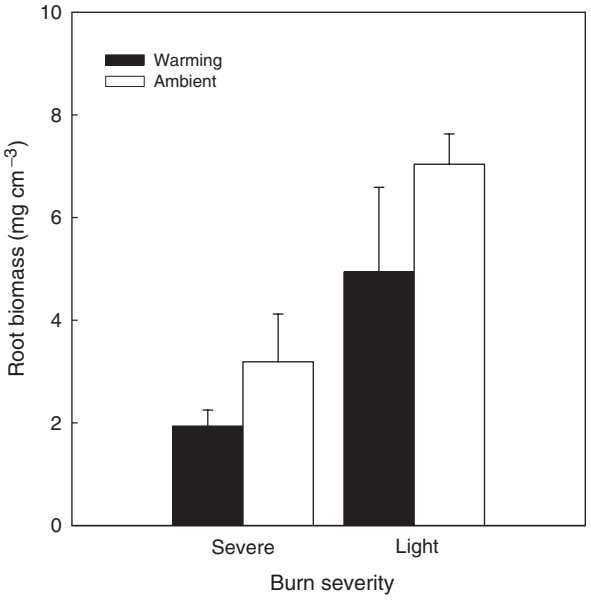

Fig. 5 Root biomass was significantly higher at ambient temperatures and light burns. Bars represent means (± SE) of six plots.

The augmentation of soil respiration under warming is consistent with previous experimental warming manipulations that produced increased decomposition rates or soil respiration in a wide range of biomes (Rustad *et al*., 2001), including arctic (Nadelhoffer *et al*., 1991) and boreal (Van Cleve *et al*., 1990) regions. In addition, our results confirm numerous modeling studies that predict significant losses of carbon from northern soils in response to warming (Schimel *et al*., 1994; Goulden *et al*., 1998; Price *et al*., 1999; Schlesinger & Andrews, 2000). In our study, higher soil respiration rates were not associated with compensatory increases in root biomass or standing pools of microbes, suggesting that postfire boreal soils may be a net source of CO_2 to the atmosphere in a warmer climate.

Our findings add to the mounting evidence that elevated temperatures can increase microbial activity – but not necessarily microbial biomass – in high-latitude soils. For example, in one experimental warming study in two arctic communities of Sweden, Jonasson *et al*. (1999) reported no net increase in microbial C, N or P. Nevertheless, mineralization rates increased. In an OTC experiment in Alaskan tundra, warming elicited no net increase in carbon flux or storage (Hobbie *et al*., 1999), although decomposition rates rose (Hobbie, 1996).

The divergent responses of soil CO_2 flux and soil microbe abundance to experimental warming in our study suggests that changes in soil respiration activity can occur without large changes in the numbers or biomass of soil microbes. This ecological response is an important consideration in quantifying microbial abundance in response to global changes, and in linking microbial activity to carbon flux measurements. The increase in soil respiration with warming observed in our study could be explained by increased metabolic activity of the existing microbes and roots. It is possible that root respiration increased with warming despite the significant decline of root biomass, if root activity increased without adding biomass. Alternatively, the metric we employed to estimate bacterial abundance (i.e., an indicator dye that provides a proxy for bacterial growth on specific carbon substrates) may be too coarse to detect biomass changes in specific, highly active bacterial groups that could be responsible for a significant portion of microbial CO_2 flux.

Fire has been shown to be a major driver of net carbon storage in boreal ecosystems because of its role in periodically exporting large amounts of carbon to the atmosphere or to deeper soil layers (Kasischke *et al*., 1995; Harden *et al*., 2000). As the level of fire severity is a measure of the proportion of carbon that is lost from an ecosystem because of combustion of organic material, it should be a good indicator of how well carbon stores are retained across a disturbance cycle. However, our data indicate that postfire rates of soil respiration are higher in lightly burned soils compared with severely burned soils. As a result, rates of carbon storage in lightly burned soils are likely to be overestimated if based on combustion losses alone. Rates of postfire respiration may be reduced in severely burned soils because of substrate limitation or reductions in fungal biomass. In comparison, soil respiration rates in a neighboring unburned black spruce forest averaged 132, 162, and 147 mg C m^{-2} h^{-1} for July 13, 17 and 21, 2002 (B. Bergner, unpublished data). These rates were consistently higher than those within the fire scar, potentially owing to a better-established root system (O'Neill *et al*., 2002, 2003) or decomposer community (Treseder *et al*., 2004) in the older ecosystem. In general, fires reduce subsequent soil respiration, and the more severe the fire, the greater the effect.

The lack of fungal recovery in our severe-burn treatment 3 years after fire may have implications for rates of vegetation colonization and plant community composition, since mycorrhizal fungi facilitate plant growth through their symbiosis with plants. Indeed, the markedly different species composition between our two burn severity treatments (see Methods) indicates a strong effect of severity on patterns of initial vegetation colonization. In addition, the hyphal biomass of both mycorrhizal and saprophytic fungi contributes to the organic soil layer. Subsequently, soil carbon pools may accumulate at a slower rate after severe fires because of the delay in fungal growth and plant colonization.

Bacteria often display greater tolerance of high soil temperatures associated with ground fire than do fungi (Neary *et al*., 1999). The ability of bacteria to remain where fungi could not in our severe-burn treatment is consistent with this pattern. Although we did not find a significant effect of warming on fungal or bacterial abundance, this result does not rule out the possibility that microbes could have been more responsive immediately after the fire, when dead material provided a pool of easily accessible substrates for decomposition.

Soil respiration in boreal regions has been previously shown to exhibit a high sensitivity to temperature changes (Burke *et al*., 1997; Nakane *et al*., 1997; Savage *et al*., 1997; Goulden *et al*., 1998; Lindroth *et al*., 1998). We found a 20% increase in soil respiration in response to a relatively moderate (0.4–0.9 °C) temperature increase. Although this level of temperature increase is consistent with recent warming trends (Keyser *et al*., 2000), global warming is predicted to raise average annual temperatures in northern ecosystems by 2–5 °C over the next century (Houghton *et al*., 2001). Thus, our warming manipulation provides a conservative measure of ecosystem responses in a warmer climate, but greater magnitudes of warming might increase the magnitude of soil respiration response.

The temperature responses of postfire soils are likely to be inherently transient, however, as succession elicits rapid changes in vegetation biomass and soil carbon inputs during the first decades after fire (Amiro *et al*., 2001). Thus, although soils may have the potential to acclimate to long-term changes in climate (Schimel *et al*., 2000; Melillo *et al*., 2002), annual- to decadal-scale responses of boreal soils are likely to be strongly influenced by transitory disturbance effects. Changes in the amount of soil carbon released to the atmosphere by fire, either due directly to combustion or to temperature stimulation of postfire respiration, may significantly affect the potential for boreal forests to act as a net sink of atmospheric carbon (Kasischke *et al*., 1995).

In conclusion, our results suggest that fire-disturbed boreal forest soils will release more carbon under global warming but less carbon in more severely burned areas, at least within a few years after fire. Thus, decreases in soil respiration associated with high-severity burns may be increasingly offset by increases in soil respiration under a warmer climate. Future research is needed to determine whether the positive response of soil fluxes to increases in temperature within fire scars will persist across subsequent successional stages. Regardless, policy makers in countries containing a significant amount of boreal forest in their territory might consider that current carbon budgets may not be maintained in the future if temperatures rise by as little as 1 °C.

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