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## RELATIONSHIPS AMONG FIRES, FUNGI, AND SOIL DYNAMICS IN ALASKAN BOREAL FORESTS

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**Abstract.** Fires are critical pathways of carbon loss from boreal forest soils, whereas microbial communities form equally critical controls over carbon accumulation between fires. We used a chronosequence in Alaska to test Read's hypothesis that arbuscular mycorrhizal fungi should dominate ecosystems with low accumulation of surface litter, and ectomycorrhizal fungi should proliferate where organic horizons are well-developed. This pattern is expected because ectomycorrhizal fungi display a greater capacity to mineralize organic compounds than do arbuscular mycorrhizal fungi. The sites were located in upland forests near Delta Junction, Alaska, and represent stages at 3, 15, 45, and 80 years following fire. Soil organic matter accumulated 2.8-fold over time. Fire did not noticeably reduce the abundance of arbuscular mycorrhizal fungi. In contrast, ectomycorrhizal colonization required up to 15 years to return to pre-fire levels. As a result, dominant mycorrhizal groups shifted from arbuscular to ectomycorrhizal fungi as succession progressed. Bacterial functional diversity was greatest in the oldest sites. Altogether, microbes that can mineralize organic compounds (i.e., ectomycorrhizae and bacteria) recovered more slowly than those that cannot (i.e., arbuscular mycorrhizae). Potential net N mineralization and standing pools of ammonium-N were relatively low in the youngest site. In addition, glomalin stocks were positively correlated with arbuscular mycorrhizal hyphal length, peaking early in the chronosequence. Our results indicate that microbial succession may influence soil carbon and nitrogen dynamics in the first several years following fire, by augmenting carbon storage in glomalin while inhibiting mineralization of organic compounds.

**Key words:** Alaskan boreal forest; Biology; chronosequence; external hyphae; fire and soil microbes; glomalin; microbial community; mineralization; mycorrhizal fungi; organic material; soil carbon and nitrogen; succession.

### INTRODUCTION

An estimated 90–290 Pg carbon (C) resides in boreal soils (Schlesinger 1977, Post et al. 1982, Chapin and Matthews 1992), accounting for 12–42% of global stocks of soil organic C (Batjes 1996). As such, feedbacks between climate and boreal regions have received much consideration as components of climate change (e.g., Kasischke and Stocks 2000a). Fires are a chronic disturbance in these systems, with return intervals of 70–500 years (Stocks 1991, Payette 1993, Kasischke et al. 2002). Historical fire records have indicated an almost threefold increase in annual area burned in North America over the past 30 years (Kasischke and Stocks 2000b, Murphy et al. 2000). Thus, fires represent an element of global change that may increase fluxes of carbon from ecosystems to the atmosphere. Carbon losses may be accentuated if microbial activity increases after fire owing to elevated soil temperatures. This hypothesized response has often been incorporated into fire models (e.g., Kasischke et

al. 2000, Kasischke and Stocks 2000a). However, empirical tests of this effect are rare.

An important consideration is that fire often reduces the abundance and diversity of fungi and bacteria (Neary et al. 1999). Microbes are affected immediately by the fire itself, and are then influenced in the long term by subsequent alterations in substrate availability, microclimate, and the presence of host plants for mycorrhizal fungi. Read (1991) has hypothesized that the amount of soil organic matter present in an ecosystem may control the dominance of major mycorrhizal groups. Specifically, he has suggested that arbuscular mycorrhizal (AM) fungi should dominate where nutrients are primarily in mineral form, because since this group only acquires inorganic compounds. In contrast, ectomycorrhizal (ECM) fungi should be most abundant in forests with a well-developed litter layer, because they produce enzymes that mineralize organic material such as proteins, cellulose, and phosphorus compounds (Abuzinadah and Read 1989, Read 1991). In extreme cases, ericoid mycorrhizal fungi should be favored on mor soils. This group can degrade even extremely recalcitrant compounds such as lignin (Haselwandter et al. 1990), chitin (Leake and Read 1990), and tannins

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PLATE 1. Three years after a severe fire in 1999, a diverse community of herbaceous plants, tree seedlings, and shrubs spreads through the understory while dead black spruce still dominate the canopy. Photo credit: K. Treseder.

(Leake 1987). This hypothesis can be applied to long-term changes in soil chemistry observed during secondary succession in boreal forests. Specifically, burned areas should be dominated by AM fungi in early stages and ECM fungi in later stages. Ericoid fungi may take over at the final stages if soils are moist enough to form bog-like conditions that inhibit decomposition.

These three groups of mycorrhizal fungi have contrasting effects on soil dynamics. Ectomycorrhizal and ericoid fungi contribute to mineralization of organic material, but AM fungi augment soil carbon storage by producing glomalin, a recalcitrant glycoprotein (Wright et al. 1996, Rillig et al. 2001). Shifts between these groups during succession have implications for carbon and nitrogen cycling. Nevertheless, few studies have concurrently measured mycorrhizal and nutrient dynamics during post-fire recovery in boreal forests.

In our study, we used a fire chronosequence in upland boreal forests of Alaska (see Plate 1) to test the hypothesis that the rate of recovery of microbial groups should be linked to the capacity of each group to decompose organic material (*sensu* Read 1991). We predicted that glomalin should be most abundant earlier in succession, owing to proliferation of AM fungi. In contrast, N mineralization should be low in the youngest site, where organic pools are relatively small. The chronosequence sites are well-drained, and host plants of ericoid fungi constitute <20% of standing biomass in any site (M. C. Mack, *unpublished data*). As such, we did not measure abundance of ericoid fungi. Instead, we assessed the functional diversity of bacteria, which represent another decomposer group that can metabolize a wide range of substrates. O'Neill et al. (2003) have found that soil respiration declines in the first several years following fire near our sites; delays in recovery of microbes that perform mineralization may be a possible mechanism underlying this response.

#### METHODS

##### Sites

We selected four study areas from a fire chronosequence in upland boreal forests near Delta Junction in

the interior of Alaska (63°55' N, 145°44' W; Fig. 1). Sites had been burned in severe fires during the summers of 1999, 1987, or 1956. A "control" site was established in 80-year-old *Picea mariana* (black spruce) forest selected to have plant species composition and tree density similar to that of the site burned in 1999. All sites are located within a 100-km<sup>2</sup> landscape on gently sloped alluvial flats. Portions or all of this chronosequence have been used to assess effects of fire on soil carbon fluxes (O'Neill 2000, O'Neill et al. 2003), soil chemistry (King et al. 2002), and hydrogen fluxes (Rahn et al. 2002).

Plant communities in the sites represent several stages of secondary succession. The 1999 burn has high plant diversity and fairly equitable representation of evergreen and deciduous shrubs, herbaceous perennials, and deciduous trees (Table 1). The same species are present in the 1987 and 1956 burn, but deciduous trees have the greatest biomass and productivity. Saplings of *P. mariana* are conspicuous in the 1956 burn. In the oldest site, *P. mariana* dominates with an understory of evergreen shrubs, lichens, and mosses (M. C. Mack, *unpublished manuscript*). Net primary productivity is highest in the 15-year-old site, and standing biomass accumulates with site age (M. C. Mack, *unpublished data*).

Soils are gelisols formed from loessal inputs carried by sediments of the Tanana River (Richter et al. 2000).

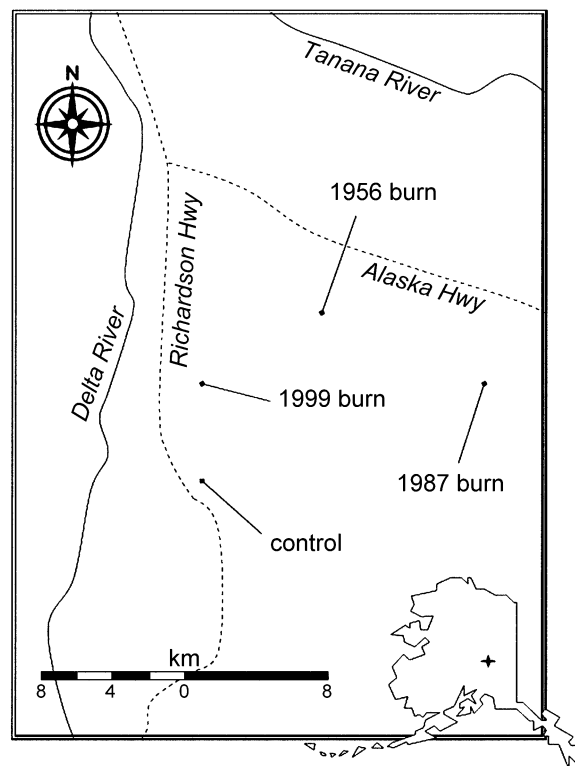


FIG. 1. Map of study area near Delta Junction, Alaska (USA).

TABLE 1. Mycorrhizal status of dominant vegetation in the Delta chronosequence.

Species†	Mycorrhizal status‡
Shrubs	
<i>Betula glandulosa</i>	ectomycorrhizal
<i>Empetrum nigrum</i>	ericoid
<i>Ledum groenlandicum</i>	ericoid
<i>Salix</i> spp.§	arbuscular + ectomycorrhizal
<i>V. uliginosum</i>	ericoid
<i>Vaccinium vitis-idaea</i>	ericoid
Herbaceous perennials	
<i>Calamagrostis canadensis</i>	arbuscular
<i>Carex bigelowii</i>	dark septate fungi
<i>Corydalis sempervirens</i>	arbuscular
<i>Epilobium angustifolium</i>	arbuscular
<i>Festuca altaica</i>	arbuscular
<i>Juncus arcticus</i>	non-mycorrhizal
<i>Lupinus arcticus</i>	dark septate fungi
Deciduous trees	
<i>Betula papyrifera</i>	ectomycorrhizal
<i>Populus tremuloides</i> §	ectomycorrhizal
Evergreen trees	
<i>Picea mariana</i>	ectomycorrhizal

† M. C. Mack, unpublished data.

‡ Schulze et al. (1994), Treu et al. (1996), Visser et al. (1998), Thormann et al. (1999), Emmerton et al. (2001), Fontenla et al. (2001).

§ Dominant canopy tree in the 1987 and 1956 burns.

|| Dominant in the understory of the 1956 burn and in the canopy of the 80-year-old control site.

Silt loams predominate, underlain by deposits of sand and gravel. In this region, permafrost is discontinuous and is not present in these sites. The oldest site has a well-developed organic horizon of 9.8 cm, on average (King et al. 2002). Fire in the 1999 burn removed approximately half of the organic horizon (King et al. 2002), and white ash deposits indicate high burn temperatures on the soil surface. The oldest and youngest sites have equivalent soil acidity, with pH of 5.5 and 5.2, respectively, in the upper 10 cm (King et al. 2002).

The regional climate is cold and dry. Mean monthly temperatures range from  $-20^{\circ}\text{C}$  in January to  $16^{\circ}\text{C}$  in July, with a record daily high of  $33^{\circ}\text{C}$  and daily low of  $-53^{\circ}\text{C}$ . July is the wettest month, with an average of 6.9 cm of rain. Winter months are driest, with averages of 0.8 cm per month, mostly as snow (National Weather Service web site).<sup>5</sup> The growing season typically lasts from bud break in May to leaf senescence in September. To measure soil temperature and moisture content, thermocouples and time-domain reflectometry (TDR) probes were installed 2, 4, and 11 cm deep in all sites except the 1956 burn. Measurements were collected in 2002 from May to August.

#### Sample collection

Our sampling regime consisted of collecting soil during the growing seasons of two consecutive years. Specific dates were: 24 July 2001; 19 May, 24 June, 25 July, and 22 August 2002. For most measurements, we

selected 10 random locations within each site, and then compiled two (in July 2001) or four (in 2002) soil cores from each location. In July 2001, measurements of N transformations were conducted on soil from six locations only, and measurements of organic material were conducted on soil from 8–15 locations. Cores were 10 cm deep by 5 cm in diameter. In the 80-year-old site, a thick moss layer was present; we defined the soil surface as the uppermost layer of dead moss tissue. Samples were kept on ice for transport back to the field laboratory in Delta Junction within four hours. In May, July, and August 2002, all cores were frozen at  $-10^{\circ}\text{C}$ . In July 2001 and June 2002, each sample was split in two. One half was frozen, and one half was stored at  $4^{\circ}\text{C}$  to be used for measurements of potential N transformation rates and bacterial diversity. Once cooled, soils were shipped to the University of Pennsylvania, Philadelphia, Pennsylvania, USA, where samples were maintained at  $4^{\circ}\text{C}$  or  $-20^{\circ}\text{C}$ , as appropriate. All soil measurements were performed on root-free soil that had been homogenized by hand-mixing. Actual numbers of samples analyzed were lower than the numbers of samples collected when some samples were discarded owing to inadequate root length (for AM or ECM colonization), difficulty viewing hyphae because of obstruction by organic matter, or damage in transit from leaky bags. We used calculations of soil bulk density (72, 94, 34, and 21  $\text{kg}/\text{m}^3$  for the 1999, 1987, 1956, and 80-year-old burns, respectively; J. Harden, unpublished data) to adjust results to an area basis based on the top 10 cm of soil.

<sup>5</sup> <http://weather.noaa.gov/>

### *Soil organic matter*

Organic matter content of soil was determined by mass loss on ignition (Storer 1984). We used root-free soils from the July 2001 sampling date. Soil from each sample was dried at 100°C for 24 h. Two replicates of 2.5 g each were heated at 360°C for 2 h in an Isotemp muffle furnace (Fisher Scientific, Philadelphia, Pennsylvania, USA). Organic material was calculated as the difference between pre- and post-ignition mass.

### *Arbuscular mycorrhizal hyphae*

Lengths of AM hyphae in the soil were determined for each 2002 sampling date, using a modified procedure from Sylvia (1992). For each sample, 10 g of air-dried soil was added to 200 mL sodium metaphosphate solution (39.5 g/L), shaken for 1 min, sonicated for 20 s, and then allowed to settle for 1 h. The solution was passed through a 425- $\mu\text{m}$  sieve, and the material retained on the sieve was discarded. The remaining solution was diluted with 400 mL deionized water, and then was shaken for 1 min. The solution was passed through a 45- $\mu\text{m}$  sieve, which retained the fungal hyphae. A squirt bottle filled with deionized water was used to transfer the hyphae to a graduated cylinder, and the volume was brought to 50 mL. The solution was transferred to a small beaker and was stirred continuously to keep the hyphae in suspension. A 10-mL subsample was collected in a syringe and then was passed through a 0.22- $\mu\text{m}$  polycarbonate filter; hyphae were thus collected on the filter. The filter was mounted on a glass slide with polyvinyl lactic acid (PVLG) slide-mounting medium and was dried at 60°C overnight. The filter was examined for the presence of fungal hyphae at 200 $\times$  magnification by using a Zeiss phase-contrast microscope equipped with Kpl8x lenses (Carl Zeiss, Thornwood, New York, USA). A point-intersect method was used to estimate hyphal lengths, with 100 points being scanned for each sample. Hyphae from AM fungi were distinguished from those of non-AM fungi (e.g., ECM fungi and saprotrophic fungi) by examining morphology. Arbuscular mycorrhizal hyphae lack septa, tend to branch angularly, and have irregular walls (Bonfante-Fasolo 1986).

### *Colonization of roots by arbuscular mycorrhizal fungi*

We used Trypan blue to stain for AM colonization (Koske and Gemma 1989) in roots from each collection date. Analyses were limited to fine roots, which we defined as <2 mm diameter. We extracted roots from the soil by spreading the soil cores onto a clean tray and pulling out all roots by hand. Fine roots were cut into 1-cm segments and approximately five segments were selected at random. We did not distinguish among roots of different plant species. Roots were heated in 2.5% potassium hydroxide at 90°C for 20 min, rinsed three times in deionized water, bleached in 0.525%

sodium hypochlorite for 20 min, and rinsed three times. Roots were acidified overnight in 1% hydrochloric acid, and then were heated in a solution of acidic glycerol and 0.05% Trypan blue for 20 min at 90°C. Finally, the samples were de-stained in acidic glycerol (50% glycerol, 45% deionized water, 0.05% hydrochloric acid) overnight, and then were mounted on glass slides with PVLG (polyvinyl lactoglycerol) medium. We used the magnified intersections method detailed in McGonigle et al. (1990) and a Zeiss phase-contrast microscope to assess the percentage of root length colonized by AM structures. At least 100 intersections were scored for each sample. Colonization by ericoid mycorrhizal fungi was not assessed.

### *Colonization of roots by ectomycorrhizal fungi*

We quantified ectomycorrhizal root tips on fine roots from each sampling date in 2002. We randomly selected ~25 cm of fine roots, rinsed them three times in deionized water, and then examined them under 40 $\times$  magnification with an Olympus SZ40 stereoscope (Olympus, Melville, New York, USA) for ectomycorrhizal tissues. A point-intersect method was used to estimate the percentage of root length covered with ectomycorrhizal sheaths (Brundett et al. 1996). Hyphal lengths of ECM fungi were not assessed because ECM hyphae are morphologically indistinguishable from non-mycorrhizal hyphae. Likewise, we were unable to quantify non-mycorrhizal biomass.

### *Functional diversity of bacteria*

Biolog EcoPlates were applied within one week of collection as a coarse index of bacterial functional diversity (Garland and Mills 1991, Garland 1997). We used saline solution to extract bacteria from unfrozen soil samples from the June 2002 collection. All procedures were aseptic. We mixed 1 g soil with 10 mL 0.87% sodium chloride, and then diluted 1:10 000. An aliquot of 150  $\mu\text{L}$  was added to each of 32 wells that comprise one-third of an EcoPlate. Each of 31 wells contains a different carbon source used by the microbial community, and the remaining well serves as a control. Microbial respiration is detected by a tetrazolium dye, which turns purple once reduced. Plates were incubated at 20°C for 6 d, after which absorbance at 590  $\mu\text{m}$  was measured using a microplate reader (EL800, Bio-tek instruments, Winooski, Vermont, USA). The number of positive wells per sample is an indication of the functional diversity of the community of eubacteria and archaea that can be effectively cultured in EcoPlates. A given well was scored as positive when the difference in absorbance between that well and the control well was greater than 0.25. In addition, the level of absorbance for a carbon source indicates the extent to which that source is metabolized. We examined absorbance levels to determine if the usage of particular carbon sources varied among sites.



### Glomalin

We used an enzyme-linked immunosorbent assay (ELISA) to determine concentrations of glomalin in our June 2002 samples (Wright and Upadhyaya 1996, Wright 2000). Glomalin was extracted from 1 g soil by adding 8 mL 50 mmol/L sodium citrate (pH 8.0), then autoclaving for 1 h at 121°C. Samples were centrifuged at 5000 g (26 000 m/s<sup>2</sup>) for 15 min, and the supernatant was reserved and stored at 4°C. The first extraction is “easily extractable” glomalin, which may be the most recently produced fraction of the glomalin pool. The extraction process was repeated as necessary until the supernatant was transparent. With the exception of the easily extractable glomalin, supernatant fractions were combined as “total” glomalin. The supernatant was assayed for glomalin concentrations using the ELISA procedure detailed in Wright (2000). Briefly, the supernatant was dried to the bottom of a microtiter plate well and was incubated with a monoclonal, glomalin-specific antibody (MAb32B11). Antibody concentrations were determined by using a microplate reader (EL800, Bio-tek instruments, Winooski, Vermont, USA) equipped with a 405-nm filter, and then comparing values to those of a glomalin standard extracted from fresh AM hyphae.

### Potential net N mineralization and nitrification

Laboratory incubations were performed within one week of collection to assess potential rates of net N mineralization and nitrification on unfrozen samples from July 2001 and June 2002. Standing pools of ammonium- and nitrate-N were determined by extracting two replicates of 5 g soil per sample with 2 mol/L potassium chloride (Keeney and Nelson 1987) and then measuring solute concentrations using an Auto-Analyzer 3 colorimeter (Bran + Luebbe; Roselle, Illinois, USA). An additional set of subsamples was incubated for six weeks, with two 5-g replicates of each sample maintained at either 15°C or 25°C in Precision 818 incubators (Precision Scientific, Winchester, Virginia, USA). These temperatures were chosen because they represent the approximate range of temperatures at the soil surface in the sites during the growing season (Fig. 2). We used two different incubation temperatures because soil CO<sub>2</sub> fluxes are controlled primarily by temperature for forests in general (Witkamp 1969, Burke et al. 1997) and these sites in particular (O'Neill et al. 2002). Incubated soils were field-moist; dry mass in the 1999 burn, 1987 burn, 1956 burn, and 80-year-old control sites was 65, 50, 35, and 60% in July 2001, and 65, 67, 55, and 46% in June 2002, respectively. Temperature treatments and respective samples were rotated among incubators each week to minimize effects of variation in incubator performance. Upon completion of the incubation period, ammonium- and nitrate-N was extracted as described before, and differ-

ences in concentrations were attributed to net N mineralization and nitrification.

### Statistics

With few exceptions, differences among sites were assessed using Kruskal-Wallis nonparametric tests, followed by Kolmogorov-Smirnov pairwise tests when indicated (Sokal and Rohlf 1995). In all cases, because we did not return to the same exact sampling locations at different sampling dates, separate statistical tests were performed for each date. For N mineralization and nitrification rates, a repeated-measures ANOVA was performed on ranked data. In many repeated-measures analyses, the unit of repetition is time. However, for the N mineralization and nitrification data, the unit of repetition was temperature. Specifically, one fraction of each sample was measured at 15°C, and a second fraction was measured at 25°C. Site was the independent variable, and either N mineralization or nitrification rate was the dependent variable. Separate tests were performed for each of the two sampling dates (July 2001 and June 2002). For EcoPlate assessments of bacterial functional diversity, we conducted a fully factorial ANOVA, with site and carbon source as the independent variables and absorbance as the dependent variable. Relationships between AM fungi and glomalin were examined by applying Pearson correlation tests. Differences are reported as significant when  $P < 0.05$ . All statistical analyses were performed using Systat 10 (SPSS 2000).

## RESULTS

### Soil microclimate

Soil temperatures declined with site age at all depths (Fig. 2). Between 1 April and 21 August 2002, mean temperatures were 7.4°, 6.7°, and 2.1°C at 11 cm depth in the 1999 burn, 1987 burn, and 80-year-old site, respectively. Soil thawed at 11 cm in the 1987 burn on 19 April, followed by the 1999 burn on 9 May, and finally in the control site on 21 May. Bud break of *Populus tremuloides* occurred on 22 May in all sites.

Compared to older sites, soils in the 1999 burn tended to be more moist near the surface and drier at depth between April and August (Fig. 2). Specifically, soil moisture at 2 cm was highest in the 1999 burn and lowest in the control site. In contrast, at 11 cm, the control site had greater soil moisture content than the 1999 or 1987 burns.

### Organic matter

Soil organic matter content increased with time after burn (Table 2). Concentrations of organic material were low two years after a burn (14.9%), and then grew 2.8-fold over the next 80 years. Differences among sites were significant in July 2001, the only sampling date (Table 3).

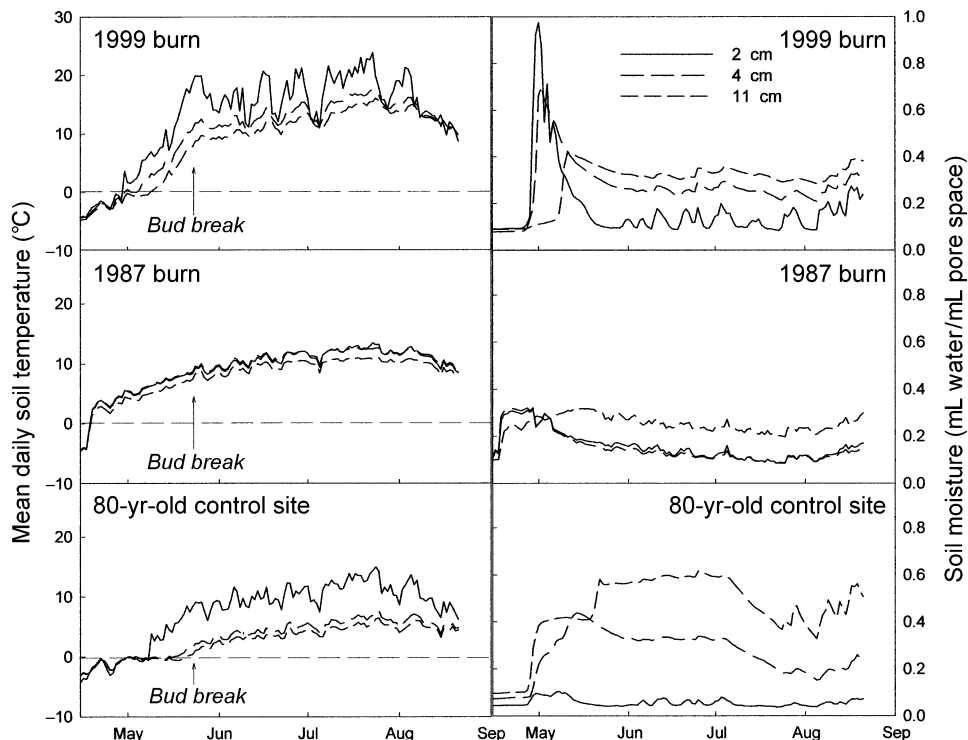


FIG. 2. Soil temperature and moisture as measured by thermocouples and TDR probes, respectively, buried in each of three sites. Lines represent daily averages of one sensor at each depth in each site. Bud break of *Populus tremuloides* was observed on 22 May 2002.

#### *Arbuscular mycorrhizal hyphae*

With the exception of the May 2002 sampling, sites were significantly different from one another in AM hyphal length (Fig. 3). In both June and July 2002, AM hyphal lengths were greatest in the 1987 burn. In July 2002, the control site had the lowest amounts of AM hyphae.

#### *Colonization of roots by arbuscular mycorrhizal fungi*

Root colonization level is a function of two variables: root length and mycorrhizal abundance. Arbuscular mycorrhizal colonization did not vary significantly among sites in any of the sampling dates (May, June, and August 2002; Fig. 4a). Moreover, the abundance of vesicles, arbuscules, or hyphae remained relatively constant across sites (data not shown). Hyphae were visible in 27%, 25%, and 28% of root lengths in May, June, and August 2002, respectively. Vesicles were most common (5%) in May 2002; and rare (<1%) in the other months. Less than 0.1% of root length was occupied by arbuscules at any time.

#### *Colonization of roots by ectomycorrhizal fungi*

In May, June, and July 2002, ECM colonization of roots was greatest in the intermediate-aged sites, lowest in the recent burn, and moderate in the control forest (Fig. 4b). Means tended to be higher in June (23.5–

76.6% root length) than in May (6.6–48.8%) and July (1.1–14.1%) for each site. However, we did not test for significant differences among sampling dates, because a repeated-measures ANOVA was not appropriate within our sampling scheme. Differences among sites were significant in May 2002, when colonization was significantly lower in the youngest site than in the older sites. Likewise, a significant site effect in June 2002 indicated that ECM colonization increased significantly between 3 and 15 years following fire, and then peaked at 45 years. Ectomycorrhizal colonization varied significantly in July as well, with higher values in the 1987 and 1956 burns than in the 1999 burn or control site.

#### *Functional diversity of bacteria*

Bacterial functional diversity, as measured with Biolog plates in June 2002 soils, was lower in the two youngest sites vs. the two oldest sites (Fig. 5). We found no evidence for shifts across sites in types of carbon metabolized, given that there was no significant site by carbon source interaction. The most extensively used carbon sources were Tween 40, Tween 80, and D-mannitol, and the least used were 2-hydroxy benzoic acid, glucose-1-phosphate, and  $\gamma$ -hydroxybutyric acid (data not shown).

#### *Glomalin*

Immunoreactive glomalin was measured in June 2002 as two fractions: easily extractable glomalin

TABLE 2. Chemistry of the Delta chronosequence soils from the top 10 cm.

Date	Incubation temp. (°C)	Burn year			80-yr-old control
		1999	1987	1956	
Potential net N mineralization (mmol N·m <sup>-2</sup> ·d <sup>-1</sup> )					
July 2001	15	0.0 ± 1.6 (6)	3.6 ± 1.6 (6)	1.3 ± 1.6 (6)	0.2 ± 1.6 (6)
	25	0.0 ± 2.9 (6)	9.2 ± 2.9 (6)	3.4 ± 2.9 (6)	0.8 ± 2.9 (6)
June 2002	15	2.9 ± 3.1 (10)	11.8 ± 3.1 (10)	11.4 ± 3.1 (10)	2.2 ± 3.3 (9)
	25	-0.2 ± 1.0 (10)	3.5 ± 1.0 (10)	3.7 ± 1.0 (10)	1.6 ± 1.1 (9)
Potential net nitrification (mmol N·m <sup>-2</sup> ·d <sup>-1</sup> )					
July 2001	15	0.0 ± 0.2 (6)	0.6 ± 0.2 (6)	0.0 ± 0.2 (6)	0.0 ± 0.2 (6)
	25	-0.1 ± 1.9 (6)	4.7 ± 1.9 (6)	0.1 ± 1.9 (6)	0.0 ± 1.9 (6)
June 2002	15	1.6 ± 0.4 (10)	2.3 ± 0.4 (10)	0.5 ± 0.4 (10)	0.2 ± 0.4 (9)
	25	0.0 ± 0.2 (10)	0.6 ± 0.2 (10)	0.0 ± 0.2 (10)	0.1 ± 0.2 (9)
Standing ammonium-N (mmol/m <sup>2</sup> )					
July 2001		1.7 <sup>a</sup> ± 18.1 (6)	55.7 <sup>a</sup> ± 18.1 (6)	43.0 <sup>a</sup> ± 18.1 (6)	3.9 <sup>a</sup> ± 18.1 (6)
June 2002		30.4 <sup>a</sup> ± 13.5 (10)	25.6 <sup>a</sup> ± 13.5 (10)	103.7 <sup>b</sup> ± 13.5 (10)	19.8 <sup>a</sup> ± 13.5 (10)
Standing nitrate-N (mmol/m <sup>2</sup> )					
July 2001		2.9 <sup>a</sup> ± 0.7 (6)	0.6 <sup>ab</sup> ± 0.8 (5)	2.0 <sup>a</sup> ± 0.7 (6)	0.0 <sup>b</sup> ± 0.7 (6)
June 2002		14.5 <sup>a</sup> ± 1.6 (10)	14.2 <sup>a</sup> ± 1.6 (10)	6.9 <sup>b</sup> ± 1.6 (10)	5.5 <sup>b</sup> ± 1.6 (10)
Organic matter (% soil mass)					
July 2001		14.9 <sup>a</sup> ± 3.3 (14)	32.6 <sup>b</sup> ± 3.2 (15)	...	42.0 <sup>b</sup> ± 4.4 (8)

Notes: Values are mean ± 1 SE with sample sizes in parentheses; where given, different letters indicate pairwise differences within a row (Tukey,  $P < 0.05$ ). Post hoc tests were not conducted for measures of potential mineralization and nitrification.

(EEG) and total glomalin (TG). These fractions mirrored one another along the chronosequence by peaking at 15 years after fire and then dropping by 45 years post burn (Fig. 6). Total glomalin content and AM hyphal lengths in June 2002 were significantly correlated (Pearson,  $r = 0.47$ ,  $df = 31$ ,  $P < 0.05$ ).

#### Potential net N mineralization, nitrification

Net N mineralization was highest in the intermediate-aged sites, and mean rates of mineralization ranged up to 11.8 mmol·m<sup>-2</sup>·d<sup>-1</sup> for both sampling times (Tables 2 and 3). We found no evidence of significant site by temperature interactions. Mineralization rates were significantly lower at 15°C than at 25°C in samples from July 2001. However, the opposite was true in June 2002, even though moisture levels were roughly equivalent in incubated soil from both sampling dates (see *Methods*).

In addition, potential net nitrification was inversely related to temperature in the June 2002 sampling, but not significantly so in July 2001 (Tables 2 and 3). Among sites, net nitrification rates peaked in the 1987 burn at both dates (Tables 2 and 3). Moreover, the degree of response to incubation temperature varied with successional stage in the June 2002 soils. The two oldest sites displayed less variation than did the younger sites, and this trend was responsible, in part, for a significant site by temperature interaction.

Patterns of standing pools of ammonium-N were not consistent among collection dates (Table 2). Differences among sites were significant in June 2002 sampling (Table 3), but not in July 2001. In particular, the 1956 burn had significantly higher concentrations of ammonium-N than did the other three sites in June

2002. In contrast, abundance of nitrate-N declined significantly as succession progressed (Tables 2 and 3), although absolute amounts varied between dates.

#### DISCUSSION

Fires in boreal forests directly and immediately alter microbial communities. Moreover, indirect effects continue for decades as secondary succession proceeds. During succession, feedbacks among soil chemistry, microclimate, plant community structure, and nutrient dynamics should influence the recovery rates of microbial groups. We can determine direct, short-term effects of forest fire in our chronosequence by comparing the 1999 burn to the adjacent 80-year-old control forest. Long-term effects can be assessed by examining trends across the chronosequence. We will discuss short-term effects of burning first, and then move on to successional processes.

#### Short-term effects

Microbial groups varied in their short-term response to fire. Specifically, we found little evidence of a decline in AM hyphae or AM colonization (Figs. 3 and 4a). Likewise, standing stocks of glomalin were not altered (Fig. 6). Either the fire had no initial effect, or the AM mycelial network recovered within a few years and restocked the glomalin pool. Arbuscular mycorrhizal fungi are relatively tolerant of high soil temperatures (Klopatek et al. 1988, Pattinson et al. 1999), which may have contributed to their resilience to fire. In contrast, studies in other biomes have frequently reported an initial decline in colonization levels or propagules (Dhillion et al. 1988, Klopatek et al. 1990, Rashid et al. 1997, Neary et al. 1999). Complete re-



TABLE 3. Statistics on soil chemistry from the top 10 cm of soil.

Measurement, date, and independent variable	df	<i>N</i>	<i>F</i>	<i>H</i>	<i>P</i>
A) Repeated-measures ANOVA					
Potential N mineralization (mmol·m <sup>-2</sup> ·d <sup>-1</sup> )					
July 2001					
Site	3, 20		4.717		0.012
Incubation temperature	1, 3		4.569		0.045
Site × temperature	3, 20		1.923		NS
June 2002					
Site	3, 35		9.018		<0.001
Incubation temperature	1, 3		21.080		<0.001
Site × temperature	3, 35		1.825		NS
Potential nitrification (mmol·m <sup>-2</sup> ·d <sup>-1</sup> )					
July 2001					
Site	3, 20		8.461		0.001
Incubation temperature	1, 3		3.790		NS
Site × temperature	3, 20		1.28		NS
June 2002					
Site	3, 35		3.860		0.017
Incubation temperature	1, 3		51.560		<0.001
Site × temperature	3, 35		3.046		0.041
B) Kruskal-Wallis					
Standing ammonium-N (mmol/m <sup>2</sup> )					
July 2001, Site		24		4.570	NS
June 2002, Site		40		17.671	<0.001
Standing nitrate-N (mmol/m <sup>2</sup> )					
July 2001, Site		23		11.024	0.012
June 2002, Site		40		22.699	<0.001
Organic matter (soil mass %)					
July 2001, Site		37		17.400	<0.001

Notes: Statistics for the ANOVA are df, *F*, and *P*; statistics for the Kruskal-Wallis test are *N*, *H*, and *P* (NS, *P* > 0.05).

covery can occur within a growing season (Dhillion et al. 1988), or may require more than 10 months (Rashid et al. 1997) or 10 years (Klopatek et al. 1990).

Ectomycorrhizal colonization tended to be lower three years after fire than in intact forest (Fig. 4b). Ectomycorrhizal fungi in coniferous forests often decline in diversity or display altered community composition following high-intensity burns (Danielson 1984, Visser 1995, Dahlberg et al. 1997, Torres and Honrubia 1997, Stendell et al. 1999, Grogan et al. 2000), although Jonsson et al. (1999) found minimal effects following a low-intensity fire. A reduction in root colonization has also been noted (Dahlberg et al. 1997, Stendell et al. 1999), with exceptions (Visser 1995, Torres and Honrubia 1997). In general, changes in community composition or colonization can be long-term; the studies just cited were conducted 4 months (Dahlberg et al. 1997) and 1 (Stendell et al. 1999), 1.5 (Grogan et al. 2000), 2 (Torres and Honrubia 1997), and 6 years (Danielson 1984) after fire. In a chronosequence of *Pinus banksiana* stands in northeastern Alberta, community composition stabilized by the 41st year of recovery (Visser 1995). Our results are consistent with these findings; ECM colonization required ~15 years to return to pre-burn levels (Fig. 4b).

Of the three microbial groups assessed in our study, bacteria displayed the strongest short-term response to fire. Bacterial functional diversity was markedly reduced even after three years of recovery (Fig. 5). Bio-log EcoPlates were used to characterize bacterial diversity, so our findings are restricted to species that can be cultured under the specific conditions present in the microtiter plates. Our results contrast somewhat with a study in Scots pine forest in Central Finland, where phospholipid fatty acid (PLFA) analysis indicated that microbial biomass had not recovered within one year of fire, and that fungi had been more severely affected than bacteria (Baath et al. 1995). The authors attributed incomplete recovery of the microbial community to changes in soil organic matter.

Altogether, our analyses indicate that microbial groups responsible for mineralization of organic material (i.e., bacteria and ECM fungi) had not recovered within three years following fire (Figs. 4b and 5). In contrast, AM fungi, which take up mineral nutrients only, were briefly affected at most (Figs. 3 and 4a). A lack of organic substrates in the soil may have compounded delays in recovery of mineralizers but not AM fungi. We also note that the three-year-old burn had fewer ECM plants than do the other sites; ECM fungi

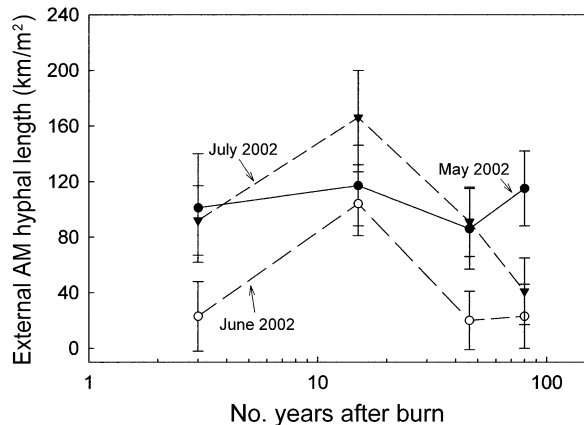


FIG. 3. Length of external arbuscular mycorrhizal hyphae extracted from the top 10 cm of soil in relation to time since burning (log scale). Symbols denote means  $\pm$  1 SE of 5–10 samples. Arbuscular mycorrhizal hyphal length varied among sites in June 2002 ( $H = 10.270$ ,  $P = 0.016$ ) and July 2002 ( $H = 11.892$ ,  $P = 0.008$ ), but not in May 2002.

may have been host-limited at early stages. Herbaceous AM plants are common in the recent burn and should facilitate re-establishment of AM fungi.

Changes in soil microclimate within the first few years after the fire were consistent with established patterns (Bonan and Shugart 1989, Van Cleve et al. 1996, Richter et al. 2000). The increase in soil temperature in the 1999 burn compared to the control site (Fig. 2) was probably due to removal of the organic horizon and overlying plant biomass, which can act as an insulating layer when intact. In addition, the recent burn contained drier soils at 11 cm depth than did the control site. Faster decomposition rates have been suggested to occur under such conditions (e.g., Bonan and Shugart 1989).

However, our results do not support an increase in microbial activity following a rise in soil temperature and aridity due to fire. We found minimal differences between the 1999 burn and the control site in potential net N mineralization and nitrification rates when soils were incubated in the laboratory (Table 2), even though June 2002 samples were drier in the recent burn compared to the control (see *Methods*). Moreover, net N mineralization and nitrification responded inconsistently to warmer incubation temperatures by increasing, decreasing, or remaining constant, depending on the sampling date and site (Table 2). Verburg et al. (1999) found that net N mineralization in a Norwegian boreal forest did not vary with temperature, because gross mineralization and immobilization of  $\text{NH}_4^+$  tended to covary.

#### Long-term effects

In other studies of secondary succession in upland black spruce forests, organic material has accumulated in the soil over decades so that at intermediate and late

stages, the majority of soil nutrients are present as organic material (Van Cleve et al. 1983, 1993, 1996, Smith et al. 2000). Likewise, we found a linear increase in soil organic matter content and a decrease in nitrate concentrations across our chronosequence (Table 2).

The sequence of mycorrhizal succession suggested by Read (1991) was loosely replicated in our fire chronosequence (Figs. 3 and 4b). In the youngest site, AM hyphae were moderately abundant, and ECM fungi were low. In the 1987 burn, both AM hyphae and ECM fungi were prevalent. Ectomycorrhizal fungi were dominant in the 1956 burn, but AM hyphae were still well-represented. Finally, AM hyphae were rarer in the oldest site, while ECM colonization was moderately high. The decline in ECM colonization between the 1956 burn and the oldest site might be attributable to the limited ability of ECM fungi to mineralize recalcitrant material (Read 1991). Black spruce litter is typically high in lignins and phenolics (Van Cleve et al. 1983), and this tree species was most abundant in the 80-year-old site. Bacteria were also most functionally diverse at this stage (Fig. 5) and could have competed more

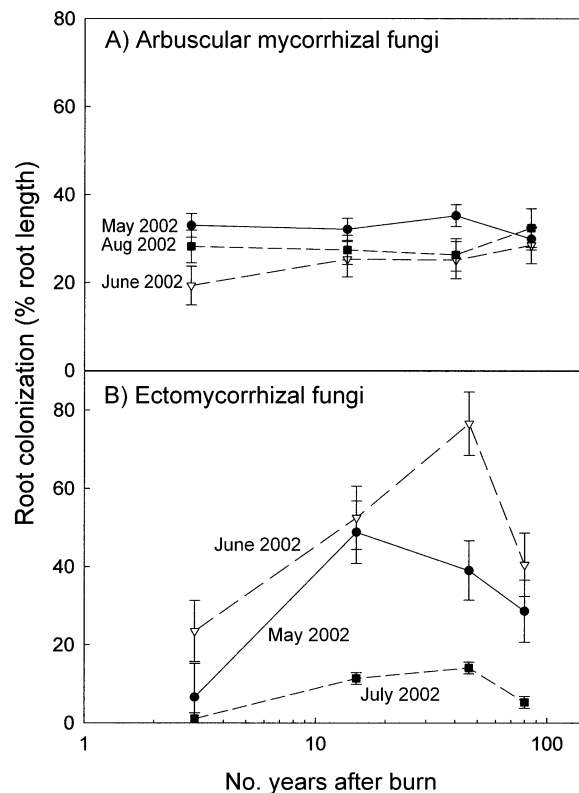


FIG. 4. Colonization of roots by (a) arbuscular mycorrhizal fungi (AM) and (b) ectomycorrhizal fungi (ECM), in relation to time since burning (log scale). Symbols are means  $\pm$  1 SE of 5–10 samples (AM) or 7–10 samples (ECM). Colonization by AM did not differ significantly across sites at any time. Variation among sites was significant for ECM in May 2002 ( $H = 15.461$ ,  $P = 0.001$ ), June 2002 ( $H = 19.141$ ,  $P < 0.001$ ), and July 2002 ( $H = 24.224$ ,  $P < 0.001$ ).

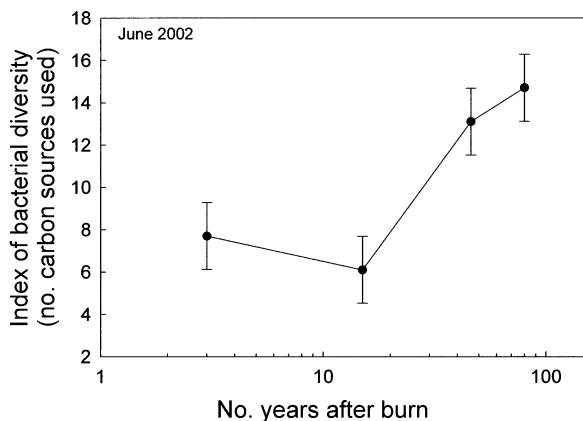


FIG. 5. Functional diversity of bacteria from soils of chronosequence sites in relation to time since burning (log scale), as measured by Biolog EcoPlates after six days of incubation. Symbols represent means  $\pm$  1 SE of 10 samples. Sites varied significantly in functional diversity ( $H = 13.961$ ,  $P = 0.003$ ), as indicated by the number of carbon sources used (of a possible 31). Absorbance values indicate the extent to which the carbon sources are metabolized; these values varied significantly among sites ( $F_{3,30} = 52.790$ ,  $P < 0.001$ ) and carbon sources ( $F_{30,90} = 17.085$ ,  $P < 0.001$ ). There was no significant site  $\times$  carbon-source interaction.

effectively with ECM fungi. The rise in bacterial functional diversity with site age may be related to increasing complexity of soil organic matter and spatial structure. We note that AM colonization of roots did not vary across sites (Fig. 4a), but colonization levels are a function of both AM and root abundance. If root production were highest in the intermediate-aged sites, this variation would account for discrepancies between colonization levels and external hyphal lengths. In general, mycorrhizal communities appear to progress through succession on a time scale similar to that of their host plants. Plants and mycorrhizal fungi may be influenced by the accumulation of soil organic matter, either directly or indirectly through their symbiotic partners.

Net N mineralization rates, and to some extent, net nitrification rates and standing pools of ammonium-N, were highest in the intermediate-aged sites (Table 2). Overall, nitrogen availability appeared to increase with succession until black spruce trees established at 45 years after fire. Delays in recovery of bacterial groups (Fig. 5) or ECM communities (Fig. 4b) may contribute to low activity in the first two decades post-burn. The rise in N transformation rates over the first two decades could also be due to accumulation of leaf litter from earlier successional plants. These species tend to have relatively low lignin : N ratios (Van Cleve et al. 1983), and should decompose relatively quickly. In contrast, slowly decomposing black spruce litter may be primarily responsible for the decline in nutrient availability at later stages. A fertilization study by Yarie and Van Cleve (1996) indicated that carbon limitation of saprotrophic activity increases over time and is least

pronounced at early stages of fire recovery in boreal upland forest. DeLuca et al. (2002) reported a decline in net N mineralization along a fire chronosequence of Swedish Scots pine forests, potentially due to greater  $\text{NH}_4^+$  immobilization in older sites. A corresponding reduction in net nitrification with age was attributed to increasing concentrations of phenolics at later successional stages (DeLuca et al. 2002).

Modeling studies indicate that the amount of C directly released from burning could be roughly equivalent to the amount lost due to post-fire changes in the ecosystem (Kasischke et al. 1995, O'Neill et al. 2003). Specifically, the removal of an insulating moss layer by fire increases subsequent soil temperatures. In turn, deeper thawing of permafrost should improve soil drainage. Together, these changes may elicit faster decomposition rates (Bonan and Shugart 1989). Soil  $\text{CO}_2$  emissions or decomposition rates in situ are often higher under warmer soil conditions that occur through temperature manipulation (Fox and Van Cleve 1983, Bonan and Van Cleve 1992, Billings et al. 1998), natural variation in climate (Schlentner and Van Cleve 1985, Goulden et al. 1998, Hirsch et al. 2002), or after forest clearing (Gordon et al. 1987). However, fire-related field studies have reported that soil respiration often declines for the first several years after fire in spite of warmer soil temperatures (Burke et al. 1997, Savage et al. 1997, O'Neill 2000, O'Neill et al. 2002); this response has been observed near our sites as well (O'Neill et al. 2003). The decline in  $\text{CO}_2$  emissions has usually been attributed to losses of root and moss respiration rather than to declines in heterotrophic respiration. However, our results indicate that fire is a considerable disturbance to the microbial community,

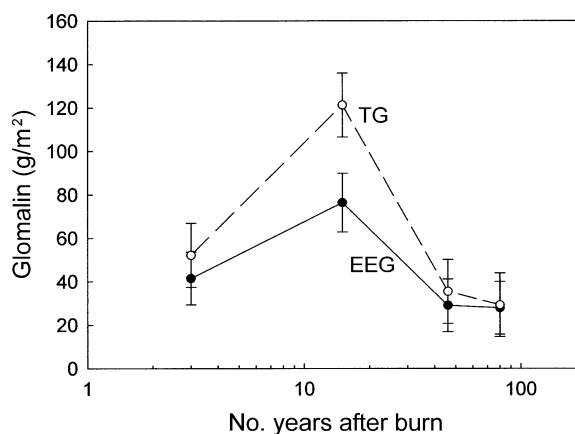


FIG. 6. Glomalin concentrations in soil from the upper 10 cm in relation to time since burning (log scale), as determined by an enzyme-linked immunosorbent assay on samples from June 2002. Glomalin is produced only by arbuscular mycorrhizal fungi and is measured as two fractions: easily extractable glomalin (EEG) and total glomalin (TG). Symbols are means  $\pm$  1 SE of 8–10 samples. Differences among sites were significant for both EEG (Kruskal-Wallis,  $H = 8.467$ ,  $P = 0.037$ ) and TG ( $H = 17.738$ ,  $P < 0.001$ ).

and soil activity might remain low until decomposer groups recover.

Fire elicited an increase in C sequestration in glomalin for the first 15 years of succession (Fig. 6), corresponding to trends in AM hyphal length (Fig. 3). In the 1987 burn, glomalin-C was 9–20 g/m<sup>2</sup> higher than baseline levels in mature black spruce stands (represented by the 80-year-old burn), given that glomalin contains 10–22% C (Rillig et al. 2001). However, because fires in black spruce forests directly remove an estimated 1000–7600 g C/m<sup>2</sup> by burning (Kasischke et al. 2000), the amount of C stored in glomalin is comparatively small. Knorr et al. (2003) reported no effect of fire frequency on glomalin stocks in oak–hickory forests of eastern North America.

### Conclusion

Overall, fire appears to produce decades-long alterations in the structure and activity of microbial communities in boreal forests, potentially due to long-term changes in soil chemistry. As a result, the documented increases in fire frequency in the northern latitudes (Kasischke and Stocks 2000b, Murphy et al. 2000) may shift regional microbial communities toward groups that exploit inorganic nutrients. It is possible that the delayed recovery of decomposers during succession may limit initial increases in soil respiration or nutrient mineralization following fire.

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