



Changes in soil chemical and biological properties after thinning and prescribed fire for ecosystem restoration in a Rocky Mountain Douglas-fir forest

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ABSTRACT

Practices such as thinning followed by prescribed burning, often termed 'ecosystem restoration practices', are being used in Rocky Mountain forests to prevent uncontrolled wildfire and restore forests to pre-settlement conditions. Prior to burning, surface fuels may be left or collected into piles, which may affect fire temperatures and attendant effects on the underlying soil. The objective of this study is to determine which pre-fire fuel management treatments best reduce fuel loadings without causing fire temperatures high enough to impair soil chemical and biological properties. Five fuel-management treatments were compared: large piles, small piles, cut and leave, slash-free areas around mature leave-trees, and unburned control. We measured key properties of forest floors and mineral soil (forest floor depth, soil pH, carbon and nutrient levels, and microbial abundances) prior to and during the first year after fire, and explored relationships among fuel loadings, fire temperatures and changes in these soil properties. Fire temperatures were above 300 °C for more than 3 h in the large-pile treatment but were lower and of shorter duration in the small-pile and cut-and-leave treatments. The most severe fire effects occurred around the leave-trees where temperatures were above 200 °C for more than 2 h, the forest floor was completely consumed, and the mature trees were killed. In the forest floors, abundances of all microbial groups were reduced and pH and availabilities of Ca^{2+} , Mg^{2+} and PO_4^{3-} were increased in all burned treatments. Forest floor C and N contents were reduced in burned plots by an average of 39% and 44% respectively, and availabilities of nitrate and sulphate were increased in the leave-tree areas only. There were few significant changes in mineral soil properties – pH and availabilities of NO_3^- , Mg^{2+} and SO_4^{2-} increased in leave-tree areas whilst PO_4^{3-} and K^+ increased under large piles. Microbial abundances had not recovered to pre-fire levels in any burned treatments after one year, which may be attributed to the persistence of significant increases in pH. Prior to the fire, microbial abundances were most closely related to N concentration in the forest floor, and C and N concentrations in the mineral soil; after fire, microbial abundances were most closely related to pH of the forest floor. Forest floor consumption and attendant changes in chemical and biological properties were most closely related to pre-fire moisture content, indicating that forest-floor moisture content may be as critical as fuel loading in determining impacts of prescribed fire on soil.

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1. Introduction

Management of fuel loadings is critical for reducing the risk of large, uncontrolled wildfires in Rocky Mountain forest ecosystems (USDA-USDI, 2000; Schmidt et al., 2002). Fire suppression has caused increased forest fuel loadings and encroachment of small-diameter saplings into forest meadows or open stands, leading to more intense wildfires, higher rates of disease and transformations of wildlife habitat (Keane et al., 2002). In developed areas where wildland fire-use programs cannot be employed, the potential for extreme wildfires is being lowered through application of forest

management practices which reduce stand density and fuel loadings (Fulé et al., 2001). Common techniques employed include mechanical thinning to reduce stand density, followed by prescribed fire to decrease the amount of surface fuels. Successful implementation of prescribed fire requires that fuels be managed such that flame lengths do not reach into mature-tree canopies (Graham et al., 2004). Fuel management options include pile-burning of leftover slash following thinning, broadcast-burning with slash in place, or both. All of these treatments result in the burning of compacted fuel near the soil surface, which increases temperatures in forest floors and soil, and may alter physical, chemical and biological properties of the soil.

Prescribed fire affects soil through consumption of the forest floor and heating of the soil, which are a function of fire temperature

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and duration. Between 2 and 37% of the forest floor mass is lost, on average, through consumption during prescribed fires (Covington and Sackett, 1984; Gundale et al., 2005). In the mineral soil, fire temperatures decrease with depth due to soil thermal conductivity (Campbell and Norman, 1998). Moist soils do not rise above 95 °C until all water has been driven off, but once this threshold is reached soil temperatures can rapidly rise to 200–300 °C (Franklin et al., 1997; Certini, 2005). Many biological mortality thresholds are reached at these temperatures, including those for seeds (50 °C), plant tissue (60 °C), fungi (100 °C) and bacteria (110 °C) (Hare, 1961; Dunn et al., 1979; Busse et al., 2005; Neary et al., 2005). Temperatures above 200 °C can volatilize nitrogen; temperatures greater than 760 °C are needed to volatilize other potentially limiting forest nutrients (Neary et al., 1999).

A recent meta-analysis of fire effects of soil C and N storage (Nave et al., 2011) indicated that prescribed fires have little effect on mineral soil, causing no significant changes in concentrations or pool sizes of C and N. In forest floors, prescribed fire did not significantly affect C and N concentrations, but reduced C and N storage by 46% and 35%, respectively. Concentrations of ammonium (NH_4^+) and nitrate (NO_3^-) are usually elevated after prescribed fire (Covington et al., 1991; Kaye and Hart, 1998; Gundale et al., 2005; Jiménez Esquilín et al., 2007). Soil available P has been reported to increase (Vázquez et al., 1993; Banning and Murphy, 2008), decrease (Kaye and Hart, 1998) or stay the same (Kaye and Hart, 1998; Andreu et al., 1996). Calcium and Mg^{2+} concentrations have been reported to increase (Pietikäinen and Fritze, 1995) or remain the same after fire (Andreu et al., 1996; Gundale et al., 2005). Increases in soil pH after forest fire are common (Pietikäinen and Fritze, 1993; Vázquez et al., 1993; Choromanska and DeLuca, 2002; Jiménez Esquilín et al., 2007), although small declines in pH have also been reported (Abril et al., 2005; Gundale et al., 2005).

Effects of fire on soil microbiological communities can be assessed by comparing the phospholipid fatty acid (PLFA) content of soils before and after fire. PLFA analysis measures the abundance of broad taxonomic groups of bacteria, fungi and actinomycetes in soil. In a native, wet sclerophyll forest in Queensland, Australia, Campbell et al. (2008) found significantly lower abundance of Gram-positive bacteria, Gram-negative bacteria and actinomycetes in soils that experienced fire every two years compared to sites with 4-year fire intervals. In *Pinus sylvestris* stands of central Finland, total PLFA abundance, as well as total bacteria and fungi and the ratio of fungi to bacterial PLFA, were significantly lower in the organic matter of a burned site 2 years after fire than in an unburned control site (Bååth et al., 1995). Díaz-Raviña et al. (2006) found that granitic and acid schist soils heated to 350 °C for 10 min under laboratory conditions had 24–40% less total PLFA abundance than unheated soils. In contrast, in forests of western Montana Gundale et al. (2005) found no significant differences in total PLFA abundance among treatments (control, thinned, prescribed fire, thinned + prescribed fire) immediately or three years after fire, and concluded that these forest management treatments had no long-lasting effects on soil microbial communities.

The aim of this study was to determine which fuel management treatment best served the purpose of reducing surface fuel loadings while minimizing negative impacts on soil properties in interior Douglas-fir forests of the Rocky Mountain trench. We measured fire temperatures, forest-floor depth and key soil properties (moisture content, C and N concentrations, pH, nutrient availability and microbial community composition (PLFA) in four fuel-management treatments and in an unburned control prior to and 10 days, 3 months and 1 year after a prescribed fire. Relationships among fuel loadings, fire temperatures and soil properties were explored, as were relationships between soil properties and microbial communities. Based on studies to date, we hypothesized that:

1. Changes in soil chemical and biological properties will be greatest in treatments with the largest fuel loadings.
2. Soil pH and concentrations of inorganic N, Ca and Mg will increase while microbial abundances will decrease in burned plots, especially in those with the highest fire temperatures.
3. Changes in soil biological and chemical properties will be sustained for at least one year following the prescribed fire.

2. Methods

2.1. Site description

The study site is located in the Rocky Mountain Trench of south-east British Columbia (BC) (49° 43' 10 N and 115° 38' 35 W, elev. 1000 m, 7–12% slope), approximately 20 km northeast of Cranbrook, BC. It is positioned on a geographic bench above the valley bottom with surrounding mountains that rise to 2500 m. The site is classified as Interior Douglas-fir Dry Mild (IDFdm2/04) under the BC Biogeoclimatic Ecosystem Classification (Pojar et al., 1986). IDF forests encompass about 5.5% of BC's land area. The adjacent valley bottom has a mean annual precipitation of 32 cm, with 30% in the form of snow (National Climate Data and Information Archive, xxxx). Annual monthly mean high and low temperatures averages are 11.4 °C and −0.37 °C, respectively. *Pseudotsuga menziesii* var. *glauca* (interior Douglas-fir) and *Larix occidentalis* (western larch) are the dominant tree species, while shrub species include *Spiraea betulifolia* (birch-leaved spirea), *Arctostaphylos uva-ursi* (kinnikinnick) *Rubus idaeus* (raspberry) and *Rosa acicularis* (prickly rose). The herb layer after thinning is dominated by *Calamagrostis rubescens* (pinegrass). The modal soil is classified as Orthic Eutric Brunisol (Soil Classification Working Group, 1998) and is less than 1 m deep. It is a well-drained, sandy loam with 30–50% coarse fragments and is non-effervescent (10% HCl) until immediately above the calcareous bedrock. Averaged forest-floor depth before fire was 4.6 cm.

A variety of silvicultural treatments were implemented by the BC Ministry of Forests and Range in this area during the previous 5 years. The largest treatment unit (TU2 – 20 ha) had been commercially thinned in 2004; all trees >30 cm were retained for residual density of 150 trees ha^{-1} . Slash was piled into small ($\sim 1 \text{ m}^3$) and large ($\sim 4 \text{ m}^3$) piles in 2008. An adjacent unit, TU5 (9 ha), was a cut-and-leave thinning treatment established in 2008, where all trees less than 30 cm were felled in the same direction and left on site. The remaining mature trees in TU5 had relatively deep forest floors (>6 cm) but small amounts of woody materials beneath them. Areas outside these TUs and the prescribed fire perimeter had low surface-fuel loadings and abundant saplings. The entire study area was 330 ha, and all plots were within 1 km of one another.

2.2. Experimental design

Fifteen plots, each of 1.25-m radius, were non-randomly placed within five different fuel management treatments within the two treatment units (TU2 and TU5). Three “large pile” plots were under slash piles about 2 m high and 2 m in diameter in TU2 (these could also be classified as “hand” piles); three “small pile” plots were under slash piles about 1 m high and 1 m in diameter in TU2; three “cut and leave” plots were under felled small trees in TU5 which had been cut in 2008 and retained red needles; three “leave-tree” plots were directly beneath remaining mature trees in TU5 with no downed wood within 3–5 m of the tree bole; and three “unburned control” plots were located just outside of the treatment units and fire perimeter.

2.3. Fuel loadings and fire temperatures

Volumes of the large and small piles were estimated using their height, length and shape (Wright et al., 2010). Fuel loadings in the small pile and the cut-and-leave treatment area were estimated using the Photo Sampling Guide (Keane and Dickinson, 2007). HOBO data loggers (Onset Computer Corporation, Bourne, MA, USA) were installed prior to the prescribed fire immediately above the forest floor in each plot, and were set to record fire temperatures every 2 s beginning 3 h before ignition time until 9 A.M., the morning following the prescribed fire.

The Big Hill prescribed fire was ignited on April 21, 2009, when air temperature was 20 °C, relative humidity was 29%, and there was a west-southwest wind of 10–20 km h⁻¹. The fire perimeter covered 400 ha, with TU 2 and 5 located approximately at the center, and was lit with drip torches around the perimeter and with a heli-torch inside.

2.4. Soil measurements

Soils were sampled 10 days before the prescribed fire and approximately 10 days, 3 months and 1 year after the fire. On each occasion, three samples each of the forest floor and mineral soil were removed from each plot, with each sample taken in a 120° angle from the first sample. Forest-floor samples 15 cm × 15 cm were first removed and the upper 10 cm of mineral soil beneath was then sampled using a soil auger (3 cm diameter). Following the fire, forest floor samples from the leave-tree treatment were collected from low spots in the soil as no forest floor remained in other areas. Two mineral soil bulk-density measurements were determined immediately adjacent to each plot. Briefly, soil was removed from a hole about 10 × 10 × 10 cm, which was then lined with a plastic bag and filled with water, and the volume of water required to reach the soil surface was used to estimate the volume of the hole. The removed soil was oven-dried and weighed and bulk density was calculated in kg m⁻³.

Forest floor and mineral soil moisture contents were determined after oven-drying 40-g samples at 70 °C for 72 h and 105 °C for 24 h, respectively. The pH of each sample was determined by adding 20 ml of 0.01 M CaCl₂ to 2 g of forest floor or 10 g of mineral soil and measuring with a Oakton 510 Series pH bench meter (Oakton Instruments, Vernon Hills, IL, USA) (Hendershot et al., 1993). Carbon and N concentrations in air-dried forest floor and soil samples were measured using a Carlo Erba NA-1500 Nitrogen/Carbon Analyzer (Fisons Instruments, Dearborn, MI, USA) at the BC Ministry of Forests and Range Analytical Laboratory in Victoria, BC. Samples were pre-ground to 100-mesh particle size using a ring grinder (Rocklabs, Auckland, New Zealand). Carbon and N contents (kg m⁻²) were calculated by multiplying concentration by the bulk density. Nutrient availability was determined *in situ* by inserting Plant Root Simulator (PRS)TM probes (Western Ag. Innovations Inc., Saskatoon, Saskatchewan; Bengtson et al., 2007). Six probes (three cation and three anion) were inserted horizontally into forest floors in each plot; another six probes were inserted vertically into mineral soil to a depth of 10 cm in each plot. Probes were incubated over three time periods: the first two summers after fire (May–August 2009 and 2010) and the overwinter period (August 2009–May 2010).

Biomass of Gram-positive bacteria, Gram-negative bacteria, actinomycetes, total bacteria, arbuscular mycorrhizae and total fungi were measured through PLFA analysis, as described by Frostegård et al. (1993). Fresh samples of forest floor and mineral soil were sieved through a 2-mm screen and freeze-dried. Fatty acids were extracted from samples (1 g of forest floor, 1.5 g of mineral soil) following the procedure of Brockett et al. (2012). Fatty acids identifying Gram-positive bacteria included *i15*, *a15:0*, *i16:0*, *i17:0* and

a17:0; those identifying Gram-negative bacteria included *i16:1ω7c*, *16:1ω9c*, *16:1ω7c*, *i17:1ω8c*, *cy17:0*, *18:1ω7c*, *18:1ω5c*, *cy19:0*. Total bacteria was the sum of Gram-positive and Gram-negative bacteria fatty acids, plus *15:0*, *17:0* *18:0*. Markers for actinomycetes were *10Me16:0*, *10Me17:0*, *10Me18:0*, *10Me19:0* for arbuscular mycorrhizae was *16:1ω5c*, for general fungi was *18:2ω6,9*. Fatty acid *18:2ω6* signatures from plant cells, rather than fungal biomass, were minimized by sieving the soil and removing visible roots and other plant materials prior to analysis. Biomarkers were identified using an Agilent 6890 N gas chromatograph with an Agilent 5973 N mass selective detector. Microbial abundances were expressed as nmol g⁻¹ dry weight soil.

2.5. Statistical analyses

Significant differences between treatments at each sampling date, as well as significant changes in each treatment relative to levels prior to the prescribed fire were determined using repeated measures ANOVA (with time and treatment as covariants), followed by Bonferroni *post hoc* pair-wise comparisons (McCune and Grace, 2002; SAS Institute Inc., Version 9.2, Cary, NC, USA). Treatment differences were attributed to the fuel management treatments; significant time effects indicated effects of the fire, and significant time by treatment interactions indicated significant effects attributable to the differential fire effects wrought by the five fuel treatments. The data met ANOVA assumptions of normality and uniformity of variance without need for transformation.

Multi-response permutation procedure (MRPP) was applied to determine if, based on all measured parameters except PRS probe data, the soils in the burned plots differed from those in control plots both before and following the prescribed fire. Principle component analysis was used to determine the relationship between pre-fire forest floor moisture content and the amount of forest floor consumed during the fire, and to explore relationships among microbial abundances and abiotic factors, such as maximum fire temperatures, fire temperature durations, soil moisture, forest floor consumption, C and N concentrations, C-to-N ratios and pH. PC-ORD Version 5.19 (MjM Software, Gleneden Beach, Oregon, USA) was used for MRPP and PCA analyses.

3. Results

3.1. Fire temperature profiles

Fuel loadings were greatly reduced in all four fire treatments. In each treatment, fire temperature profiles were similar in two plots, but different in the third plot. In the large-pile treatment, piles were completely consumed except for a few small-diameter branches on the pile edge. Maximum fire temperatures at the forest floor surface in the three large-pile plots reached 427°, 668° and 715 °C, respectively (Fig. 1). In large-pile plot 1, beneath a parabola-shaped pile of 4.9 m³, fire temperatures were above 100 °C for over 12 h and over 300 °C for 6 h. In large-pile plot 2 (half-cylinder shape, 9.4 m³) there were two distinct heat pulses, the first above 450 °C for over 30 min and the second above 150 °C for 30 min. In large-pile plot 3, beneath a half-ellipsoid pile of 5.2 m³, temperatures were above 400 °C for 1 h and above 100 °C for more than 2 h.

In the small-pile treatment area, small-diameter fuels (<10 cm) were completely consumed, while larger fuels (>10 cm) remained intact. Maximum fire temperatures in the three small-pile plots were 203°, 60° and 69 °C, respectively (Fig. 1). In small-pile plot 1, temperatures were above 40 °C for 2 h but temperatures greater than 80 °C were sustained for only 20 min. In small-pile plot 2, temperatures remained above 40 °C for 2 h and above 20 °C for 6 h. In small-pile plot 3, temperatures remained above 30 °C for 4 h.

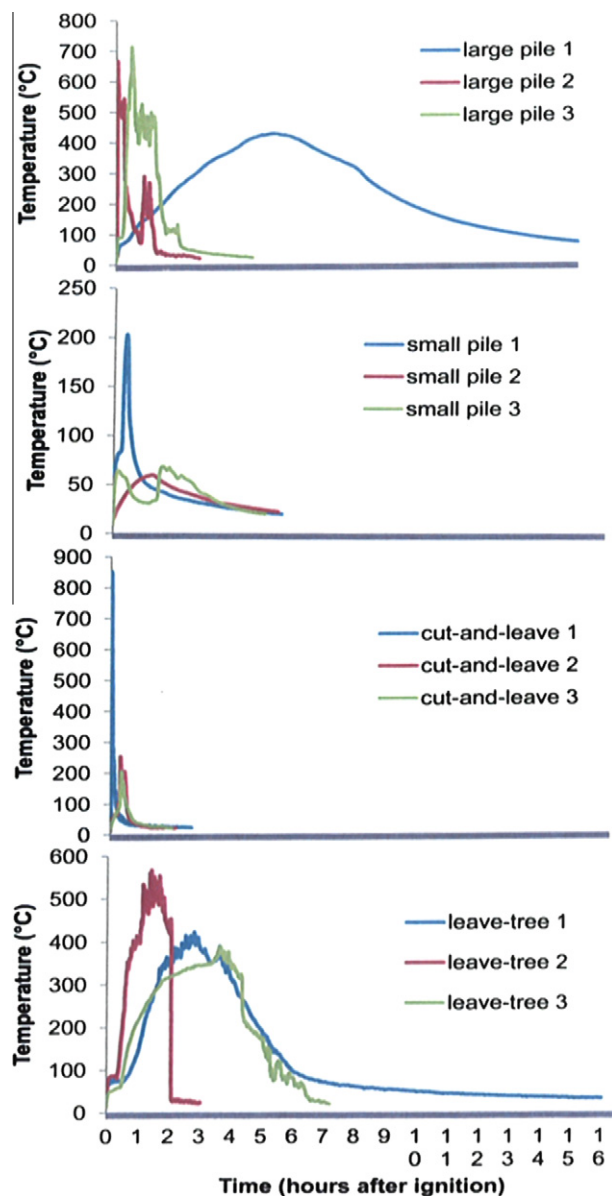


Fig. 1. Fire temperature profiles in each of the three plots in the large-pile, small-pile, cut-and-leave, and leave-tree treatments.

In the cut-and-leave thinning treatment area, all needles and branches were consumed, with only the boles remaining. Maximum fire temperatures in the three plots were 853°, 254° and 202 °C (Fig. 1). Temperatures did not remain above 50 °C for more than 40 min in any of these plots.

In the leave-tree treatment where the mature trees were the plot center, all litter within 1.25 m of the tree was consumed, leaving only an ash layer less than 0.5 cm deep. Maximum temperatures reached 411°, 568°, and 389 °C in leave-tree plots 1, 2 and 3, respectively (Fig. 1). Two of the plots had temperatures above 200° for 4 h, while the third had temperatures above 200° for 2 h. All three plots remained near their maximum temperature for nearly 30 min before and after the maximum temperature were reached. The sudden decline in temperature after 19:00 in leave-tree plot 2 probably indicates data-logger malfunction.

Post-fire declines in forest floor depth were significant in the leave-tree treatment (Table 1). Forest floors were deepest in this treatment prior to fire (6.6 cm), but were completely consumed during the prescribed fire (Fig. 2). Average forest floor mass

consumption during the fire was 62%, 56% and 40% in the large-pile, small-pile and cut-and-leave treatments, respectively. The forest floor in the leave-tree treatment was also the driest prior to fire, contributing to a significant negative correlation between pre-fire moisture content and consumption of the forest floor (Fig. 3).

Despite differences in temperature profiles amongst the three plots of each treatment, between-plot variation was not significant in the two-way ANOVA, whilst between-treatment variance was often significant. The greatest time-by-treatment interaction effects, indicative of differential responses to fire amongst the treatments, were in the forest floor (Table 1). In the mineral soil, there were fewer significant treatment effects and similar changes with time often occurred in both burned and control plots (Table 1). Therefore we present the responses of the two soil layers separately.

3.2. Forest floor

Carbon concentrations in the forest floor were significantly higher in the leave-tree plots than beneath the small piles before fire (Table A1). Significant decreases in C concentrations after fire occurred only in the leave-tree plots. The forest floors in the unburned control plots remained between 33.9 and 38.3% C throughout the study (Table A1). The total amount of C (kg m^{-2}) in the forest floor before fire was significantly greater in the large-pile treatment compared to the other treatments (Fig. 4). After the fire, forest floor C content was significantly reduced in the large-pile and leave-tree treatments. Forest-floor N concentrations were highest in the cut-and-leave treatment throughout the study, and were not significantly affected by prescribed fire (Table 1, Table A1). Total N content of the forest floor was significantly higher in the large-pile treatment than in other treatments before fire (Fig. 4), and significantly decreased in the large-pile and leave-tree treatments after fire.

Forest floor pH in all burned plots increased significantly after the fire (Table 1), especially in the leave-tree treatment in which the residual forest floor was mostly ash (Fig. 5). After one year, forest floor pH was still significantly elevated in all fire treatments. The forest floor in the unburned control plots remained between pH 4.75 and 5.0 throughout the study.

Abundances of Gram-positive bacteria, Gram-negative bacteria, actinomycetes, total bacteria, arbuscular mycorrhizae and fungi in forest floors decreased significantly in all burned treatments after the prescribed fire, and had not recovered to pre-fire levels one year after the prescribed fire (Table 1, Fig. 5). Abundances were particularly low in the 10-day sampling of the leave-tree plots; this is because the ash was sampled on this occasion. Thereafter, pockets of residual forest floor were located (usually in small depressions) and sampled to give a more representative measure of the burned forest floor.

PRSTTM-probes were only used after the prescribed fire, so no comparisons can be made with pre-fire nutrient availability. Availability of Ca^{2+} , Mg^{2+} and PO_4^{3-} in the forest floor were elevated in all burned treatments on at least one occasion (Fig. 6). Forest floor NO_3^- and SO_4^{2-} availability were significantly elevated in the leave-tree plots (Fig. 6). Ammonium and K^+ availability in burned plots were not significantly different from the unburned control at any time (Table 2).

3.3. Mineral soil

Fire-induced changes in chemical and biological properties of the mineral soil were much less pronounced than those in the forest floors (Table 1, A1 and A2). The only significant change in mineral soil pH after fire was a pH increase in the leave-tree treatment. Soil C concentrations did not change significantly after the

Table 1

Two-way ANOVA results for all measured variables in forest floor and mineral soil. Bold indicates a statistically significant treatment effect or time effect, or a significant interaction between the two.

Layer	Variable	Treatment effect		Time effect		Treatment x time	
		F-value	p-value	F-value	p-value	F-value	p-value
Forest floor	Depth	5.22	0.0008	32.59	0.0001	13.99	0.0001
	Moisture	53.98	0.0001	104.71	0.0001	22.18	0.0001
	pH	195.41	0.0001	152.73	0.0001	15.22	0.0001
	% Carbon	5.48	0.0013	8.53	0.0002	2.88	0.006
	Total carbon	10.67	0.0001	36.18	0.0001	4.06	0.0023
	% Nitrogen	11.34	0.0001	2.67	0.0603	1.09	0.3978
	Total nitrogen	10.27	0.0001	22.3	0.0001	2.14	0.06
	Ammonium	2.02	0.1304	1.03	0.3233	0.14	0.9671
	Nitrate	4.31	0.0112	0.15	0.7023	2.23	0.1026
	Phosphate	4.56	0.0088	2.5	0.1295	3.37	0.029
	Calcium	19.74	0.0001	4.61	0.0443	0.96	0.4499
	Potassium	1.89	0.1525	0.12	0.7326	1.59	0.2147
	Magnesium	12.96	0.0001	21.63	0.0002	1.55	0.2253
	Sulphate	10.86	0.0001	24.45	0.0001	2.38	0.0857
	Gram-positive	17.67	0.0001	69.9	0.0001	5.15	0.0001
	Gram-negative	7.25	0.0001	116.93	0.0001	8.71	0.0001
	Actinomycetes	18.15	0.0001	72.49	0.0001	3.01	0.0014
	Total bacteria	12.83	0.0001	112.1	0.0001	7.57	0.0001
	Arb. mycorr.	9.08	0.0001	68.87	0.0001	3.97	0.0001
	General fungi	50.25	0.0001	177.45	0.0001	11.48	0.0001
Mineral soil	Moisture	91.59	0.0001	180.73	0.0001	12.77	0.0001
	pH	84.08	0.0001	2.81	0.0441	2.78	0.0029
	% Carbon	3.45	0.0163	1.65	0.193	0.73	0.717
	% Nitrogen	5.72	0.001	3.61	0.0212	0.98	0.4814
	Ammonium	0.78	0.5535	2.68	0.1172	0.77	0.5595
	Nitrate	9.41	0.0002	0.27	0.6075	1.53	0.2322
	Phosphate	4.59	0.0086	0.05	0.8238	0.87	0.5006
	Calcium	11.73	0.0001	1.02	0.3236	2.54	0.0717
	Potassium	2.98	0.0441	1.51	0.2337	2.23	0.1021
	Magnesium	7.05	0.001	3.14	0.0918	0.52	0.7237
	Sulphate	5.9	0.0026	18.1	0.0004	1.33	0.2946
	Gram-positive	5.71	0.0004	30.4	0.0001	1.84	0.0527
	Gram-negative	4.8	0.0015	31.32	0.0001	1.47	0.1491
	Actinomycetes	4.62	0.0019	31.43	0.0001	1.58	0.1114
	Total bacteria	5.09	0.001	32.12	0.0001	1.55	0.1208
	Arb. mycorr.	13.17	0.0001	40.8	0.0001	1.67	0.088
	General fungi	4.12	0.0041	5.55	0.0015	2.04	0.0292

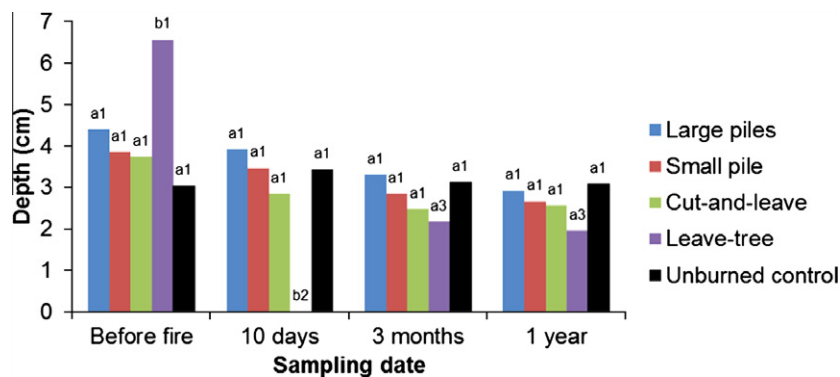


Fig. 2. Forest floor depth in the five fuel treatments prior to and during the first year following prescribed fire. Different letters on top of bars indicate significant differences ($p < 0.05$) between treatments (within a sampling date). Different numbers on top of bars indicate significant differences ($p < 0.05$) between sampling dates (within a treatment).

prescribed fire in any treatment and pre-fire differences persisted throughout the study. Mineral-soil N concentrations significantly differed among treatments and times, but the interaction between the two was not significant, indicating no effect of the fire treatments. Abundances of the various microbial groups declined with time (before fire to one year after), in both treated and control plots. Significantly greater abundances of Gram-negative bacteria, actinomycetes, total bacteria and arbuscular mycorrhizae occurred in the mineral soil of large-pile plots compared to unburned

control plots throughout the study. Nutrient availability tended to be elevated in the leave-tree and/or large-pile treatments. Nitrate, Mg^{2+} and SO_4^{2-} were highest in the leave-tree treatment; PO_4^{3-} and K^+ in the large-pile treatments. Ammonium availability did not significantly differ among treatments.

The muted effects of the burn treatments on the properties of mineral soils compared to forest floors were borne out by the MRPP analysis. Based on all measured parameters except nutrient availability (PRS probes), the forest floors in all plots were similar

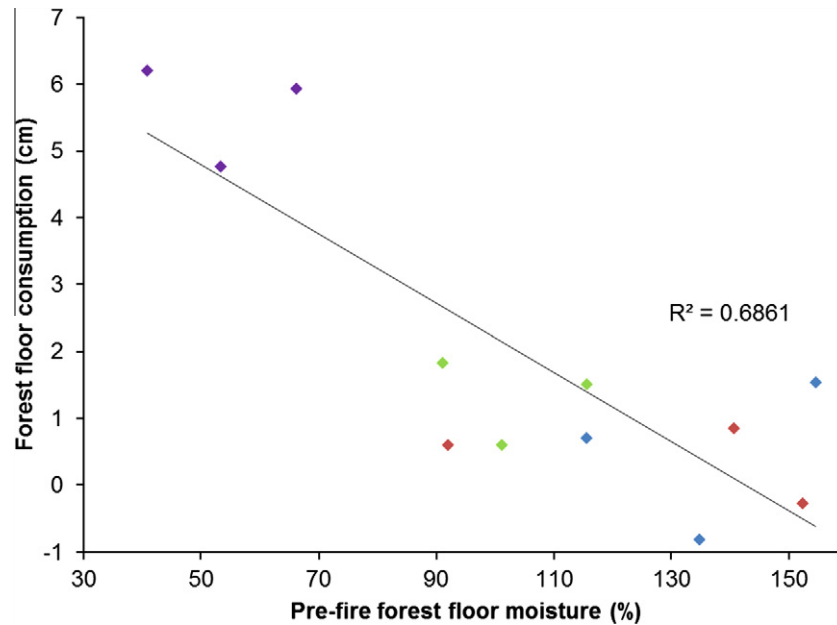


Fig. 3. Relationship between pre-fire moisture content of the forest floor and the depth of forest floor consumed during the prescribed fire. Blue diamonds represent large-pile, red = small-pile, green = cut-and-leave, purple = leave-tree treatments.

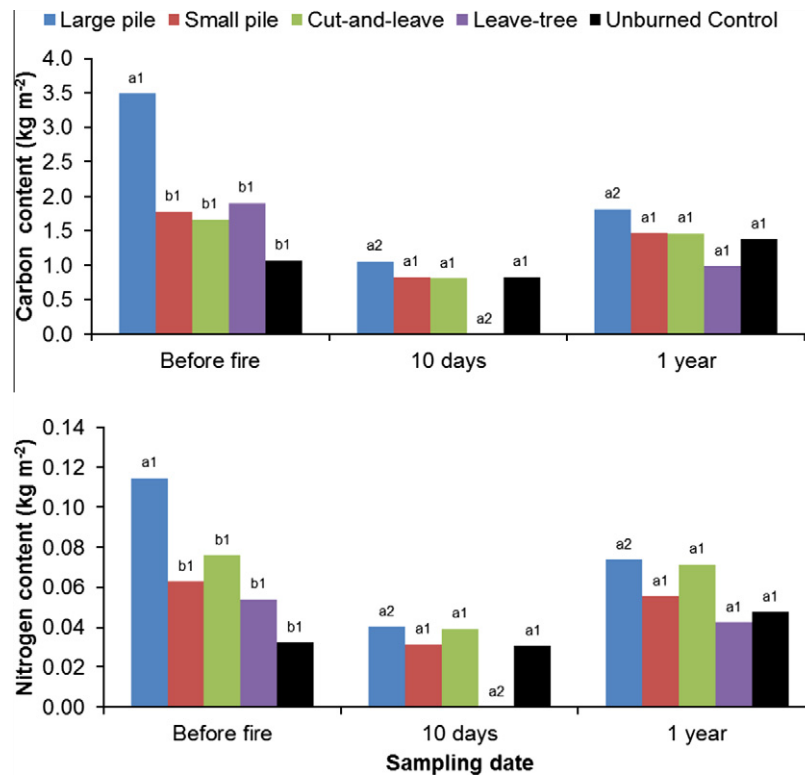


Fig. 4. Total carbon and nitrogen content of the forest floor (kg m^{-2}) in the five fuel treatments prior to and during the first year following prescribed fire. Different letters above bars indicate significant differences ($p < 0.05$) between treatments (within a sampling date). Different numbers above bars indicate significant differences ($p < 0.05$) between sampling dates (within a treatment).

prior to fire; one year after fire, forest floors in each of the burned treatments were significantly different than those in unburned controls (Table 2). Mineral soils in areas to be burned were similar to those in the unburned control plots before the prescribed fire, with the exception of the large piles (Table 2). After one year, only the soil in the small-pile treatment significantly differed from that in the unburned control plots.

3.4. Relationships among microbial and abiotic properties

Prior to fire, microbial abundances in the forest floor were most highly correlated with the N concentration and C:N ratio of the forest floor (Table 3). During the three post-fire sampling periods, microbial abundances were most strongly correlated with forest floor pH (Table 3). Fire-induced increases in pH 10 days after the fire

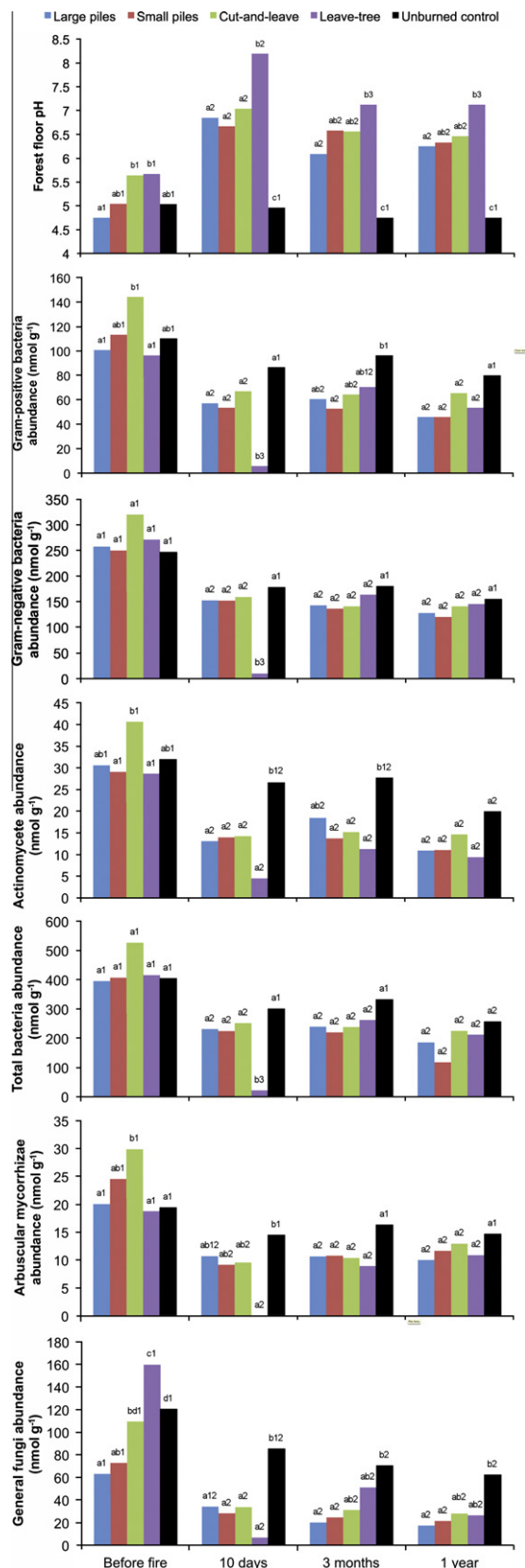


Fig. 5. pH and abundances of various microbial groups in the forest floors in the five fuel treatments prior to and during the first year following prescribed fire. Different letters above bars indicate significant differences ($p < 0.05$) between treatments (within a sampling date). Different numbers above bars indicate significant differences ($p < 0.05$) between sampling dates (within a treatment).

were associated with declines in all microbial groups, with r^2 values ranging between 0.53 and 0.78 (Fig. 7). There was a strong negative correlation between microbial abundances 10 days after fire and the depth of forest floor consumed during the fire (Fig. 8). In turn, there was a positive correlation between forest floor consumption and forest floor pH 10 days after fire ($r^2 = 0.65$). After 1 year, microbial abundances were still strongly correlated with pH, and also with moisture content (Table 3). In the mineral soil, abundances of all microbial groups except fungi were strongly positively correlated with soil C and N concentrations throughout the study, especially prior to fire (Table 3, Fig. 9).

4. Discussion

The findings of this study were not entirely consistent with our hypotheses. Our first hypothesis – that changes in soil chemical and biological properties would be greatest in treatments with the largest fuel loadings – would have been supported if post-fire changes were greatest in the large-pile treatment and least in the leave-tree treatment. Effects of the large-pile treatment were greater than other slash treatments for a few variables (C and N loss in forest floor and PO_4^{3-} and K^+ availability in mineral soil), but for most response variables there was little difference between the large-pile, small-pile and cut-and-leave treatments. Contrary to our hypothesis, the greatest fire effects occurred in the leave-tree plots, in which there was no slash within 3–5 m of the living tree boles.

Our second hypothesis was that the greatest changes in soil chemical and biological properties would occur in treatments in which fire temperatures were highest. The longest durations of high temperatures ($>300^\circ\text{C}$) occurred in the large-pile and leave-tree treatments, and these were the treatments with the greatest reductions in forest floor mass and significant changes in some chemical properties of mineral soil (pH , NO_3^- , Mg^{2+} , SO_4^{2-} in leave-tree; PO_4^{3-} and K^+ in large-pile). For most other variables (microbial abundances and forest floor chemistry), there was little difference in responses between the large-pile and leave-tree treatments and the small-pile and cut-and-leave treatments, in which temperatures were lower and/or of shorter duration.

The unexpectedly high temperatures and pronounced effects of fire (including mortality of the trees) in the leave-tree plots may be attributable to the lower moisture contents of the forest floors in these plots. Moisture contents of the forest floor and the mineral soil were significantly lower in the leave-tree and unburned control plots than in other burned plots both before fire and 10 days after. This indicates that fuel moisture content rather than fuel loading had the greatest influence on the severity of fire effects on soil properties in this experiment. This suggests that forest-floor moisture content may be as critical as fuel loading in determining impacts of prescribed fire on soil.

Consistent with conclusions from the meta-analyses by Johnson and Curtis (2001) and Nave et al. (2011), we found no significant effect of prescribed fire on mineral soil C and N content. The only significant losses of C and N were associated with combustion of the forest floor in the large-pile and leave-tree treatments, which lost 24 and 19 Mg C ha^{-2} respectively and 827 and 540 kg N ha^{-2} , respectively. Thus fire-induced losses of C and N from these fuel management treatments (under similar conditions) largely depend on the amount of forest floor consumed during the fire. Reductions in forest floor C and N storage in these prescribed fire treatments (excluding leave-tree plots) were 39% and 44%, respectively, which is similar to the average values of 46% and 35% reported by Nave et al. (2011).

The significant increase in forest floor pH, PO_4^{3-} , Ca^{2+} , and Mg^{2+} throughout all burned treatments is consistent with previous

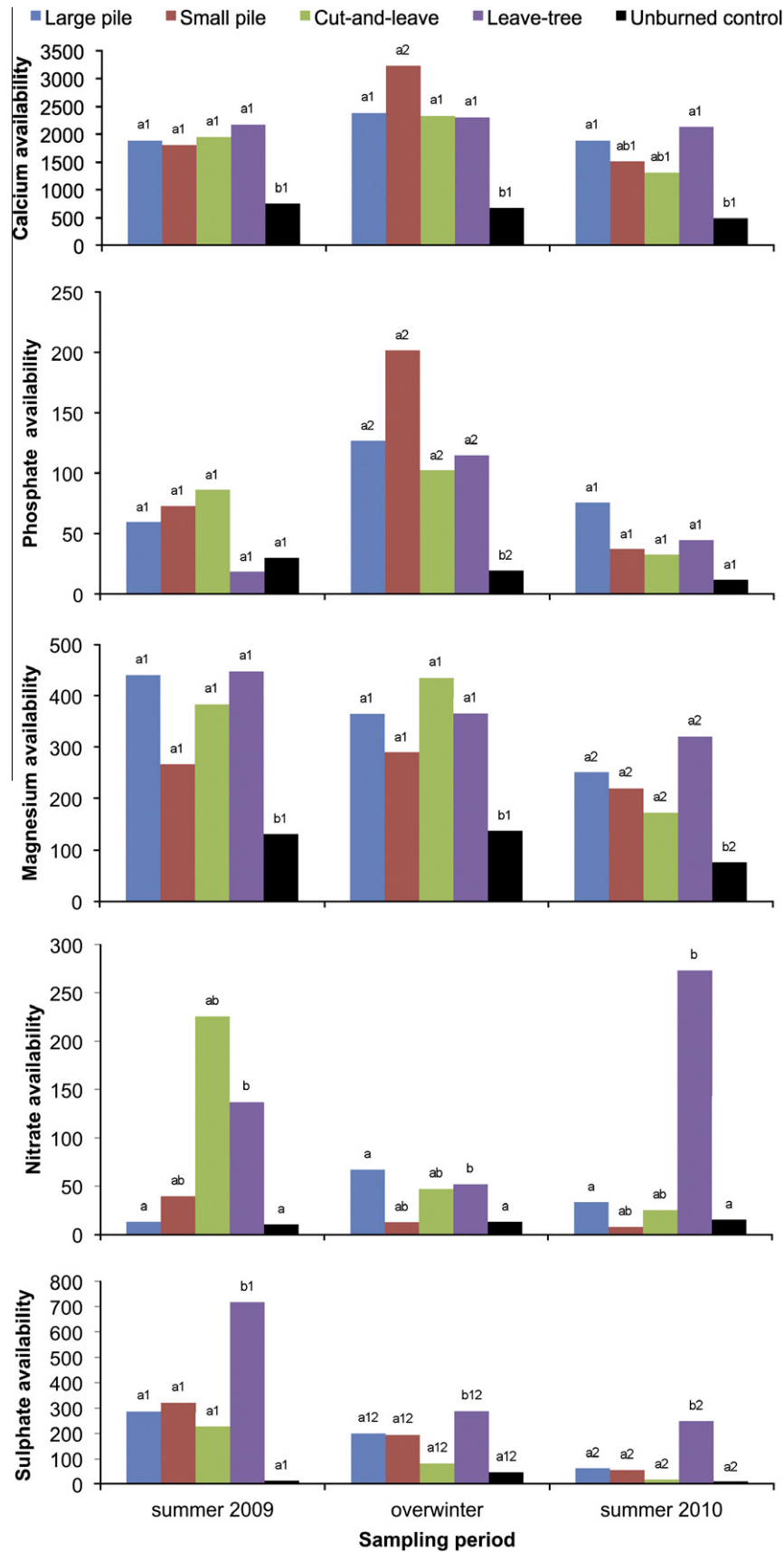


Fig. 6. Availability of nutrients in forest floor ($\mu\text{g } 10 \text{ cm}^{-2}$) assessed by PRS probes in the five fuel treatments during the three time periods after the prescribed fire. Different letters above bars indicate significant differences ($p < 0.05$) between treatments when averaged over all sampling periods. Different numbers above bars indicate significant differences ($p < 0.05$) between sampling periods (within a treatment). Different numbers above bars within the same sampling period indicate significant difference ($p < 0.05$) between sampling periods when averaged over all treatments.

Table 2

Multi-response permutation procedure results comparing forest floor and mineral soils in unburned and burned soil in each fuel management treatment prior to and 1 year after the prescribed fire. Bold numbers indicate significant differences between the treatment and control plots.

Layer	Sampling date	Treatments compared	A value	p-value
Forest floor	Before fire	Unburned control vs. large pile	−0.06	0.64
		Unburned control vs. small pile	−0.03	0.49
		Unburned control vs. cut-and-leave	−0.27	0.06
		Unburned control vs. leave-tree	−0.19	0.52
	1 year after	Unburned control vs. large pile	0.50	0.02
		Unburned control vs. small pile	0.52	0.02
		Unburned control vs. cut-and-leave	0.29	0.03
		Unburned control vs. leave-tree	0.35	0.03
Mineral soil	Before fire	Unburned control vs. large pile	0.27	0.04
		Unburned control vs. small pile	−0.14	0.85
		Unburned control vs. cut-and-leave	0.09	0.14
		Unburned control vs. leave-tree	−0.07	0.73
	1 year after	Unburned control vs. large pile	−0.06	0.71
		Unburned control vs. small pile	0.18	0.04
		Unburned control vs. cut-and-leave	−0.01	0.52
		Unburned control vs. leave-tree	−0.11	0.80

Table 3

Principal component analysis r^2 values and variability explanation for correlations between microbial abundances and selected abiotic variables in the two soil layers before and after the prescribed fire. Bold values indicate significant correlations.

Layer	Variable	Before fire	10 days	3 months	1 year
Forest floor	Floor depth	0.174	−0.752	−0.28	−0.219
	Moisture	−0.049	−0.537	−0.318	0.607
	pH	0.206	0.852	0.732	0.720
	%C	−0.039	−0.759	−0.077	−0.490
	%N	0.457	−0.435	0.155	−0.155
	C:N	−0.574	−0.525	−0.374	−0.438
	1st axis	75%	88%	79%	82%
Mineral soil	Floor depth	−0.508	−0.095	−0.217	−0.374
	Moisture	−0.282	−0.166	−0.740	−0.409
	pH	0.215	0.040	0.130	0.455
	%C	0.785	0.540	0.680	0.682
	%N	0.764	0.574	0.656	0.490
	C:N	0.054	−0.130	0.008	−0.572
	1st axis	76%	74%	73%	77%

studies (Pietikäinen and Fritze, 1993; Bååth et al., 1995; Arocena and Opio, 2003; Jiménez Esquilín et al., 2007). The only change in mineral soil pH during the first year after fire occurred in the leave-tree treatment in which the forest floor was converted to ash. This may occur to a lesser extent in other treatments in the future as ash and base cations from the surface are leached into the soil. Availability of PO_4^{3-} in both forest floor and mineral soil were higher in most burned plots compared to the unburned control, as also reported by Giovaninni and Lucchesi (1997). Sulphate and nitrate availabilities increased only in the leave-tree plots in which the forest floor was converted to ash. Although S is lost through volatilization during fire, elevated availability of S has been reported immediately after fire (Tiedemann and Anderson, 1980; Feller, 1988; Wohlgemuth et al., 2006). The increase in availability of NO_3^- following fire is consistent with previous studies (Covington et al., 1991; Kaye and Hart, 1998; Gundale et al., 2005; Jiménez Esquilín et al., 2007) and is attributable to elevated nitrification in response to elevated pH, Ca^{2+} and Mg^{2+} levels. The lack of increase in ammonium availability in burned plots was unexpected and may indicate active nitrification in these soils, such that ammonium is quickly converted to nitrate.

The strong relationship between the fire-induced declines in abundance of all microbial groups and the pH of the forest floor indicates that pH was the major determinant of the abundance and structure of forest floor communities in post-fire forest floors. This is consistent with many studies in which pH has been found to be a major factor influencing soil microbial communities (Frostegård et al., 1993; Bååth et al., 1995; Högborg et al., 2007; Lauber et al.,

2009). However, comparing prescribed burning and ash fertilization, both of which increase the soil pH, Fritze et al. (1994) found that changes in humus PLFA profiles were not explained by changes in pH. Furthermore, experimental heating of humus, which did not change the pH, nevertheless altered microbial community structure (Pietikäinen et al., 2000). Changes in the chemical properties of humus after fire (Bååth et al., 1995; Pietikäinen and Fritze, 1995) or toxicity induced by smoldering (Fritze et al., 1998) may also be behind fire-induced alterations to soil microbial communities.

The negative correlation between pH and bacterial abundance was unexpected as bacterial abundance and the bacterial:fungal ratio tend to increase with increasing pH (Alexander, 1977). In this experiment, the increase in pH was greatest in the forest floor of the leave-tree plot which was nearly completely consumed in the fire, which drove the strong correlations between forest floor reduction and post-fire pH and abundances of bacteria and fungi. This may indicate that combustion of the forest floor actually drove the changes in microbial abundance and community composition, but was not the most highly correlated, perhaps due to the difficulty in precisely measuring this parameter.

Microbial abundances had not recovered to pre-fire levels one year after fire. Microbial communities in some treatments increased after 3 months, but none had returned to pre-fire levels after one year. This may be related to the substantial increases in pH after fire, which remained after one year. pH was the factor most closely related to microbial abundance in the forest floor, so it could be that the microbial community will not return to its pre-fire state until the pH also returns to pre-fire level. In a chronosequence of

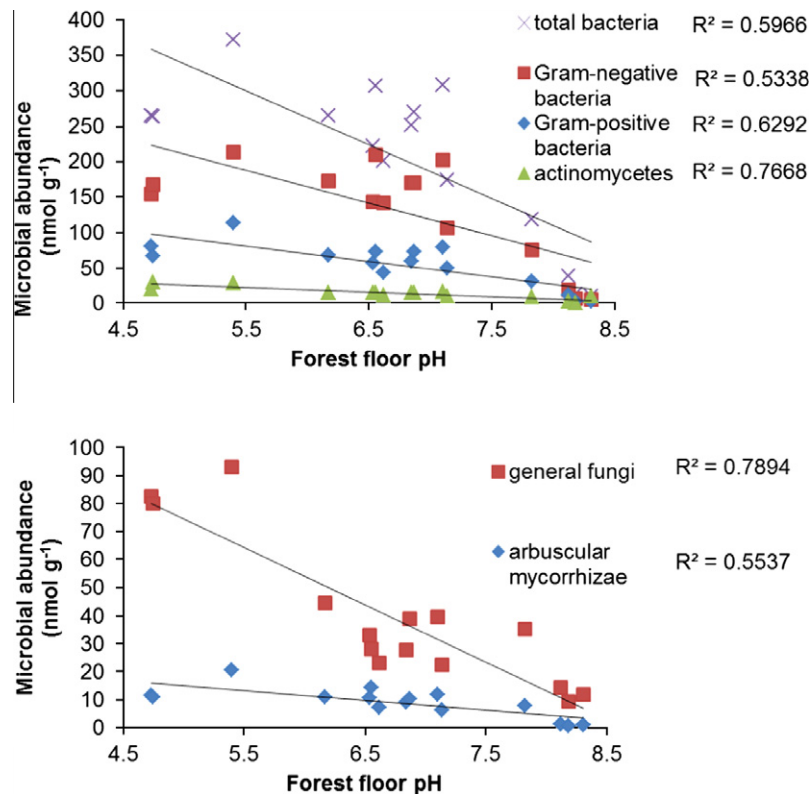


Fig. 7. Relationship between forest floor pH and abundance of various microbial groups in the forest floors 10 days after the prescribed fire.

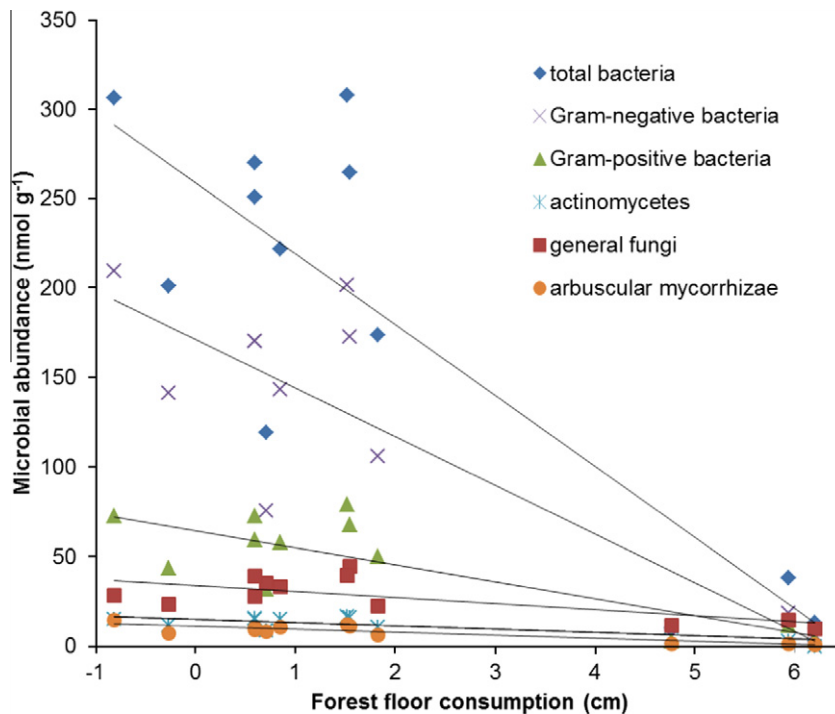


Fig. 8. Relationship between the depth of forest floor consumed during the prescribed fire and the abundance of various microbial groups in the forest floor.

Finnish forests following clearcut-harvesting and slashburning, Pietikäinen and Fritze (1993) determined that soil microbial biomass and activity returned to pre-fire levels after 12 years. Campbell et al. (2008) found that sites that were burned every four years did not have significantly different PLFA abundance than

unburned control sites, indicating that microbial communities may recover to pre-fire levels within four years of prescribed fire.

Prior to the fire, microbial community abundance in the forest floor was most closely (positively) related to forest floor N concentration, while that in the mineral soil was positively associated

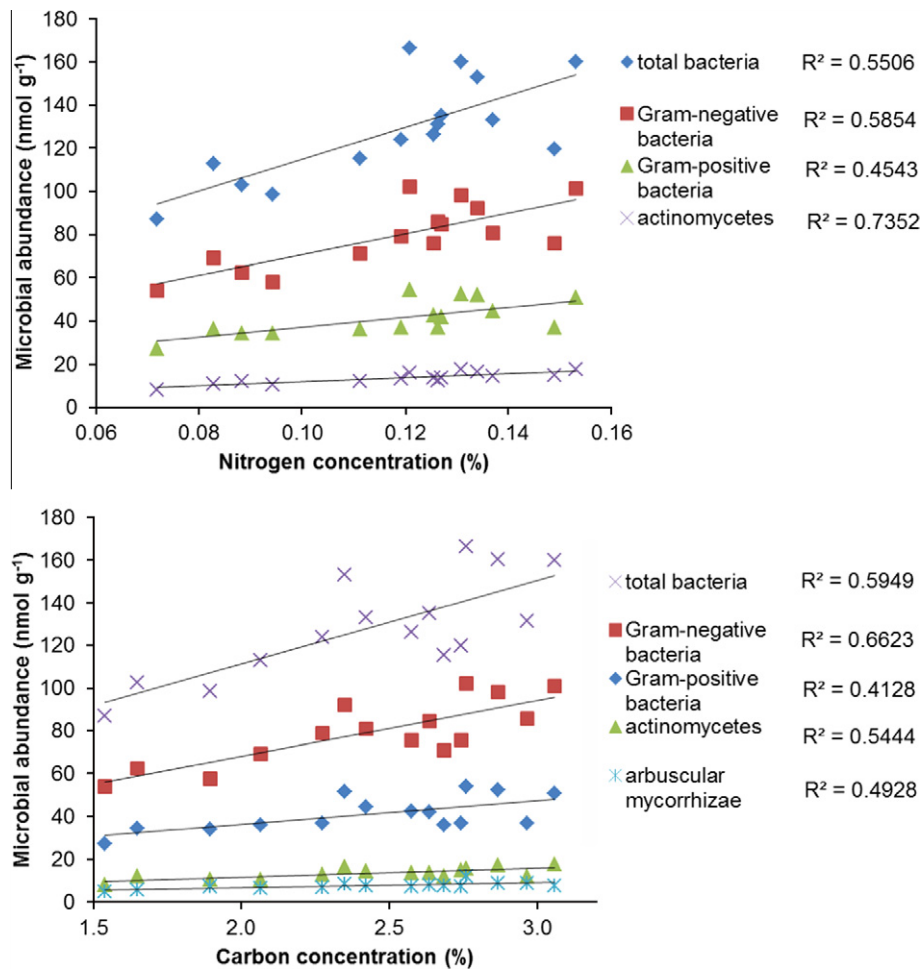


Fig. 9. Relationship between nitrogen and carbon concentrations and abundance of various microbial groups in the mineral soil before the prescribed fire.

with concentrations of C and N (presumably reflecting organic matter content). Relationships between soil organic matter or C content and microbial community structure have been reported in forest soils (Yang et al., 2010; Brockett et al., 2012), grassland soils (Grayston et al., 2004; Katsalirou et al., 2010) and agricultural soils (Yao et al., 2006; Franklin and Mills, 2009). Declines in C content with depth have also been related to changes in soil microbial communities in forest soils (Leckie, 2005; Grayston and Prescott, 2005). Högborg et al. (2007) also reported a strong correlation between microbial PLFA and C:N ratio of the humus layer in Swedish forests.

This study also sheds light on the suggestion by White et al. (1979) that PLFAs degrade rapidly upon cell death, and so do provide a reasonable indication of abundance of live microorganisms. Significantly lower PLFA levels were detected in all burned treatments 10 days after fire. This finding indicates that not only was there bacterial and fungal mortality associated with the fire treatment, but that their phospholipid fatty acids had degraded enough in 10 days that they were not detected with the PLFA analysis.

The unexpected finding of the greatest negative impacts of fire on soil in the leave-tree treatment, in which slash had been removed from within 3–5 m of each mature tree, has significant implications for management. The high temperatures (above 300 °C for over 3 h) and near complete combustion of the forest floor in this treatment appeared to result from the low moisture content of the forest floor. Forest floors in the large-pile, small-pile and cut-and-leave treatments were moister than in the leave-tree treatment, and soils were still frozen before the fire under some of

the piles. Therefore piles may actually reduce fire impacts on soils during spring-time prescribed fires, by shading the forest floor and thereby allowing it to stay moist and cool. The effect could be enhanced by constructing piles such that they allow moisture to penetrate to the forest floor while blocking solar radiation and evaporation. The architecture of the mature-tree canopy may also have contributed to the low moisture content of the forest floor around the boles by restricting precipitation penetration and snow accumulation under the canopy. Pruning of some of the mature-tree branches to allow more precipitation to collect before fires could further reduce the likelihood of sustained high fire temperatures and complete forest-floor consumption around mature trees. Raking the forest floor material away from the bole or building a fireline around mature trees would also reduce fire temperatures and hence, cambium heating and the potential for flaming combustion beneath the canopy, which contributed to the mortality of leave-trees in this treatment.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2012.02.025.

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