Forest Ecology and Management 256 (2008) 59–67

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Influence of coarse wood and pine saplings on nitrogen mineralization and microbial communities in young post-fire *Pinus contorta*

Kristine L. Metzger [a,1], Erica A.H. Smithwick [a,2], Daniel B. Tinker [b], William H. Romme [c], Teri C. Balser [d], Monica G. Turner [a,*]

[a] Department of Zoology, University of Wisconsin, Madison, WI 53706, United States
[b] Department of Botany, University of Wyoming, Laramie, WY 82071, United States
[c] Department of Forest Sciences, Colorado State University, Fort Collins, CO 80526, United States
[d] Department of Soil Science, University of Wisconsin, Madison, WI 53706, United States

ARTICLE INFO

Article history:
Received 24 October 2007
Received in revised form 18 March 2008
Accepted 20 March 2008

Keywords:
Fire ecology
Coarse woody debris
Lipid analysis
Nitrification
Rocky Mountains
Yellowstone National Park

ABSTRACT

Nitrogen (N) limits productivity in many coniferous forests of the western US, but the influence of post-fire structure on N cycling rates in early successional stands is not well understood. We asked if the heterogeneity created by downed wood and regenerating pine saplings affected N mineralization and microbial community composition in 15-yr old lodgepole pine (*Pinus contorta* var. *latifolia*) stands established after the 1988 fires in Yellowstone National Park (Wyoming, USA). In three 0.25-ha plots, we measured annual *in situ* net N mineralization in mineral soil using resin cores ($n = 100$ per plot) under pine saplings, downed wood (legacy logs that survived the fire, and fire-killed trees that had fallen and were contacting or elevated above the ground), and in bare mineral soil. Annual *in situ* net N mineralization and net nitrification rates were both greater in bare mineral soil (8.4 ± 0.6 and 3.6 ± 0.3 mg N kg_{soil}^{-1} yr^{-1}, respectively) than under pine saplings, contact logs, or elevated logs (ca. 3.9 ± 0.5 and 0.8 ± 0.1 mg N kg_{soil}^{-1} yr^{-1}, respectively). Net nitrification was positively related to net N mineralization under all treatments except for elevated logs. In laboratory incubations using ^{15}N pool dilution, NH_4^+ consumption exceeded gross production by a factor of two in all treatments, but consumption and gross production were similar among treatments. Contrary to our initial hypothesis, microbial community composition also did not vary among treatments. Thus, two- to three-fold differences in *in situ* net N mineralization rates occurred despite the similarity in microbial communities and laboratory measures of gross production and consumption of NH_4^+ among treatments. These results suggest the importance of microclimate on *in situ* annual soil N transformations, and differences among sites suggest that broader scale landscape conditions may also be important.

1. Introduction

Wildfires have numerous direct effects on soil nitrogen (N) availability (Wan et al., 2001; Smithwick et al., 2005; Certini, 2005), which limits productivity in many northern coniferous forests (Vitousek and Howarth, 1991). Wildfires also initiate plant community dynamics and introduce a subsequent pulse of coarse wood in burned forests (Clark et al., 1998; Ferguson and Elkie, 2003; Tinker and Knight, 2000), creating structural heterogeneity locally and across the landscape. This heterogeneity includes individual plants that accumulate nutrients and produce litter of varying quality, and physical formations such as coarse wood that modify the soil microenvironment and provide substrate for decomposers (Busse, 1994; Harmon et al., 1986). Previous studies showed that the amount, position and age of coarse wood influenced local litter decomposition rates within young post-fire stands of lodgepole pine (*Pinus contorta* var. *latifolia* [Engelm. ex Wats.] Critchfield), and these local differences scaled up to the landscape (Remsburg and Turner, 2006). However, whether the coarse wood also influences soil processes in young post-fire stands is not known. Downed wood has been shown to lower total and microbial N, increase microbial C:N ratios, and lower N_2O production and denitrification enzymatic activity in mixed forests

* Corresponding author at: Department of Zoology, Birge Hall, University of Wisconsin, 430 Lincoln Drive, Madison, WI 53706, United States.
Tel.: +1 608 262 2592; fax: +1 608 265 6320.
E-mail address: turnermg@wisc.edu (M.G. Turner).
[1] Current address: Department of Zoology, University of British Columbia, Vancouver, BC, Canada V6T 1Z4.
[2] Current address: Department of Geography, The Pennsylvania State University, University Park, PA 16802, United States.

0378-1127/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2008.03.043

(Hafner and Groffman, 2005), but other studies in conifer forests show minimal effects (Spears et al., 2003; Laiho and Prescott, 2004; Spears and Lajtha, 2004; Brais et al., 2005). Given that forest fires are common and increasing in western US landscapes (Westerling et al., 2006), we were interested in whether the heterogeneity created by downed wood and pine saplings in post-fire stands might influence soil biogeochemistry. If so, such variation could suggest mechanisms that are important in the functioning of young post-fire forests, particularly with regard to spatial heterogeneity in process rates, and could potentially facilitate extrapolation to the broader landscape.

Extensive severe fires in Yellowstone National Park (YNP) in 1988 created ~25 million metric tons of standing dead wood (Tinker and Knight, 2001). Many of the trees killed by the fires have now fallen, and coarse wood is abundant in the post-fire forest. Because relatively little pre-fire coarse wood was consumed in the fires (~8%; Tinker and Knight, 2000), legacy coarse wood, i.e., downed wood from the previous stand also contributes to within-stand structure. In addition, post-fire regeneration of lodgepole pine has been extensive yet variable, with sapling densities ranging from 0 to >500,000 ha^{-1} (Turner et al., 2004). Thus, coarse wood and pine saplings are the main structural components of these post-fire stands.

The presence of coarse wood and lodgepole pine saplings may potentially influence soil N dynamics in many ways. Coarse wood provides locations for N immobilization and fixation (Brunner and Kimmins, 2003) and serves as a substrate for decomposition (Busse, 1994; Fahey and Knight, 1986; Harmon et al., 1986). Newly introduced coarse wood begins as a net N sink due to initially high C:N ratios, whereas older, decayed coarse wood becomes a net N source (Holub et al., 2001; Laiho and Prescott, 2004; Spears et al., 2003). The position of coarse wood may also modify soil N dynamics; decomposition is slow for standing wood (Harmon et al., 1986) but accelerates once the wood establishes contact with the ground (Busse, 1994). As a result, standing versus fallen wood may affect nutrient input to underlying mineral soil differently with regard to leaching of dissolved organic carbon (C) (Spears et al., 2003) and subsequent formation of soil organic matter. Pine saplings may also modify soil N dynamics, primarily through plant nutrient uptake and litter production. In Rocky Mountain forests, lodgepole pine needles decompose slowly (Fahey and Knight, 1986), and local accumulations of needle litter may slow net N mineralization rates (e.g., Stump and Binkley, 1993). In addition to effects on substrate quality and quantity, downed wood and pine saplings modify local microclimatic conditions, which can affect microbial community composition (Sinsabaugh et al., 1993) and subsequent N availability (Balser et al., 2001; Waldrop et al., 2000). However, it is not known whether microbial communities are sensitive to the variation in saplings and wood that is typical of post-fire forest stands.

The objective of this study was to determine whether the position and age of coarse wood ≥20 cm diameter and the presence of pine saplings influenced N mineralization rates and microbial communities in 15-yr old post-fire lodgepole pine stands in Yellowstone National Park (YNP), Wyoming, USA. With regard to downed wood, we expected that soils under legacy wood would have higher N mineralization relative to the other wood classes due to higher levels of labile C and N (Fahey, 1983) compared to soils under less decayed wood. We also expected N mineralization to be low under pine saplings because of the low quality of pine needle litter (Fahey and Knight, 1986; Stump and Binkley, 1993). Finally, we hypothesized that models to predict N mineralization would be improved by inclusion of metrics describing microbial community composition, substrate (initial NH_4^+ pool, extractable C) and percent cover of overlying vegetation. Because coarse wood and pine sapling densities vary so much across the burned landscape, our overarching goal was to determine whether these features might be associated with local differences in soil N dynamics in the young post-fire forests and, in turn, potentially be important across the landscape.

2. Study area and methods

2.1. Study sites

Yellowstone National Park (YNP), Wyoming, USA, encompasses approximately 9000 km^2 and is characterized by cold, snowy winters and dry, mild summers. Our study was conducted at three sites in the central and southern portions of YNP that experienced stand-replacing fires during 1988: Biscuit Basin, Lewis Canyon, and Riddle Lake (Table 1). The three sites were all on infertile soils

Table 1
Summary of general stand characteristics and soil properties in three 0.25-ha post-fire lodgepole pine sites

Site characteristic	Site		
	Biscuit Basin	Lewis Canyon	Riddle Lake
Sapling density (stems ha^{-1})	18,100	11,333	7,000
Elevation (m)	2,228	2,377	2,437
Lodgepole pine ANPP (mg ha^{-1} yr^{-1})[1]	11.5	6.6	2.2
Herbacous ANPP (mg ha^{-1} yr^{-1})[1]	0.5	1.2	1.2
Basal area of fallen coarse wood (m^2 ha^{-1})	20.1	18.2	17.9
Soil properties			
pH	4.8 (0.04)[a]	4.3 (0.04)[b]	4.5 (0.03)[b]
K (kg ha^{-1})[2]	424.2 (50.7)[a,b]	358.2 (23.4)[b]	442.7 (31.3)[a]
Ca (kg ha^{-1})[2]	1411.2 (29.2)[a]	644.5 (29.4)[c]	1137.9 (32.7)[b]
P (kg ha^{-1})[3]	24.0 (2.1)[a]	9.8 (0.7)[c]	18.0 (1.2)[b]
Mg (kg ha^{-1})[2]	237.8 (7.6)[a]	106.9 (7.5)[c]	173.5 (10.3)[b]
Total N (%)[4]	0.07 (0.01)	0.07 (0.01)	0.07 (0.04)
Organic matter (%)[5]	2.8 (0.1)[b]	4.2 (0.1)[a]	3.9 (0.1)[a]
C:N ratio[6]	23.2[b]	34.8[a]	32.3[a]

Soil and vegetation were sampled in 2002 (stand age = 14 yrs). Soil properties are average values from five composite samples. ±1 standard error is in parentheses. Significant differences among means by site were determined by Tukey's Studentized Range with $\alpha = 0.05$.

[1] See Turner et al. (2004) for methods.
[2] Atomic absorption after extraction with H_2SO_4 (Schulte et al., 1987).
[3] Truog method.
[4] Micro-Kjeldahl procedure (Jackson, 1958).
[5] Dry combustion using the Tekmar-Dohrman 183 TOC Boat Sampler DC-190 (Tekmar-Dohrman, Mason, OH).
[6] Assuming a carbon-to-organic matter ratio of 0.58.

derived from rhyolite, minimal topographic relief and were dominated by lodgepole pine both before and after the 1988 fires. Pine sapling densities were moderate (7000–18,100 stems ha^{-1}) with respect to the wide range of post-fire regeneration in Yellowstone (Kashian et al., 2004). Sites were selected for their similar parent material, tree density, and coarse wood abundance, but soil chemical composition, aboveground net primary productivity, and pH were found to vary by site (see Table 1).

As an indicator of weather conditions during our study, we obtained temperature and precipitation data for the two weather stations nearest to our sites. The Old Faithful weather station (WY6845; 44°27′N latitude, 110°50′W longitude) is located 3.4 km of the Biscuit Basin site, and the Lewis Lake Divide station (WY10E09S; 44°12′N latitude, 110°39′W longitude) is located within 6.8 and 19.7 km of the Lewis Canyon and Riddle Lake sites, respectively. Summers typically are dry at both stations (average precipitation of 1.5–2.5 cm mo^{-1} in June, July and August), but winter precipitation is greater at Lewis Lake. During the 12 months of our study, total precipitation at Old Faithful was 48 cm, which is 78% of the 1979–2005 annual average; the three warmer months (August 2002 and June, July 2003) were extremely dry ($<$1 cm mo^{-1}, which is 26–50% of the monthly averages). Total precipitation at Lewis Lake was 115.1 cm, which is 90% of the 1981–2007 annual average; the three warm months were also very dry ($<$1 cm mo^{-1}, which is 30–60% of the monthly averages). Average daily temperature and the maximum and minimum temperatures during each month of our study showed no pronounced differences from the longer-term averages.

2.2. Field sampling

Sampling was conducted in a 0.25-ha plot (50 m × 50 m) at each of the three sites during the summers of 2002 and 2003. We examined five treatments, including bare mineral soil and four structural classes (saplings, elevated logs, contact logs, and legacy logs); all logs were ≥20 cm in diameter. Bare mineral soil sampling areas were devoid of aboveground plant vegetation and located adequately far (≥2 m) from neighboring vegetation to reduce the chance of fine roots reaching the sampling area. Pine sapling sampling areas were located directly under the branches of a lodgepole pine tree at least 2 m in height. Elevated logs were trees killed in the 1988 fires that fell to rest ~10 cm from the ground. Contact logs were trees killed in the 1988 fires, but which had fallen to rest on the ground. Both elevated and contact logs had bark absent but sound wood present, similar to decay condition class 2 and 3 (Triska and Cromack, 1979). Legacy logs had fallen before the 1988 fires, and they had bark detached or absent and little or no structural integrity, similar to condition class 4 and 5 (Triska and Cromack, 1979). All treatments (structural features or bare mineral soil) were separated by ≥2 m. To measure *in situ* N mineralization, each of the five treatments was replicated 20 times per plot (n = 100 per plot, 300 total across the three sites), with replicates distributed to ensure spatial coverage within each stand. Microbial community composition and ^{15}N pool dilution studies were conducted using 8 of the 20 replicates of each treatment per plot, with two selected at random from each quarter of the plot to assure spatial coverage (n = 40 per plot, 120 total).

Mineral soil was sampled under all structural classes; there was essentially no organic layer observed in any of the stands. For elevated and contact logs, logs were carefully rolled away for sampling using peaveys and replaced in their original positions. For legacy logs, woody material was carefully removed, the underlying mineral soil was sampled, and the woody material was replaced. At each sampling location, mineral soil was collected to a depth of 15 cm (within the active rooting zone) using clean PVC cores (5 cm diameter) during the summer of 2002. Soil samples for microbial analysis (described below) were placed immediately into coolers and shipped overnight to the University of Wisconsin (Madison, WI, USA). Another set of soil samples was air-dried and composites were used for analysis of general soils characteristics. At each sampling location, we installed ion-exchange resin cores to initiate year-long incubations for determination of *in situ* net N mineralization (described below).

At each sampling location we measured the percent cover of herbaceous vegetation, mineral soil, lodgepole pine litter, and coarse wood in 30-cm diameter rings centered on the resin core (described below) with cover values summing to 100%. Herbaceous litter was a minor contribution to total percent cover under all structural features. Gravimetric soil moisture was determined by oven drying 20 g of wet soil at 70 °C for 24 h. Soil pH was measured after adding 5 g soil to 10 ml of a $CaCl_2$ (0.01 M) solution using a Mettler Toledo InLab 430 pH meter with a glass electrode.

2.3. In situ net N mineralization

We used field incubations (July 2002–2003) of ion exchange resin in intact soil cores (5 cm × 15 cm PVC tubes) to determine annual net nitrification and total net N (NO_3^- + NH_4^+) mineralization (Binkley and Hart, 1989). Samples consisted of intact soil cores with ion exchange resin bags placed at the bottom to collect ions leached from the confined soil core (DiStefano and Gholz, 1986). Resin bags were constructed by weighing 20 g of cation + anion exchange resin beads (J.T. Baker Laboratory Chemicals, Phillipsburg, New Jersey, USA) into nylon stocking material.

Initial soil samples were collected to the same depth (15 cm) adjacent to each resin core using a clean PVC tube. The field-moist soil was homogenized, sieved through a 2-mm mesh soil sieve, and a 20-g sub-sample of soil was extracted in 75 mL of 2 M KCl to determine initial NH_4^+ and NO_3^- levels at the onset of incubation. At the end of the year-long incubation, all soil above the resin bag in the PVC tube was collected, weighed and homogenized and a 20-g sub-sample was extracted in 75 mL of 2 M KCl. All soil samples were processed within 24 h of return to the lab. Resin bags were refrigerated, then air dried and extracted with 75 mL of 2 M KCl. Extracts were filtered with 0.7-μm, sample-rinsed, filter paper and analyzed colorimetrically for NH_4^+–N and NO_3–N using a flow-injected autoanalyzer (Lachat Instruments, Milwaukee, WI). Net N mineralization was calculated as the post-incubation quantity of NH_4^+–N and NO_3–N in both the soil and resin bag minus the quantities in the pre-incubation soil. The final N product was then divided by the mass of soil (particle sizes $<$2 mm) in the column above the resin by assuming that N production leached from the soil is collected in the resin bags and therefore distributed equally among the soil. Nitrification was similarly calculated as the NO_3–N in both the soil core and resin bag minus the quantity in the pre-incubation soil. Net transformation values are presented as mg N kg_{soil}^{-1} yr^{-1}.

2.4. Gross NH_4^+ production and consumption

Gross rates of NH_4^+ production and consumption were calculated using ^{15}N isotope dilution (Hart et al., 1994) on a subset of the samples (8 per treatment per plot), using 24-h soil incubations. We mixed 1 ml of ^{15}N ammonium sulphate ($(^{15}NH_4)_2SO_4$ (98 atom % ^{15}N) at a concentration of 17.81 μg N ml^{-1}) into 30 g of soil. Solution was mixed in the soil for $<$10 s per sample using a vortexer to ensure even distribution of the label. Fifteen grams of the 30 g of soil was transferred to a new container and 75 ml of 2 M KCl was added to create the initial (t = 0) sample. Samples were shaken for 30 min, and filtered using KCl-rinsed, Whatman No. 2 filters. The remaining soil

(approximately 15 g) was incubated at constant temperature and moisture for 24 h, long enough for the NH_4^+ pool to dilute isotopically but short enough that remineralization was unlikely (Murphy et al., 2003). Thirty $\mu g^{15}N$ (1 $\mu g^{15}N\ g_{soil}^{-1}$) was added to the sample in total. After the incubation period, the soil was extracted and filtered as described above. Extractants were frozen (−18 °C) until further analysis. Samples were diffused using a ^{15}N diffusion procedure that volatilizes extracted N as NH_3, which is then collected on an acidified filter disk (Brooks et al., 1989; Herman et al., 1995). Diffusion efficiency was evaluated using standards until 90–95% recovery of sample was obtained. Samples were stored in 5 mm × 8 mm aluminum capsules (Elemental Microanalysis Ltd., Mason, Ohio) and analyzed by mass spectrometry (Europa Integra, UC-Davis Stable Isotope Facility, California).

Gross rates were determined from changes in atom percentage of ^{15}N excesses (APE) above background values and from N pool sizes of pre-and post-incubated soils. Pool sizes of all samples (NH_4–N) were determined on a Lachat QuikChem (Lachat Instruments, Milwaukee, Wisconsin, USA) autoanalyzer. Gross NH_4^+ mineralization was calculated using the equations from Kirkham and Bartholomew (1954). We did not perform laboratory assays of gross production and consumption of NO_3^- because of cost.

2.5. Microbial community composition

We used microbial lipid analysis to analyze microbial community composition on freeze-dried soil. The procedure is based on the extraction of 'signature' lipid biomarkers from the cell membrane and wall of microorganisms. All glassware was baked at 475 °C for 4 h to remove any organic contaminants. We extracted, purified and identified lipids in 1-g samples of lyophilized soil. Briefly, lipids were extracted from 1 g of freeze-dried soil using a chloroform–methanol extraction with a phosphate buffer (potassium phosphate (3.6 ml), methanol (8 ml), and $CHCl_3$ (4 ml)) in 25-ml glass tubes, shaken for 1 h and centrifuged. Supernatant was then decanted to 30-ml tubes and potassium phosphate buffer and chloroform were re-added and vortexed for 30 s. The phases were allowed to separate overnight at room temperature. The top layer was aspirated off, saving the chloroform phase, and the volume was reduced in a RapidVap. We then followed the procedure for FAME as given by Microbial ID Inc.; sodium hydroxide was added for saponification and the solution was heated in a water bath for 30 min, followed by mild alkaline methanolysis.

A 2 μl injection of the methyl-ester derivatives of the extracted phospholipids were analyzed using a Hewlett-Packard 6890 Gas Chromatograph equipped with a flame ionization detector and split/splitless inlet and a 25 mm × 0.2 mm inside diameter × 0.33 μm film thickness Ultra 2 (5% phenyl, 95% methyl) capillary column (Agilent Technologies, Loveland, CO) using N_2 as the carrier gas, and H_2 and air to support the flame. Gas chromatograph conditions are set by the MIDI Sherlock program (MIDI, Inc. Newark, DE). Peaks were identified using bacterial fatty acid standards and Sherlock peak identification software (MIDI, Inc. Newark, DE). Fatty acids were quantified by comparisons of peak areas from the sample compared with peak areas of two internal standards, 9:0 (nonanoic methyl ester) and 19:0 (nonadeconoic methyl ester), of known concentration. In all statistical analyses we used only fatty acids that were identifiable, present at >0.5 mole% (moles of a given lipid/total moles lipid per sample) and in at least 5% of the soil cores (n = 65 lipids from 97 cores).

Terminology to describe fatty acids is described elsewhere (Arao, 1999; Bååth and Anderson, 2003; Steenworth et al., 2003). The total μmol lipid g^{-1} soil was used as an index of microbial abundance (Balser and Firestone, 2005; Hill et al., 1993; White et al., 1979; Zelles et al., 1992). The relative contribution of lipids was determined by calculating the mole%. In addition, ratios of indicator lipids were calculated to characterize the response of the microbial community to stressful environmental conditions (Kieft et al., 1994). Specifically, the ratio of iso- to anteiso- branched lipids, a potential indicator of microclimatic stress (Kieft et al., 1994), and cyclo-/pre-cyclo, a potential indicator of nutritional stress (Wilkinson et al., 2002) were calculated.

2.6. Extractable organic carbon

As a relative index of bio-available C in mineral soil, we extracted 20 g of soil in 0.5 M K_2SO_4 to extract anthrone-reactive carbon (Balser and Firestone, 2005). The method measures cold-soluble hexose sugars, which are related to microbial activity (DeLuca, 1998). Extracts were frozen pending analysis and then processed on a carbon analyzer (I.O. Corp, College Station, TX) at the University of Wisconsin.

2.7. Statistical analyses

The relative influence of site and structural class on net nitrification, net N mineralization, and gross NH_4^+ production and consumption were evaluated using nested ANOVA with site as a main effect and treatment (i.e., structural class) nested in site. Significant differences in net N mineralization rates among treatments were assessed using Tukey's Studentized Range (HSD; α = 0.05). Linear regression was used to test relationships between net nitrification and net N mineralization by treatment. This estimates relative nitrification (i.e., nitrification as a proportion of net N mineralization), and we examined the significance of the relationship (p), the slope of the line (β) and the explained variation (r^2). *In situ* net N mineralization values were log transformed prior to analysis to achieve normality. All statistical analyses were completed using SAS (v.9.1, SAS Institute, Cary, N.C.).

Microbial community composition (mole fraction of lipids) was analyzed using non-metric multidimensional scaling (NMS) ordination. NMS was chosen because it avoids the assumption of linear relationships among variables and it uses rank distance, minimizing errors produced by the "zero-truncation" problem common to community data (McCune and Grace, 2002). Microbial data were arcsine-root transformed before running the ordinations. Ordinations were run using the "slow and thorough" autopilot option in PCOrd Version 4 (MjM Software Design), using 40 runs starting from random configurations with the real data and checked against 50 runs with randomized data to ensure a better-than-random solution. Initial results suggested a three-dimensional solution. However, examination of screen plots suggested a two-dimensional solution was sufficient to explain most of the variation in the dataset. Thus, NMS was rerun, specifying two dimensions and the best starting configuration. To determine whether microbial community composition differed among structural classes and sites, we used multiple response permutation procedures (MRPP) (McCune and Grace, 2002) using Euclidean distance measures. In addition, the NMS ordination was used to develop summary variables for use in stepwise linear regression (see below).

Stepwise linear regression with forward selection was used to determine whether *in situ* net nitrification and net N mineralization rates could be predicted at the soil core level from microbial community composition, soil characteristics or aboveground percent cover (n = 87 with full data). Scores from the first and second axis of the microbial community ordination and relative abundance of microbial groups were used as indicators of microbial community composition. Soil pH and extractable organic carbon were used as indicators of soil characteristics.

Table 2
Summary of nested ANOVA results for annual *in situ* net nitrification and net nitrogen (N) mineralization rates across three sites (Biscuit Basin, Riddle Lake, Lewis Canyon) and five structural classes (bare, elevated, pine, legacy, contact)

Response	F	p	R^2
Net nitrification			
Site	5.59	0.0042	
Class (site)	6.28	<0.0001	
Full model	6.10	<0.0001	0.23
Net N mineralization			
Site	2.55	<0.0797	
Class (site)	3.20	<0.0003	
Full model	0.13	0.0002	0.13

For all models, d.f. site = 2, d.f. class (site) = 12; n = 300. Data were log transformed prior to analysis.

3. Results

3.1. In situ net N mineralization

In situ rates of net nitrification differed significantly among sites, with higher rates observed at Biscuit Basin than at Lewis or Riddle, but net N mineralization did not vary among sites (Table 2). Among treatments, net nitrification was highest for bare mineral soil (3.6 ± 0.3 mg N kg_{soil}^{-1} yr^{-1}) and lowest under elevated logs (0.8 ± 0.1 mg N kg_{soil}^{-1} yr^{-1}) (Table 2, Fig. 1). Net N mineralization was also highest under bare soil (8.4 ± 0.6 mg N kg_{soil}^{-1} yr^{-1}) compared to the rest of the treatments, which did not differ significantly from each other (Table 2, Fig. 1). Variance in net N mineralization rates was generally low, with coefficients of variation (on transformed data) <15% within treatments.

Net nitrification was a substantial proportion of net N mineralization under most of the treatments, as indicated by the estimate of the slope (β) when net nitrification was regressed against net N mineralization. Net nitrification increased with net N mineralization in bare soil and soils under legacy logs (both $\beta = 0.47$, $r^2 = 0.50$, $p < 0.0001$), and also increased less steeply but still significantly under pine saplings ($\beta = 0.32$, $r^2 = 0.46$, $p < 0.0001$) and contact logs ($\beta = 0.27$, $r^2 = 0.31$, $p < 0.0001$). These significant positive relationships suggest that NH_4^+ availability partially controlled nitrification rates in these treatments. In contrast, nitrification did not increase with net N mineralization rates under elevated logs ($p > 0.05$), suggesting that factors other than substrate availability may have limited nitrification in this treatment.

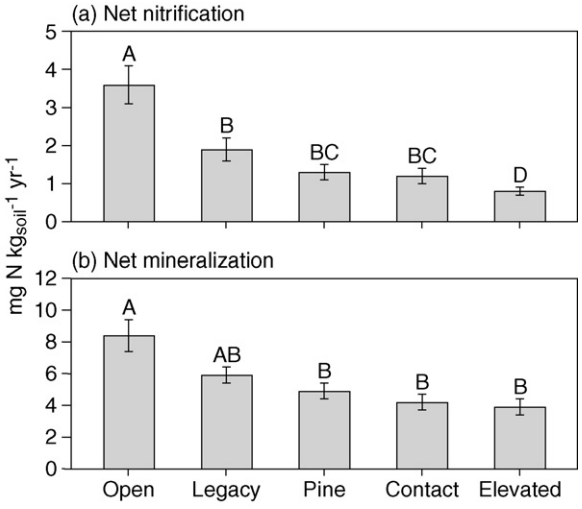

Fig. 1. Mean (±1 S.E.) annual *in situ* (a) net nitrification, and (b) net N mineralization measured from July 2002 to July 2003 in bare mineral soil and under coarse wood and pine saplings in three post-fire lodgepole pine stands.

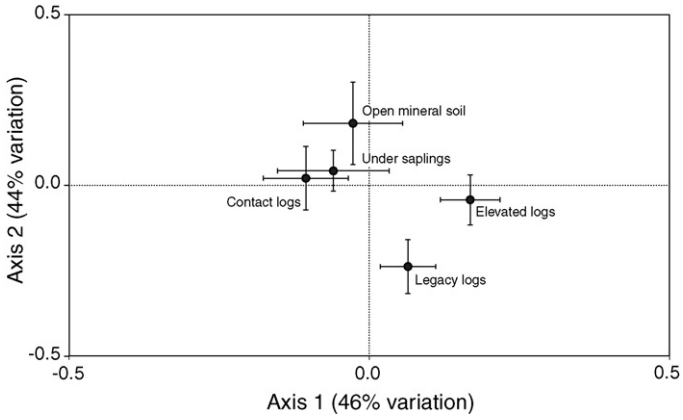

Fig. 2. Results from non-metric scaling ordination of lipid composition showing mean lipid composition score (±1 S.E.) among five structural classes (n = 24) in three post-fire lodgepole pine stands. Points closer to +1 or −1 are more strongly correlated with the ordination axes. Non-metric multidimensional scaling explained 90% variation, with axis 1 explaining 46% and axis 2 explaining 44%.

3.2. Gross NH_4^+ production and consumption

Neither rates of gross NH_4^+ production nor consumption differed among treatments. However, rates of NH_4^+ consumption were higher than rates of NH_4^+ production for all treatments ($t = 3.7492$, d.f. = 192, $p = 0.0002$), averaging 1.47 ± 0.08 and 0.84 ± 0.04 μg NH_4^+ g^{-1} d^{-1}, respectively. As a result, net NH_4^+ production was negative (average = -0.36 ± 0.05 μg NH_4^+ g^{-1} d^{-1}) and did not differ among treatments.

3.3. Microbial community composition

MRPP identified no significant differences in microbial community composition among treatments ($A = 0.005$, $p = 0.26$). In addition, post-hoc averaging of NMS axis scores by treatment identified no strong differences in microbial community composition (Fig. 2), supporting the MRPP results. The relative abundance (mole %) of lipids also did not differ among treatments ($p > 0.05$; data not shown). Among treatments, total microbial abundance was higher under elevated and legacy wood (106.3 ± 14.7 nmol g^{-1} and 110.5 ± 17.0 nmol g^{-1}, respectively) compared to contact (88.2 ± 10.7 nmol g^{-1}), pine (76.9 ± 9.4 nmol g^{-1}) and bare mineral soil (81.3 ± 12 nmol g^{-1}), but these differences were not statistically significant. Fungal abundance was higher under contact (14.4 ± 2.8 nmol g^{-1}) and elevated logs (15.2 ± 2.1 nmol g^{-1}) compared to legacy logs, pine saplings, or bare mineral soil (average = 11.6 ± 0.2 nmol g^{-1}), but again, these differences were not significant. Dominant bacterial lipids in the dataset included 15:0, 15:0iso, 15:0anteiso, 15:1ω8c, 16:0iso, 17:0anteiso, 17:0cyclo, and 17:1ω7c. The fungi-to-bacteria ratio ranged from 1.9 ± 0.4 (under pine saplings) to 3.6 ± 1.2 (under legacy wood); ratios under contact, elevated and bare mineral soil were intermediate (2.9 ± 0.9, 2.9 ± 0.6, and 2.1 ± 0.6, respectively), but differences were not significant. The microbial lipid iso- to anteiso- ratio, a measure of stress, differed among treatments (Fig. 3c). The ratio was significantly higher in soils under legacy logs than soils under contact or elevated logs, with bare soil and pine sapling treatments having intermediate values (Fig. 3c).

Total lipid abundance did vary among sites, ranging from 80.8 ± 4.9 nmol g^{-1} (mean ± 1 S.E.) and 81.2 ± 9.8 nmol g^{-1} at Biscuit

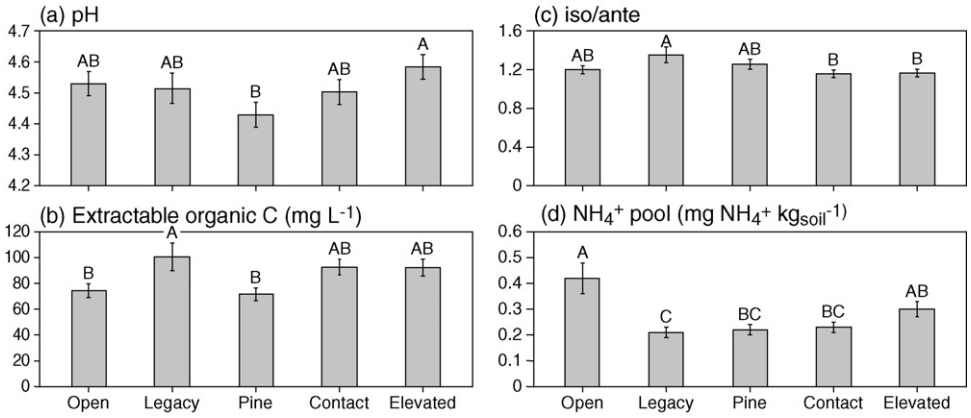

Fig. 3. Summary of significant differences among treatments of (a) pH, (b) extractable organic carbon, (c) microbial lipid iso- to anteiso- ratio, a measure of stress, and (d) initial NH_4^+ pool. Significance among class means was assessed using Tukey's Studentized Range test with $\alpha = 0.05$.

Table 3
Summary of stepwise regression with forward selection to predict initial NH_4^+ pool size and *in situ* annual nitrification and net N mineralization

Response	Predictor	Partial R^2	P	Full model
Initial NH_4^+ pool				$R^2 = 0.30$, $F = 8.15$, $p < 0.0001$
	+ Extractable organic C	0.14	0.004	
	+ %Mineral soil	0.08	0.0053	
	− %Lupine	0.04	0.0340	
	+ Axis 1	0.03	0.0777	
Net nitrification				$R^2 = 0.05$, $F = 4.51$, $p = 0.0368$
	+ %Mineral soil	0.05	0.0368	
Net N mineralization				$R^2 = 0.15$, $F = 3.42$, $p = 0.0126$
	+ Axis 1	0.06	0.0309	
	+ Iso/ante-iso	0.03	0.0959	
	+ %Mineral soil	0.03	0.1300	
	+ Extractable organic C	0.03	0.0803	

Data were log transformed prior to analysis. Significance level for inclusion in the model was 0.15. For all models, $n = 81$. The sign associated with each significant predictor indicates a positive or negative correlation.

Basin and Riddle Lake, respectively, to 124.3 ± 15.4 nmol g^{-1} at Lewis Canyon. Microbial community composition also differed significantly among sites (MRPP, $A = 0.075$, $p < 0.00001$). Fungal abundance (18:1ω9 + 16:1ω5; excluding 18:2ω3, which was not uniformly present in the dataset) was higher at Lewis Canyon (19.4 ± 2.9 nmol g^{-1}) compared to Biscuit Basin (10.8 ± 0.6 nmol g^{-1}) or Riddle Lake (10.6 ± 1.3 nmol g^{-1}).

3.4. Soil chemistry and substrate

Soil chemistry and substrate conditions differed slightly among treatments (Fig. 3). Soils under legacy logs had the highest concentrations of K_2SO_4-extractable organic carbon (101.1 ± 10.6 mg L^{-1}), high iso/ante ratios, but low initial NH_4^+ pools (Fig. 3). Under the bare soil treatment, extractable carbon was significantly lower (74.4 ± 5.4 mg L^{-1}) than under legacy logs, but the initial NH_4^+ pool was significantly greater. Soils under pine saplings were also low in extractable C and initial NH_4^+ compared to soils under legacy logs. Soils under contact and elevated logs were generally intermediate for both extractable C and initial NH_4^+. The initial NO_3^- pool was virtually undetectable in all samples (average = 0.014 mg NO_3^- kg_{soil}^{-1}), and therefore treatment differences were not assessed.

3.5. Predicting N mineralization

A combination of substrate and microbial information produced significant models of *in situ* net N mineralization when all treatments were pooled, but the amount of variation explained was low, ranging from 5 to 16% (Table 3). Percent mineral soil accounted for the largest proportion of model variation, presumably due to the bare soil treatment having the highest mineralization rates. In addition, extractable organic carbon and microbial community composition (axis scores) provided small but significant contributions to the final models.

4. Discussion

Variation in coarse wood and lodgepole pine saplings is substantial across the post-fire Yellowstone landscape (Turner et al., 2004; Remsburg and Turner, 2006). Our study suggests that the presence of these components lowered annual *in situ* net N mineralization and nitrification relative to bare soil, but had minimal effect on laboratory-derived rates of gross production and consumption of NH_4^+ or microbial community composition. *In situ* net nitrification and N mineralization rates were highest in bare soil and lowest under recently fallen trees that were elevated slightly above the ground.

The higher rates of nitrification and net N mineralization in the bare soils could reflect several different mechanisms. First, microbes in the bare soil could be C limited. Reduced inputs of litter could reduce the availability of labile C for microorganisms and hence reduce microbial assimilation of nitrate, resulting in an accumulation of nitrate in the soil (e.g., Hart et al., 1994; Magill and Aber, 2000; Prescott et al., 2003). Extractable organic C was relatively low in the bare soil microsites, which is consistent with the potential for C limitation. Second, it is possible that abiotic

conditions in bare soil caused greater turnover of the microbial community and contributed to high net N mineralization rates. Freeze–thaw and wetting–drying cycles influence N release via lysing of microbial cells and the leaching of N from bacteria (DeLuca et al., 1992; Halverson et al., 2000; Lipson and Monson, 1998); these cycles may be more pronounced in open sites and may partially explain the localized accumulation of N. The similarity among treatments in laboratory rates of potential gross NH_4^+ production and consumption also suggests that *in situ* differences in microclimate conditions could have influenced net rates.

Drier microclimate conditions under the elevated fallen trees have been observed previously at our sites, and this may depress N cycling rates. Remsburg and Turner (2006) recorded drier soil conditions throughout an annual cycle and slower litter decomposition rates under elevated logs, and they suggested that the flow of water along the length of the bole (Graham, 1925) may produce a rain shadow and a local moisture deficit. Although only a snapshot, the percent soil moisture in the initial soils (July 2002) of the resin core incubations also corroborate this pattern. Under elevated logs, initial soil moisture averaged 4.1% (S.E. 1%), whereas initial soil moisture under the other treatments ranged from 6.2% to 7.4% (S.E. all $<1.0\%$). Thus, soil under elevated logs appeared to be drier compared to the other treatments. The absence of a relationship between net nitrification and net N mineralization under elevated logs further suggests that moisture conditions rather than substrate could have limited net nitrification, as discussed by other researchers (e.g., Robertson, 1982; Killham, 1990). We also observed lower iso/ante-iso microbial lipid ratios under elevated and contact logs, compared to legacy wood, which may be a microbial response to increased moisture stress (Kieft et al., 1994), although temperature stress has also been noted (Suutari and Laakso, 1994; Petersen and Klug, 1994; Annous et al., 1997).

Interestingly, our results suggested spatial variation in relative nitrification with within-stand structure, even though net nitrification is frequently a small fraction of net N mineralization in undisturbed coniferous forests (Binkley and Hart, 1989; Chapin et al., 2002). Positive relationships between net nitrification and net N mineralization were observed among stands during the first four years after fire in the Greater Yellowstone Ecosystem (Turner et al., 2007), in forest soils of the Pacific Northwest (Hart et al., 1997), and in post-fire jack pine (*Pinus banksiana*) (Yermakov and Rothstein, 2006). Our study revealed finer-scale variation in relative net nitrification within stands. In particular, the absence of an increase in net nitrification with net N mineralization under the elevated coarse wood suggests that elevated logs could reduce nitrate availability (and hence the nutrient pool for some herbaceous plants) in the post-fire stands for some years to come.

The net N mineralization rates we measured and the potential for detecting differences among treatments may have been influenced by weather. Specifically, the summer months of June, July and August were extremely dry, with only 25–50% of average precipitation received in each month. In a 2-yr study of N mineralization under different treatments in cut and uncut juniper forests, Bates et al. (2002) found that the differences in weather between years (from moderately dry to very wet) overwhelmed treatment differences. Further, during the moderately dry year, they observed higher rates of N mineralization in the cut intercanopy zone compared to positions under downed wood or live trees, similar to our findings. Therefore, differences among open sites and those under downed wood or saplings might be more evident with moister conditions.

Although we developed significant models to predict N mineralization rates, much of the variation remained unexplained. Some of this unexplained variation may reflect unmeasured fine-scale spatial heterogeneity in fine root biomass. Effects of large root gaps on extractable nitrate have been documented in mature lodgepole pine (Parsons et al., 1994), but the dynamics of fine roots are notoriously variable and difficult to measure. For example, Jones et al. (2003) investigated the controls on fine-root dynamics in longleaf pine (*Pinus palustris*) with creation of canopy gaps and removal of understory vegetation. Even with a very intensive and detailed study, only a small portion of fine-root growth variation could be explained by their measured variables (Jones et al., 2003). Fine root biomass and turnover in our stands likely vary in a complex manner. Another unmeasured factor that may affect N mineralization rates is the accumulated charcoal in the soil, which is associated with elevated rates of nitrification (DeLuca et al., 2006; MacKenzie and DeLuca, 2006). Laboratory experiments on soils from ponderosa pine (*Pinus ponderosa*) forests demonstrated no effect of NH_4^+ additions on nitrification, whereas addition of field-collected charcoal increased net nitrification, gross nitrification and nitrification potential and decreased the concentrations of phenolics in the soil (DeLuca et al., 2006). Our sites all received substantial charcoal inputs with the 1988 fires, but the fine-scale spatial variability in accumulations is probably high. The joint variation in labile carbon from root and litter inputs along with charcoal concentrations could strongly influence N transformations.

In the pool dilution analyses, the higher rates of gross NH_4^+ consumption compared to gross production in all treatments suggest substantial microbial immobilization of NH_4^+ in these 15-yr-old post-fire stands. Spears et al. (2003) also found consumption of NH_4^+ to exceed gross production. Immobilization may be stimulated by pool dilution methodology (Hart et al., 1994; Murphy et al., 2003). However, microbial immobilization of N has also been an important sink for inorganic N in other coniferous forests following disturbances (e.g., Vitousek and Melillo, 1979; Vitousek and Matson, 1985; Yermakov and Rothstein, 2006).

Our results are consistent with several other studies that show a limited imprint of coarse wood on nutrient cycling in some forests. The contribution of coarse wood to N cycling may be low because it represents a very small fraction of the total soil N pool (Fahey et al., 1985; Busse, 1994; Laiho and Prescott, 1999). Spears et al. (2003) also found little evidence for an influence of coarse wood on soil nutrient cycling in the H.J. Andrews Experimental Forest. In a recent review, Laiho and Prescott (2004) suggest that the role of coarse wood may vary considerably among forest types, but they found little evidence that coarse wood plays an important role in nutrient cycling in northern coniferous forests. Moreover, our study suggests that previously documented patterns of within-stand variation in decomposition rates (Remsburg and Turner, 2006) did not translate into significant patterns in annual soil net N mineralization.

The lack of differences in annual rates of N mineralization does not preclude the possibility that important seasonal variation in N cycling or microbial communities is present among treatments but not detected by the long incubations used in our study. Moreover, although our focus was on fine-scale (within-stand) differences, the results indicated differences among sites and suggest the potential for broad-scale (among-stand) differences in N cycling rates and soil microbial communities. Indeed, Levitt (2006) found that summer inorganic N availability, measured with free resin bags in 25 stands burned in the 1988 fires, varied 15-fold among stands and declined with increasing lodgepole pine density. Our finding that net N mineralization rates were elevated locally in the absence of coarse wood and pine saplings also suggests that stands with lower tree densities and less coarse wood might have higher N mineralization rates and greater fine-scale spatial variation in

rates, whereas high-density stands with abundant recently introduced coarse wood may have lower N mineralization rates and less fine-scale variability in rates.

In summary, we observed relatively few significant differences in net N mineralization and microbial communities associated with within-stand structure created by coarse wood and pine saplings; net nitrification was most responsive. We suspect that greater microclimatic variability and reduced C availability over the full year may contribute to the higher rates of N mineralization in the bare soil microsites, whereas dry conditions may explain reduced rates of N mineralization under elevated logs. The lack of significant differences among treatments in the laboratory results is consistent with an important role of *in situ* microclimate on N mineralization rates. Finally, lipid analyses of microbial communities showed minimal difference among treatments, but they did differ among sites, suggesting that broader scale processes exert strong influences at local scales. Mechanisms governing net N mineralization at local, within-stand scales may be contingent on broader scale climatic and landscape conditions.

Acknowledgments

We are grateful for the hard work of our 2002 and 2003 Yellowstone field and lab research assistants: Nicole DeCrappeo, Katie McKendrick, Elizabeth Schwartz, Anders Olsen, Aaron Thiel, Kevin Tita, Alysa Remsburg, Randy Walsh, Heather Lyons, Matt Williamson, Sarah Egolf, and Jamie Corcoran. We are very grateful to Ryosuke Fujinuma, Harry Read and the Balser and Turner labs for technical and intellectual support. Phil Farnes graciously shared his error-checked data for weather stations in Greater Yellowstone. Constructive comments on early drafts of this manuscript were provided by Daniel M. Kashian, Jennifer M. Fraterrigo and three anonymous reviewers. This research was funded by a grant from the Andrew W. Mellon Foundation.

References

Annous, B.M., Becker, L.A., Bayles, D.O., Labeda, D.P., Wilkinson, B.J., 1997. Critical role of anteiso-$C_{15:0}$ fatty acid in the growth of *Listeria monocytogenes* at low temperatures. Appl. Environ. Micro. 63, 3887–3894.

Arao, T., 1999. In situ detection of changes in soil bacterial and fungal activities by measuring ^{13}C incorporation into soil phospholipid fatty acids from ^{13}C acetate. Soil Bio. Biochem. 31, 1015–1020.

Bååth, E., Anderson, T.-H., 2003. Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA-based techniques. Soil Bio. Biochem. 35, 955–963.

Balser, T., Kinzig, A., Firestone, M.K., 2001. Linking soil microbial communities and ecosystem functioning. In: Kinzig, A., Pacala, S., Tilman, D. (Eds.), The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions. Princeton University Press, Princeton, New Jersey, pp. 265–293.

Balser, T.C., Firestone, M.K., 2005. Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. Biogeochemistry 73, 395–415.

Bates, J.D., Svejcar, T.J., Miller, R.F., 2002. Effects of juniper cutting on nitrogen mineralization. J. Arid Environ. 51, 221–234.

Binkley, D., Hart, S., 1989. The components of nitrogen availability assessments in forest soils. Adv. Soil Sci. 10, 57–112.

Brais, S., Sadi, F., Bergeron, Y., Grenier, Y., 2005. Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation to site productivity. Forest Ecol. Manage. 220, 216–226.

Brooks, P.D., Stark, J.M., McInteer, B.B., Preston, T., 1989. Diffusion method to prepare soil extracts for automated nitrogen-15 analysis. Soil Sci. Soc. Am. J. 53, 1707–1711.

Brunner, A., Kimmins, J.P., 2003. Nitrogen fixation in coarse woody debris of *Thuja plicata* and *Tsuga heterophylla* forests on northern Vancouver Island. Can. J. Forest Res. 33, 1670–1682.

Busse, M.D., 1994. Downed bole-wood decomposition in lodgepole pine forest of central Oregon. Soil Sci. Soc. Am. J. 58, 221–227.

Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oceologia 143, 1–10.

Chapin, F.S., Matson, P.A., Mooney, H.A., 2002. Principles of Terrestrial Ecosystem Ecology. Springer-Verlag, New York.

Clark, D.F., Kneeshaw, D.D., Burton, P.J., 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Can. J. Forest Res. 28, 284–290.

DeLuca, T.H., 1998. Relationship of 0.5 M K_2SO_4 extractable anthrone reactive carbon to indices of microbial activity in forest soils. Soil Biol. Biochem. 30, 1293–1299.

DeLuca, T.H., Keeney, D.R., McCarty, G.W., 1992. Effect of freeze-thaw events on mineralization of soil nitrogen. Biol. Fert. Soils 14, 116–120.

DeLuca, T.H., MacKenzie, M.D., Gundale, M.J., Holben, W.E., 2006. Wildfire-produced charcoal direction influences nitrogen cycling in ponderosa pine forests. Soil Sci. Soc. Am. J. 70, 448–453.

DiStefano, J.F., Gholz, H.L., 1986. A proposed use of ion exchange resins to measure nitrogen mineralization and nitrification in intact soil cores. Comm. Soil. Sci. Plant. Anal. 17, 989–998.

Fahey, T.J., 1983. Nutrient dynamics of above-ground detritus in lodgepole pine (*Pinus contorta* ssp *latifolia*) ecosystems. Southeastern Wyoming. Ecol. Monogr. 53, 51–72.

Fahey, T., Knight, D.H., 1986. Lodgepole pine ecosystems. BioScience 36, 610–617.

Fahey, T., Yavitt, J.B., Pearson, J.A., Knight, D.H., 1985. The nitrogen cycle in lodgepole pine forests, southeastern Wyoming. Biogeochemistry 1, 257–275.

Ferguson, S.H., Elkie, P.C., 2003. Snag abundance 20, 30, and 40 years following fires and harvesting in boreal forests. Forestry Chron. 79, 541–549.

Graham, S.A., 1925. The felled tree trunk as an ecological unit. Ecology 6, 397–411.

Hafner, S.D., Groffman, P.M., 2005. Soil nitrogen cycling under litter and coarse woody debris in a mixed forest in New York State. Soil Biol. Biochem. 37, 2159–2162.

Halverson, L.J., Jones, T.M., Firestone, M.K., 2000. Release of intracellular solutes by four soil bacteria exposed to dilution stress. Soil Sci. Soc. Am. J. 64, 1630–1637.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Leinkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.

Hart, S.C., Binkley, D., Perra, A., 1997. Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity. Soil. Biol. Biochem. 29, 1111–1123.

Hart, S.C., Nason, G.E., Myrold, D.D., Perry, D.A., 1994. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. Ecology 75, 880–891.

Herman, D.J., Brooks, P.D., Ashraf, M., Azam, F., Mulvaney, R.L., 1995. Evaluation of methods for nitrogen-15 analysis of inorganic nitrogen in soil extracts. II. Diffusion methods. Comm. Soil Sci. Plant Anal. 26, 1675–1685.

Hill, T.C.J., McPherson, E.F., Harris, J.A., Birch, P., 1993. Microbial biomass estimated by phospholipid phosphate in soils with diverse microbial communities. Soil Biol. Biochem. 25, 1779–1786.

Holub, S.M., Spears, J.D.H., Lajtha, K., 2001. A reanalysis of nutrient dynamics in coniferous coarse woody debris. Can. J. Forest Res. 31, 1894–1902.

Jackson, M.L., 1958. Soil Chemical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Jones, R.H., Mitchell, R.J., Stevens, G.N., Pecot, S.D., 2003. Controls of fine root dynamics across a gradient of gap sizes in a pine woodland. Oecologia 134, 132–143.

Kashian, D.M., Tinker, D.B., Turner, M.G., Scarpace, F.L., 2004. Spatial heterogeneity of lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park, Wyoming, USA. Can. J. Forest Res. 34, 2263–2276.

Kieft, T.L., Ringelberg, D.B., White, D.C., 1994. Changes in ester-linked phospholipid fatty acid profiles of subsurface bacteria during starvation and desiccation in a porous medium. Appl. Environ. Microbiol. 60, 3292–3299.

Killham, K., 1990. Nitrification in coniferous forest soils. Plant Soil 128, 31–44.

Kirkham, D., Bartholomew, W.V., 1954. Equations for following nutrient transformations in soil utilizing tracer data. Soil Sci. Soc. Am. Proc. 18, 33–34.

Laiho, R., Prescott, C.E., 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. Can. J. Forest Res. 29, 1592–1603.

Laiho, R., Prescott, C.E., 2004. Decay rate and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can. J. Forest Res. 34, 763–777.

Levitt, E.A., 2006. Sources of variation in soil nitrogen availability among postfire lodgepole pine stands in Yellowstone National Park. MS Thesis, University of Wisconsin, Madison, Wisconsin, 55 pp.

Lipson, D.A., Monson, R.K., 1998. Plant-microbe competition for soil amino acids in the alpine tundra: effects of freeze-thaw and dry-rewet events. Oecologia 113, 406–414.

MacKenzie, M.D., DeLuca, T.H., 2006. Charcoal and shrubs modify soil processes in ponderosa pine forests of western Montana. Plant Soil 287, 257–266.

Magill, A.H., Aber, J.D., 2000. Variation in soil net mineralization rates with dissolved organic carbon additions. Soil Biol. Biochem. 32, 597–601.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, USA.

Murphy, D.V., Recous, S., Stockdale, E.A., Fillery, I.R.P., Jensen, L.S., Hatch, D.J., Goulding, K.W.T., 2003. Gross nitrogen fluxes in soil: theory, measurement and application of ^{15}N pool dilution techniques. Adv. Agron. 79, 69–118.

Parsons, W.F.J., Knight, D.H., Miller, S.L., 1994. Root gap dynamics in lodgepole pine forest: nitrogen transformations in gaps of different size. Ecol. Applic. 4, 354–362.

Petersen, S., Klug, M., 1994. Effects of sieving, storage, and incubation temperature on the phospholipid fatty acid profile of a soil microbial community. Appl. Environ. Microbiol. 60, 2421–2430.

Prescott, C.E., Hope, G.D., Blevins, L.L., 2003. Effect of gap size on litter decomposition and soil nitrate concentrations in a high-elevation spruce-fir forest. Can. J. Forest Res. 33, 2210–2220.
Remsburg, A.J., Turner, M.G., 2006. Amount, position, and age of coarse wood influence litter decomposition in postfire *Pinus contorta* stands. Can. J. Forest Res. 36, 2112–2123.
Robertson, G.P., 1982. Factors regulating nitrification in primary and secondary succession. Ecology 63, 1561–1573.
Schulte, E.E., Peters, J.B., Hodgson, B.R., 1987. Wisconsin Procedures for Soil Testing, Plant Analysis and Feed & Forage Analysis. Department of Soil Science, University of Wisconsin, Madison, WI.
Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., McClaugherty, C.A., Rayburn, L., Repert, D., Weiland, T., 1993. Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. Ecology 74, 1586–1593.
Smithwick, E.A.H., Turner, M.G., Mack, M.C., Chapin III, F.S., 2005. Post-fire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. Ecosystems 8, 163–181.
Spears, J.D.H., Lajtha, K., 2004. The imprint of coarse woody debris on soil chemistry in the western Oregon Cascades. Biogeochemistry 71, 163–175.
Spears, J.D.H., Holub, S.M., Harmon, M.E., Lajtha, K., 2003. The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, U.S.A. Can. J. Forest Res. 33, 2193–2201.
Steenworth, K.L., Jackson, L.E., Calderon, F.J., Stromberg, M.R., Scow, K.M., 2003. Soil microbial community composition and land use history in cultivated and grassland ecosystems of coastal California. Soil Bio. Biochem. 35, 489–500.
Stump, L.M., Binkley, D., 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Can. J. Forest Res. 23, 492–502.
Suutari, M., Laakso, S., 1994. Microbial fatty acid and thermal adaptation. Critical Rev. Microbiol. 20, 285–328.
Tinker, D.B., Knight, D.H., 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3, 472–483.
Tinker, D.B., Knight, D.H., 2001. Temporal and spatial dynamics of coarse woody debris in harvested and unharvested lodgepole pine forests. Ecol. Model. 141, 125–149.
Triska, F.J., Cromack Jr., K., 1979. The role of wood debris in forests and streams. In: Waring, R.H. (Ed.), Forests: Fresh Perspectives from Ecosystem Analysis. Oregon State University Press, Corvallis, Oregon, pp. 171–190.
Turner, M.G., Tinker, D.B., Romme, W.H., Kashian, D.M., Litton, C.M., 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7, 751–775.
Turner, M.G., Smithwick, E.A.H., Metzger, K.L., Tinker, D.B., Romme, W.H., 2007. Inorganic nitrogen availability following severe stand-replacing fire in the Greater Yellowstone Ecosystem. Proc. Natl. Acad. Sci. 104, 4782–4789.
Vitousek, P., Howarth, R.W., 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13, 87–115.
Vitousek, P.M., Matson, P.A., 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. Ecology 66, 1360–1376.
Vitousek, P.M., Melillo, J.M., 1979. Nitrate losses from disturbed forests: patterns and mechanisms. Forest Sci. 25, 605–619.
Waldrop, M.P., Balser, T.C., Firestone, M.K., 2000. Linking microbial community composition to function in a tropical soil. Soil Biol. Biochem. 32, 1837–1846.
Wan, S., Hui, D., Luo, Y., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol. Applic. 11, 1349–1365.
Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313, 940–943.
White, D.C., Davis, W.M., Nickels, J.S., King, J.D., Bobbie, R.J., 1979. Determination of the sedimentary microbial biomass by extractable lipid phosphate. Oecologia 40, 51–61.
Wilkinson, S.C., Anderson, J.M., Scardelis, S.P., Tisiafouli, M., Taylor, A., Wolters, V., 2002. PLFA profiles of microbial communities in decomposing conifer litters subject to moisture stress. Soil Biol. Biochem. 34, 189–200.
Yermakov, Z., Rothstein, D.E., 2006. Changes in soil carbon and nitrogen cycling along a 72-year wildfire chronosequence in Michigan jack pine forests. Oecologia 149, 690–700.
Zelles, L., Bai, Q.Y., Beck, T., Beese, F., 1992. Signature fatty acids in phospholipids and lipopolysaccharides as indicators of microbial biomass and community structure in agricultural soils. Soil Biol. Biochem. 24, 317–323.