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Restoration treatments in a Montana ponderosa pine forest: Effects on soil physical, chemical and biological properties

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Abstract

Low-elevation ponderosa pine ecosystems of the inland northwestern United States experienced frequent, low-severity fire that promoted open stands dominated by large diameter ponderosa pine (*Pinus ponderosa*). Fire exclusion has led to increased stand densities, often due to proliferation of less fire-tolerant species and an increased risk of stand-replacing wildfire. These fundamental changes have spurred interest in forest restoration treatments, including thinning, prescribed burning and thinning combined with prescribed burning. We examined the response of numerous soil physical, chemical and biological parameters to these treatments 1 and 3 years post-treatment, using a replicated field experiment. Individual restoration treatments were implemented in 9 ha units. We observed significantly lower C:N in the O horizon and higher O horizon and mineral soil NH_4^+ concentrations in both BURN and THIN/BURN treatments during year 1. Soil NH_4^+ remained elevated through year 3 in the THIN/BURN treatment. Net N mineralization, nitrification and NO_3^- concentration were significantly greater in the THIN/BURN than all other treatments during year 1 and net nitrification rates remained elevated through year 3. A high C:N substrate decomposed more rapidly in both BURN treatments relative to the unburned treatments. Treatments had no immediate effect on the soil microbial community; however, phospholipid fatty acid profiles differed 16–18 weeks following treatments due to higher actinomycetes in the THIN/BURN treatment. The large scale of our treatment units resulted in significant variation in fire severity among prescribed burns as a function of variation in fuel quantity and distribution, and weather conditions during burn days. Correlation analysis revealed that variation in fine fuel consumed was tightly correlated with net N mineralization and net nitrification. These differences in soil characteristics may influence stand productivity and understory species composition in the future.
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Keywords: Ponderosa pine; Fuels management; Nitrogen cycling; Microbial community; Prescribed fire; Thinning; Restoration

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1. Introduction

Lower elevation ponderosa pine ecosystems of the Rocky Mountain West (US) historically experienced a frequent, low-intensity fire regime that promoted dominance of large diameter ponderosa pine (*Pinus ponderosa*) (Arno, 1980; Barrett and Arno, 1982; Arno et al., 1995a; Fule et al., 1997; Mast et al., 1999; Moore et al., 1999). The historical fire regime likely maintained more rapid nutrient cycling that corresponded with a diverse understory community of grasses and forbs (Hall, 1977; Mutch et al., 1993; Kaye and Hart, 1998; Moore et al., 1999; Smith and Arno, 1999). An abrupt change in this historical disturbance regime occurred upon Euro-American settlement of the West in the late 1800s and early 1900s (Arno, 1980; Barrett and Arno, 1982; Arno et al., 1995a; Fule et al., 1997; Mast et al., 1999; Moore et al., 1999). A century of fire exclusion may have allowed less fire-tolerant species to become more dominant and C rich organic matter to accumulate (MacKenzie et al., 2004). Some investigators hypothesize that these changes in forest structure and composition have resulted in reduced nutrient turnover relative to historical conditions (Covington and Sackett, 1984; Kaye and Hart, 1998; MacKenzie et al., 2004).

Land managers throughout the West are introducing surrogates of natural disturbance into the ponderosa pine community in an effort to reduce the risk of stand-replacing wildfire. Management strategies to accomplish these goals often include silvicultural thinning or thinning followed by prescribed burning. A third option, less often employed, is the use of prescribed fire by itself. These restoration treatments likely affect ecosystem function in dramatically different ways (Moore et al., 1999). Central to ecosystem function are the numerous processes that occur within the soil that determine resource availability to the plant community. These belowground processes may ultimately influence site productivity, and initial composition and successional trajectory of the understory community. Thus, understanding these belowground responses to alternative restoration treatments may lead to more informed management decisions that may ultimately determine the success of restoration efforts.

Several studies focused on N cycling suggest that important belowground differences exist following these restoration treatments. Comparisons of prescribed fire with unburned controls (White, 1986; Covington and Sackett, 1992; Monleon et al., 1997) consistently show that prescribed fire results in a substantial short-term increase in N mineralization and the availability of inorganic N. Additional studies (Kaye and Hart, 1998; DeLuca and Zouhar, 2000) have also included thinning treatments among these comparisons. Kaye and Hart (1998) found that both thinning and prescribed burning increased N mineralization and inorganic N availability relative to the control in the southwestern US, whereas DeLuca and Zouhar (2000) found that only prescribed fire increased inorganic N pools in western Montana. Few studies have reported how other soil nutrient pools respond to restoration treatments.

The objective of our research was to determine how the initial application of restoration treatments, in a long-term restoration process, affect an array of soil physical, chemical and biological properties. These treatments included silvicultural cutting, cutting followed by prescribed burning, prescribed burning alone and an untreated control. To our knowledge, no published studies have simultaneously examined these restoration treatments under an experimental design where treatments are both replicated and implemented at a scale representative of operational restoration projects. Most studies evaluating fuel management and restoration in ponderosa pine have been conducted at the scale of 1 ha or smaller (Covington and Sackett, 1984, 1992; White, 1986; Monleon et al., 1997; Kaye and Hart, 1998). Larger treatment units allow a more natural spread of fire through stands and better reflect the heterogeneous effects of harvesting activities on fuel distributions compared to studies conducted at smaller scales. This experimental design allows us to examine differences among restoration treatments as well as examine within-treatment variation, variation that is likely to occur in operational-sized restoration projects. Finally, this study provides an analysis of ponderosa pine restoration in the northern half of its range, where far less research has been conducted.

2. Materials and methods

Our study is part of the Fire and Fire Surrogates (FFS) national study network, which includes 13 research sites utilizing similar experimental designs and sampling protocols. The FFS study is a multiyear interdisciplinary study investigating the effectiveness of restoration treatments (cutting and burning) for reducing wildfire hazard. It is also examining treatment effects on vegetation, soils, insects, diseases, birds and small mammals, and wood utilization.

We implemented our study in an approximately 100-year-old second-growth ponderosa pine/Douglas-fir forest at the University of Montana's Lubrecht Experimental Forest in western Montana. Mean annual air temperature is 7 °C and mean annual precipitation is 50 cm, with 44% falling as snow (Nimlos, 1986). We used a blocked experimental design consisting of three 36 ha blocks. Soil in block 1 is a clayey-skeletal, mixed Eutric Haplocryalfs. Soil within block 2 is a loamy-skeletal, mixed, frigid Typic Dystrocryepts. Soil in block 3 is a fine-silty, mixed Eutric Haplocryalfs. Experimental units ranged in elevation from 1230 to1388 m. Each block was quartered into square 9 ha units and assigned one of four treatments (CONTROL, BURN, THIN and THIN/BURN). We could not randomly assign one burn treatment in two of the blocks because positioning required consideration of pre-existing firebreaks. All other treatments were randomly assigned. We measured most response variables prior to treatment implementation and determined that no pre-existing differences existed among treatments (data not presented). Year 1 response data were collected in the summer of 2002 and year 3 response data were collected in the summer of 2004. Several variables (Tables 3 and 5) thought to be highly dynamic were sampled at three separate times during 2002. These are reported as weeks 1, 4–5 and 16–18.

2.1. Restoration treatments

Our restoration treatments were designed to initiate the long-term process of moving stand density, structure and species composition toward historical conditions, and to reduce hazard of stand-replacing wildfire. Restoration targets for these stand characteristics were based on old photographs, early stand descriptions (Anderson, 1933), investigations of old-growth ponderosa pine in western Montana (Arno et al., 1995b; Fiedler, 2000) and ongoing uneven-aged silvicultural research (Fiedler, 1995, 1999). We employed a broad rather than discrete interpretation of historical reference conditions to guide our restoration treatment prescription development. This approach is consistent with Allen et al. (2002) and Brown et al. (2004) who suggest that reconstructed historical reference conditions are most useful when used as general guides in prescription development, rather than rigid restoration prescriptions, per se.

All stands were very similar prior to treatment implementation. Basal area density among the four treatments ranged from 20.6 to 23.8 m^2/ha (trees >10 cm diameter). Measured in basal area, pretreatment stands were approximately 60% seral species composition (primarily ponderosa pine) and 40% late-successional Douglas-fir. All treatment areas had nearly balanced uneven-aged diameter distributions prior to treatment, with individual tree diameters ranging from 10 cm to nearly 70 cm.

Our restoration prescription set a target reserve basal area of 11 m^2/ha (trees >10 cm diameter) for each of the six units receiving cutting. Target stand structures were uneven-aged, with a long-term goal of one-half to two-third of the basal area in trees ≥50 cm diameter. Target species composition over the long-term is ≥90% basal area composition of ponderosa pine. Units receiving cutting treatments were leave-tree marked. We used low thinning to remove most pole-sized trees (ladder fuels), improvement cutting to remove most shade-tolerant Douglas-fir from the mid and upper canopy and selection cutting to reduce overall stand density enough to induce regeneration of shade-intolerant ponderosa pine. Harvests were conducted by private contractors in the winter of 2000/2001 on frozen, snow-covered soil. A cut-to-length system was used to cut and limb trees on site, leaving non-merchantable materials in place as a buffer between logging equipment and the soil. Merchantable timber was transported from the stand to a landing area, using forwarders.

Similar to the cutting treatments, the goal of prescribed burning was to reduce fuel loads and to move existing stand structure and composition toward historical conditions. Thus, some tree mortality was desired as an objective of the treatment. We conducted six separate prescribed broadcast burns in the spring of 2002, with the first fire occurring on May 1 and the last fire occurring on June 25. Fires were initiated with drip torches along transects in each 9 ha unit. While all burns were conducted using the same methodology, unavoidable variation in weather conditions among burn days and the volume and spatial distribution of fuels within each 9 ha unit led to variation in fire behavior among the six burns (Table 1).

Target basal areas were achieved to the nearest 0.1 m^2/ha on all six units receiving restoration cutting. Mortality due to burning was about 10% in the BURN treatment and about 15% in the THIN/BURN. Treatment significantly increased basal area composition of seral species on the THIN and THIN/BURN treatments (from about 60 to 75%), but not on the BURN or CONTROL. Post-treatment, the CONTROL had about 2000 saplings (1–10 cm diameter)/ha remaining, the THIN and BURN treatments about 1000 ha^{-1} and the THIN/BURN about 100 ha^{-1}.

2.2. Field methods

Within each 9 ha treatment unit, we established a 6 × 6 grid, yielding 36 permanent reference points. We randomly chose 10 of these points as permanent center points for ten 20 m × 50 m plots. We sub-sampled at each of these 10 plots by collecting soil samples from two opposing corners to form a single composite sample per plot. These 10 composite samples were independently analyzed and averaged, yielding a single datum from each treatment replicate ($n = 3$).

We collected mineral soil samples from a depth of 0–10 cm, using a standard 2.5 cm soil probe. We transported all soil samples to the laboratory in a cooler, where they were refrigerated overnight prior to extraction and analysis. We measured net N mineralization, ammonification and nitrification via the buried bag method (Eno, 1960). Under this method, soil samples are collected and homogenized, a portion is analyzed immediately, and a portion is placed in a polyethylene bag and returned to the soil for a 1-month period. Differences in NH_4^+ and NO_3^- measured at the beginning and the end of this in situ incubation reflect net ammonification and nitrification. These incubations were initiated in June and ended in July of each year the analysis was conducted. We also collected and analyzed samples for phospholipid fatty acid (PLFA) profiles and microbial biomass. Due to the high cost of this analysis, the 10 sub-samples from each unit were homogenized and analyzed as a single sample. These samples were handled with latex gloves to avoid contamination of samples with non-soil-borne PLFA, sifted through a 2 mm sieve in the field, and immediately placed in a cooler with dry ice. Samples were transported to the laboratory immediately upon collection, where they were stored in a sub-zero freezer until analysis. We measured decomposition by placing two tongue depressors horizontally between the surface of the mineral soil and the organic horizon at each plot. Depressors were oven-dried (100 °C), weighed and placed in the field in November 2002. The first set of depressors was collected in May 2003. The second set was collected in June 2004. Upon collection, depressors were oven-dried (100 °C), brushed clean and weighed. Decomposition is reported as mass% lost during the entire incubation period.

We also measured soil physical properties, including exposed mineral soil, bulk density and organic horizon thickness. Exposed mineral soil was measured throughout each 20 m × 50 m plot. Soil bulk density and organic horizon thickness were sub-sampled on the corners of each 20 m × 50 m plot, as described above. Bulk density was measured using a standard bulk density slide hammer. Bulk density cores were returned to the laboratory, oven-dried (105 °C),

Table 1
Summary of wind speed, relative humidity, temperature, fine fuels and duff consumed on six separate prescribed fires at Lubrecht Experimental Forest, 2002

	Burn 1	Burn 2	Burn 3	Burn 4	Burn 5	Burn 6
Date	5/1/2002	5/15/2002	5/31/2002	6/6/2002	6/14/2002	6/25/2002
Treatment	THIN/BURN	BURN	THIN/BURN	THIN/BURN	BURN	BURN
Wind speed (km h^{-1})	3.2–8.0	1.6–4.8	4.8–9.7	6.4–12.9	1.6–4.8	1.6–4.8
R.H. range (%)	28–42	35–46	20–29	27–45	20–41	26–48
Temperature range (°C)	11.6–13.3	8.9–11.6	17.8–26.7	13.9–17.8	19.4–28.3	19.4–29.4
Fine fuels consumed (Mg ha^{-1})	14.67	3.00	22.24	14.99	1.66	4.35
Duff (O_e, O_a) consumed (%)	14.2	17.4	14.4	10.4	2.0	13.3

weighed and density calculated as mass per core volume. Organic horizon thickness was measured from the top of the O_i horizon to the bottom of the O_a horizon. Complete organic horizon (O_i, O_e and O_a) samples were collected within a 15.2 cm diameter ring. Samples were oven-dried (65 °C) and weighed. The mass of each sample per ring area was used to report total C and N data on an area basis.

We estimated surface fuels in all units before and after treatment implementation by randomly placing two 15.2 m long transects at the 36 permanent sampling points in each treatment unit. Fuel loads (<7.6 cm) along each transect were estimated following the protocol of Brown et al. (1982). We defined fine fuels as consisting of 100-h fuels (2.5–7.6 cm), 10-h fuels (0.6–2.5 cm), 1-h fuels (0–2.5 cm) and litter (O_i). We estimated duff (O_e and O_a) depth reduction from burning by placing four 8-in. spikes around the 36 reference points in each unit. We pushed spikes level with the top of the duff layer prior to burning. Duff thickness in reference to the top of this spike was measured following burning.

2.3. Laboratory methods

Exchangeable Ca^{2+}, Mg^{2+}, Na^+, K^+, extractable P, soil pH and total C and N were measured on oven-dried soil (65 °C). Exchangeable Ca^{2+}, Mg^{2+}, Na^+ and K^+ were extracted by placing 10 g of dry soil into 50 ml of 1 M NH_4Cl solution. Soil suspensions were shaken for 1 h and extracted as described above. Concentrations of Ca^{2+}, Mg^{2+}, Na^+ and K^+ in extracts were analyzed via inductively coupled plasma spectrophotometery (Thermo Elemental Corp.). Available P was estimated by extracting 5 g of dry soil in 1 M NH_4F as described above. Phosphate in these extracts was measured on a segmented flow analyzer (Auto Analyzer II) using the method described by Murphy and Riley (1962). Soil pH was measured on a 2:1 suspension of 0.01 M $CaCl_2$:soil. Total C and N of both soil and O horizon were measured by dry combustion analysis on a Fissions Elemental Analyzer (Milano, Italy).

Net N mineralization, nitrification, amino N and microbial respiration were measured on fresh, field moist soils, 1 day after soil collection. Extractable NH_4^+ and NO_3^- were extracted by shaking 25 g (dry weight equivalent) of soil in 50 ml of 2 M KCl followed by filtration through Whatman #42 filter paper. Extracts were analyzed on a segmented flow analyzer (Auto Analyzer III, Bran Luebbe, Chicago, IL) using the Berthelot reaction (Willis et al., 1993) and cadmium reduction method (Willis and Gentry, 1987), respectively. Amino N was measured on these same extracts using the ninhydrin method (Moore, 1968) and polyphenols by the Prussian Blue method (Stern et al., 1996). Basal soil respiration was measured by incubating 50 g dry weight equivalent soil in a sealed container with 20 ml 1 M NaOH traps for 3 days (Zibilske, 1994).

Soil microbial community structure was assessed by phospholipid fatty acid analysis according to the methods of White and Ringelberg (1998). Phospholipid fatty acids were extracted from 3 g of soil from composite samples into a buffered methanol/chloroform solution. Phospholipids were separated from other lipids by silicic acid chromatography and derivatized to fatty acid methyl esters (FAMEs) for quantification by gas chromatography. FAMEs were quantified on an HP 6890 series gas chromatograph and verified by GC–MS and by using columns of differing polarity. The 28 most abundant PLFAs served as continuous variables for principle components (PC) analysis. PC axes generated from the PLFA profiles indicate relative differences in microbial community structure. Changes in populations of groups of micro-organisms were tracked using specific fatty acids as biomarkers. The fungal PLFA 18:2ω6 was used to estimate the contribution of fungi (Frostegård and Bååth, 1996). The ratio of 18:2ω6 to the bacterial PLFAs (i15:0, a15:0, 15:0, i16:0, 16:1ω9, 16:1ω7t, i17:0, a17:0, 17:0, cy17:0, 18:1ωt and cy19:0) was used to estimate the relative contributions of fungi and bacteria (Frostegård and Bååth, 1996). The 10-methyl branched fatty acids (10me16:0, 10me17:0 and 10me18:0) were used to track actinomycetes (Kroppenstedt, 1985). Total PLFA (nmol/g) extracted from samples was used as an estimate of microbial biomass.

3. Statistical analysis

We performed all statistical analyses in SPSS Version 11.0. We first determined whether each variable met parametric assumptions. When all these assumptions were adequately met, a blocked ANOVA was performed under the general linear model where treatment was entered as a fixed factor and block was entered as a random factor. When block was not a significant factor at an alpha of 0.05, the comparison was repeated using a one-factor ANOVA. When data did not meet parametric assumptions, or could not be transformed to meet these assumptions, a non-parametric Kruskal–Wallis test was performed. Using Pearson's correlation coefficients, we further investigated whether any simple linear relationships existed between fire severity (measured as fine fuels consumed) and each response variable, which could explain some of the notable variation among the six burned units.

4. Results and discussion

4.1. Soil carbon and nitrogen

The total C capital in the organic horizon was significantly higher in the THIN treatment and lower in both the BURN and THIN/BURN treatments relative to the CONTROL during the first year (Table 2). This difference was a function of differences in O horizon depth among the treatments, and not differences in C or N concentration, which did not differ among treatments (Table 2). Despite no detectable differences in total C and N concentration in the O horizon, both the BURN and THIN/BURN treatments resulted in a diminished C:N ratio during

Table 2
Total C and N (mean ± S.E., $n = 3$) in the organic horizon and mineral soil (0–10 cm) following restoration cutting (THIN), burning (BURN) and restoration cutting followed by burning (THIN/BURN) at Lubrecht Experimental Forest, MT

Variable	CONTROL	THIN	BURN	THIN/BURN	p[a]
O horizon					
C (Mg ha^{-1})					
Year 1[b]	19.9 ± 4.2	28.4 ± 1.4	16.9 ± 4.1	14.6 ± 1.4	*
Year 3[b]	19.2 ± 1.3	20.7 ± 2.7	14.3 ± 1.2	14.4 ± 3.6	ns
N (Mg ha^{-1})					
Year 1[b]	0.48 ± 0.10	0.61 ± 0.03	0.43 ± 0.09	0.42 ± 0.05	ns
Year 3[b]	0.43 ± 0.03	0.49 ± 0.01	0.34 ± 0.03	0.35 ± 0.10	ns
C (g kg^{-1})					
Year 1[b]	351 ± 28	392 ± 7	363 ± 19	353 ± 30	ns
Year 3[b]	426 ± 17	366 ± 44	412 ± 18	375 ± 9	ns
N (g kg^{-1})					
Year 1[b]	9 ± 0.6	9 ± 0.1	10 ± 0.2	10 ± 0.7	ns
Year 3[b]	10 ± 0.6	9 ± 0.2	10 ± 0.5	9 ± 0.6	ns
C:N					
Year 1[c]	40.8 ± 0.4	45.3 ± 1.1	37.7 ± 2.8	34.4 ± 0.7	**
Year 3[b]	45.2 ± 0.9	42.1 ± 5.9	42.9 ± 3.3	42.4 ± 3.9	ns
Mineral soil					
C (g kg^{-1})					
Year 1[b]	23.1 ± 4.0	18.9 ± 1.3	18.6 ± 1.7	24.0 ± 2.5	ns
Year 3[c]	24.9 ± 1.0	16.9 ± 1.4	21.6 ± 0.4	20.6 ± 3.6	ns
N (g kg^{-1})					
Year 1[b]	1.0 ± 0.1	0.9 ± 0.0	0.8 ± 0.0	1.1 ± 0.1	ns
Year 3[b]	0.9 ± 0.2	0.5 ± 0.1	0.8 ± 0.0	0.8 ± 0.1	ns
C:N					
Year 1[b]	21.0 ± 1.0	20.3 ± 0.6	20.9 ± 0.3	21.1 ± 0.1	ns
Year 3[b]	29.8 ± 3.6	30.3 ± 3.9	25.6 ± 1.2	28.1 ± 3.2	ns

[a] p-Value: ns > 0.1, *: <0.1, **: <0.05.
[b] One-factor ANOVA.
[c] Kruskal–Wallis.

the first year (Table 2). The differences observed during the first year became non-significant by year 3. This is likely the result of scorched canopy inputs in both BURN treatments and decomposition of logging residues in the THIN treatment that made treatments more similar to one another. No significant differences were detected for total C, N or C:N in the mineral soil during year 1 or 3 (Table 2).

While no differences could be detected in the soil or organic horizon total N pool, substantial changes occurred within the inorganic fraction of this pool (Table 3). The most notable treatment effects were detected during weeks 1 and 4–5, where substantial increases in NH_4^+ occurred following fire in both the O horizon and mineral soil. This difference was greatest immediately following fire in the O horizon

Table 3
O horizon and mineral soil (0–10 cm) extractable NH_4^+, NO_3^-, amino N and phenols (mean ± S.E., $n = 3$) 1, 4–6 and 16–18 weeks following prescribed fire at Lubrecht Experimental Forest, MT

	CONTROL	THIN	BURN	THIN/BURN	p[a]
O horizon					
NH_4^+–N					
Week 1[b]	6.0 ± 0.8	6.0 ± 4.6	45.9 ± 9.9	88.3 ± 4.6	****
Weeks 4–5[b]	1.0 ± 0.6	4.4 ± 1.9	8.9 ± 2.5	9.9 ± 1.8	**
Weeks 16–18[b]	2.0 ± 1.6	5.1 ± 3.4	6.3 ± 2.0	9.3 ± 4.7	ns
NO_3^-–N					
Week 1[c]	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	ns
Weeks 4–5[c]	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.6 ± 0.4	ns
Weeks 16–18[c]	1.2 ± 1.2	0.7 ± 0.3	1.0 ± 0.0	2.1 ± 1.1	ns
Amino N					
Week 1[c]	8.9 ± 8.7	2.9 ± 1.9	8.4 ± 8.4	0.0 ± 0.0	ns
Weeks 4–5[d]	15.7 ± 6.2	13.3 ± 7.9	1.9 ± 1.9	1.6 ± 1.6	ns
Weeks 16–18[b]	9.9 ± 2.9	6.5 ± 3.3	4.3 ± 3.9	4.7 ± 3.7	ns
Phenols					
Year 1[b]	4.7 ± 0.2	5.1 ± 0.3	5.3 ± 0.2	4.5 ± 0.1	*
Mineral soil					
NH_4^+–N					
Week 1[b]	0.2 ± 0.1	0.9 ± 0.3	3.1 ± 1.2	3.4 ± 0.8	**
Weeks 4–5[b]	0.9 ± 0.1	0.8 ± 0.1	2.3 ± 0.3	5.3 ± 1.0	****
Weeks 16–18[b]	0.4 ± 0.1	0.7 ± 0.4	1.9 ± 1.3	2.4 ± 1.0	ns
Year 3[b]	1.1 ± 0.3	1.0 ± 0.2	1.3 ± 0.2	1.9 ± 0.2	*
NO_3^-–N					
Week 1[b]	0.00 ± 0.00	0.00 ± 00.00	0.00 ± 0.00	0.00 ± 0.00	ns
Weeks 4–5[c]	0.00 ± 0.00	0.01 ± 0.01	0.03 ± 0.02	0.17 ± 0.09	*
Weeks 16–18[b]	0.31 ± 0.31	0.83 ± 0.02	0.86 ± 0.04	0.57 ± 0.28	ns
Year 3[b]	0.11 ± 0.04	0.16 ± 0.04	0.23 ± 0.02	0.13 ± 0.03	ns
Amino N					
Week 1[b]	11.0 ± 1.4	11.0 ± 2.8	6.0 ± 1.4	13.4 ± 4.6	ns
Weeks 4–5[b]	4.6 ± 1.4	5.9 ± 0.2	9.4 ± 3.0	1.3 ± 1.1	ns
Weeks 16–18[d]	12.2 ± 5.3	6.8 ± 1.4	10.1 ± 2.9	8.2 ± 5.8	ns
Phenols					
Year 1[b]	1.9 ± 0.07	2.0 ± 0.08	1.9 ± 0.03	1.8 ± 0.05	ns
Year 3[b]	2.2 ± 0.7	1.3 ± 0.1	0.9 ± 0.5	1.6 ± 0.4	ns

p-Value: ns > 0.1, *: <0.1, **: <0.05, ***: <0.01, ****: <0.001.
[a] mg kg^{-1}dry soil.
[b] One-factor ANOVA.
[c] Kruskal–Wallis.
[d] Blocked ANOVA.

and diminished over time. The high NH_4^+ concentration in the O horizon appeared to cause a delayed pulse of NH_4^+ in the mineral soil, which remained elevated through year 3 in the THIN/BURN. All treatments showed an increase in NO_3^- levels at weeks 16–18, which corresponded with the beginning of the wet season. Soil NO_3^- levels were significantly higher in the THIN/BURN treatment at weeks 4–5, corresponding with peak levels of NH_4^+ in the mineral soil. The greater response in the THIN/BURN relative to the BURN is likely a function of greater fuel consumption in this treatment.

These data are supported by several other studies that have reported that NH_4^+ concentration following prescribed fire increased between 2 and 20 times that of reference plots (White, 1986; Covington and Sackett, 1992; Monleon et al., 1997; Kaye and Hart, 1998; DeLuca and Zouhar, 2000). The magnitude increase of O horizon and mineral soil NH_4^+ we observed following prescribed fire is within the range reported among these studies.

To determine whether the increase in inorganic N we detected in both BURN treatments was partially the result of post-fire mineralization and not simply residual accumulation, we conducted a 1-month in situ soil incubation to measure net N mineralization and nitrification rates. This analysis demonstrated that both net N mineralization and nitrification were higher in the THIN/BURN treatment relative to the other treatments (Table 4) during year 1, with net nitrification remaining elevated through year 3. This suggests that the large inorganic N pool found in the THIN/BURN treatment was not only the direct result of burning, but also the product of post-fire mineralization. Additionally, the significantly higher rates of net nitrification we detected 1 and 3 years following the THIN/BURN treatment, combined with only a minimal increase in soil NO_3^- detected during the same period, suggests that NO_3^- is rapidly removed from the soil solution through mechanisms such as plant uptake, immobilization, leaching or denitrification.

Several factors could explain why the higher net N mineralization and nitrification rates occurred in the THIN/BURN treatment and not the BURN treatment, relative to the control. One possibility is that the more severe fires experienced in the THIN/BURN treatment relative to the BURN treatment (Table 1) resulted in a greater alteration of organic substrates ultimately affecting microbial transformation of soil organic N. In support of this idea, research has demonstrated that soil heating can alter organic substrate fractions, ultimately affecting mineralization rates (White, 1994; Fernandez et al., 1997; Pietikainen et al., 2000). One way in which fire may act to stimulate mineralization and nitrification is to degrade recalcitrant organic N substrates into labile organic N substrates such as amino groups. It has been demonstrated that amino N is a highly labile N pool, the magnitude of which is equal to the total inorganic N pool in grassland and forest ecosystems (Jones et al., 2005). The amino N pool reflects the balance between microbial uptake, ammonification and enzymatic or thermal degradation of proteins (DeLuca and Keeney, 1993). An additional mechanism by which fire could stimulate N mineralization and nitrification is by altering or eliminating soluble phenols, which have been shown to increase during secondary succession (MacKenzie et al., 2004). Phenols may diminish net N mineralization and nitrification through a variety of mechanisms, including stimulation of N immobilization, complexation of inorganic N or microbial

Table 4
Net N mineralization, ammonification, nitrification and decomposition (mean ± S.E., $n = 3$) following prescribed fire at Lubrecht Experimental Forest, MT

	CONTROL	THIN	BURN	THIN/BURN	p[a]
Net N mineralization[b]					
Year 1[c]	2.3 ± 0.6	3.6 ± 2.1	3.2 ± 0.8	6.9 ± 0.6	*
Year 3[d]	5.7 ± 1.7	5.0 ± 0.9	7.2 ± 2.3	8.0 ± 0.8	ns
Net ammonification[b]					
Year 1[d]	2.0 ± 0.7	2.5 ± 1.1	2.8 ± 0.9	3.6 ± 0.7	ns
Year 3[d]	3.9 ± 0.9	3.2 ± 0.7	5.1 ± 2.2	5.1 ± 0.9	ns
Net nitrification[b]					
Year 1[e]	0.3 ± 0.1	1.1 ± 0.9	0.4 ± 0.2	3.2 ± 0.7	**
Year 3[d]	0.2 ± 0.1	0.0 ± 0.0	0.3 ± 0.2	0.7 ± 0.1	*
Decomposition (%)					
Year 1[d]	24.3 ± 0.4	24.9 ± 0.2	30.3 ± 1.4	28.4 ± 1.2	***
Year 3[d]	32.0 ± 1.6	32.7 ± 1.7	34.7 ± 3.6	42.3 ± 5.3	*

Decomposition is reported as mass% lost during an in situ incubation.

[a] p-Value: ns > 0.1, *: <0.1, **: <0.05, ***: <0.01.

[b] $\mu g\ g^{-1}$ 30 day^{-1}.

[c] Blocked ANOVA.

[d] One-factor ANOVA.

[e] Square-root transformed; non-transformed values reported.

inhibition (White, 1994; Northrup et al., 1995; Aerts, 1999; Hattenschwiler and Vitousek, 2000).

To explore these hypotheses, we measured soluble amino N concentration as a measure of labile organic N and total soluble phenol concentrations as a measure of bioavailable C. These analyses revealed no significant treatment differences in amino N concentration across all times in either the O horizon or the mineral soil, whereas total phenols in the O horizon were lowest in the THIN/BURN treatment relative to all other treatments (Table 3). This decline in total phenols may not have occurred in the BURN treatment because loss of phenols during combustion in this treatment may have been offset by a substantial deposition of scorched needles shortly after burning, replenishing the O horizon with fresh organic material rich in phenols. In contrast, much of the canopy fuels in the THIN/BURN treatment were transferred to the O horizon prior to burning during the harvest operation and were likely oxidized more completely. Other factors we did not measure, such as soil moisture and temperature, likely have a greater effect on net mineralization and nitrification patterns.

Decomposition, another microbe-mediated transformation, occurred significantly faster in the BURN and THIN/BURN treatments relative to the THIN and CONTROL (Table 4) during the first year, whereas decomposition in the THIN/BURN treatment exceeded all other treatments by year 3. The tongue depressors used to measure decomposition had a C:N greater than 200:1; thus, decomposition was likely influenced heavily by nitrogen availability in the soil. The higher inorganic N concentrations in the BURN and THIN/BURN treatments likely enhanced the ability of the soil microbial community to decompose this high C:N substrate. Differences in soil moisture and temperature may also have contributed to the higher rate of decomposition in the BURN and THIN/BURN treatments.

Because decomposition and nutrient mineralization are dependent on the soil microbial community, we compared microbial community structure, biomass and basal respiration rates among the treatments (Table 5). Restoration treatments may alter the soil microbial community structure and activity directly through heating, or indirectly by changing the physiochemical environment or the availability of substrates. Immediately following burning, O horizon respiration significantly differed among treatments, with the highest respiration occurring in the THIN treatment and the lowest respiration occurring in the BURN treatment. Differences in O horizon respiration were only temporary, with no significant differences found in later sampling periods. No differences in soil microbial biomass were detected during the first year; however, higher microbial biomass was found in the CONTROL compared to all other treatments during year 3. Soil respiration did not differ among treatments at any sampling time.

One and 4–5 weeks after the prescribed fire, no treatment effects were detected in the PLFA data, suggesting restoration treatments did not exert a strong direct effect on soil microbial community composition. In contrast, PLFA PC 2 was significantly different among treatments at weeks 16–18 (Table 5). This PC axis was heavily influenced by differences in actinomycete markers (10me16:0, 10me17:0 and 10me:18:0), which were significantly higher in the THIN/BURN treatment (Table 5). By year 3, the phospholipid fatty acid data no longer demonstrated any significant differences in microbial community composition. Many studies have shown that soil heating results in a substantial short-term loss of microbial biomass, activity or a shift in community structure (Pietikainen and Fritze, 1993, 1995; Choromanska and DeLuca, 2002; Korb et al., 2003). It is likely that the low-severity prescribed burning experienced in this study did not transfer enough energy into the soil to cause a direct restructuring of the microbial community.

4.2. Soil chemical properties

Restoration treatments had no significant effects on concentrations of soil exchangeable Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, extractable P or pH (Table 6) during years 1 and 3. These results were unexpected because it has been documented that the return of several elements from vegetation to soil is enhanced by both fire and harvesting. Fire is known to leave behind an ash rich in Ca, Mg, K and P because C and N volatilize at much lower temperatures (Neary et al., 1999). Additionally, condensation of alkali metals following fire is known to increase soil pH in many systems (Fisher and Binkley, 2000). Likewise, a rapid return of several nutrients from litter following harvest has been documented, with K showing the greatest mobility

Table 5
Soil microbial properties (mean ± S.E., $n = 3$) following prescribed fire at Lubrecht Experimental Forest, MT

	CONTROL	THIN	BURN	THIN/BURN	p[a]
Duff respiration (mg CO_2 g^{-1} day^{-1})					
Week 1[b]	3.5 ± 0.1	3.8 ± 0.1	3.0 ± 0.1	3.4 ± 0.1	***
Weeks 4–5[b]	3.4 ± 0.1	3.2 ± 0.3	2.9 ± 0.5	3.6 ± 0.2	ns
Weeks 16–18[b]	3.2 ± 0.4	4.0 ± 0.3	3.0 ± 0.3	2.2 ± 1.1	ns
Soil respiration (mg CO_2 g^{-1} day^{-1})					
Week 1[b]	0.6 ± 0.0	0.5 ± 0.6	0.6 ± 0.3	0.6 ± 0.2	ns
Weeks 4–5[c]	0.7 ± 0.00	0.8 ± 0.23	0.6 ± 0.01	0.7 ± 0.07	ns
Weeks 16–18[c]	0.6 ± 0.04	0.6 ± 0.03	0.5 ± 0.16	0.6 ± 0.08	ns
Year 3[c]	0.6 ± 0.01	0.6 ± 0.13	0.6 ± 0.03	0.5 ± 0.02	ns
Microbial biomass (nmol PLFA g^{-1})					
Week 1[b]	315.7 ± 45.1	295.2 ± 56.2	296.1 ± 41.1	269.0 ± 21.5	ns
Weeks 4–5[b]	281.0 ± 17.8	320.9 ± 19.2	282.4 ± 21.5	312.8 ± 43.0	ns
Weeks 16–18[b]	395.9 ± 22.4	333.1 ± 47.7	289.9 ± 26.7	305.2 ± 49.0	ns
Year 3[b]	397.2 ± 40.5	336.2 ± 19.7	257.9 ± 16.8	311.3 ± 38.0	*
PLFA PC 1					
Week 1[b]	0.38 ± 0.44	0.29 ± 1.01	−0.77 ± 0.44	0.10 ± 0.11	ns
Weeks 4–5[b]	0.08 ± 0.15	−0.26 ± 0.93	−0.05 ± 0.73	0.24 ± 0.58	ns
Weeks 16–18[b]	−0.36 ± 0.57	0.01 ± 0.66	0.36 ± 0.56	−0.01 ± 0.79	ns
Year 3[b]	−0.93 ± 0.41	0.08 ± 0.42	0.11 ± 0.79	0.75 ± 0.38	ns
PLFA PC 2					
Week 1[b]	0.66 ± 0.01	0.24 ± 0.72	−0.30 ± 0.50	−0.60 ± 0.40	ns
Weeks 4–5[b]	0.07 ± 0.15	−0.26 ± 0.93	−0.05 ± 0.73	0.24 ± 0.58	ns
Weeks 16–18[b]	−1.01 ± 0.59	0.28 ± 0.06	−0.35 ± 0.26	1.09 ± 0.47	**
Year 3[b]	−0.14 ± 0.90	−0.26 ± 0.57	0.33 ± 0.09	0.08 ± 0.77	ns
Actinomycetes (mol%)					
Week 1[b]	8.17 ± 0.37	8.23 ± 0.52	8.13 ± 0.38	8.70 ± 0.63	ns
Weeks 4–5[b]	8.61 ± 0.19	7.82 ± 0.81	7.75 ± 0.58	7.59 ± 0.29	ns
Weeks 16–18[b]	7.30 ± 0.10	8.02 ± 0.26	7.99 ± 0.31	8.85 ± 0.35	**
Year 3[b]	7.47 ± 0.24	8.12 ± 0.09	8.27 ± 0.26	8.76 ± 0.54	ns

PLFA principle components have no units, with PC 1 accounting for 35, 39 and 27%, and PC 2 accounting for 15, 14 and 21% of the variation in PLFA data during week 1, 4–5 and 16–18, respectively.
[a] p-Value: ns > 0.1, *: <0.1, **: <0.05, ***: <0.01.
[b] One-factor ANOVA.
[c] Kruskal–Wallis.

and Ca the least mobility (Klemmedson et al., 1985; Entry et al., 1991; Klemmedson, 1992).

Several factors may explain why we did not find elevated concentrations of these soil chemical properties following treatments. Substantial patchiness existed throughout the 9 ha treatment units as a result of heterogeneous fuel distribution and irregular fire behavior. Treatment averages, therefore, may not reflect the range of processes that occurred within patches. The prescribed fires experienced in this study may not have been severe enough on average to generate sufficient ash necessary to increase soil ion concentrations. Additionally, increased concentrations of these ions in the upper surface of the soil may have been diluted by analyzing composite samples of the 0–10 cm depth.

4.3. Soil physical characteristics

Restoration treatments had a pronounced effect on the depth of the organic horizon (O_i, O_e and O_a), where both BURN and THIN/BURN treatments resulted in a diminished depth, and the THIN treatment resulted in a thicker O horizon, relative to the CONTROL (Table 7). By year 3, O horizon thickness remained diminished in both burn treatments; whereas, the O horizon in the THIN treatment did not differ

Table 6
Soil chemical variables (mean ± S.E., $n = 3$) in response to restoration cutting (THIN), burning (BURN) and restoration cutting followed by burning (THIN/BURN) at Lubrecht Experimental Forest, MT

	CONTROL	THIN	BURN	THIN/BURN	p[a]
Ca (mg kg^{-1})					
Year 1[b]	1588.9 ± 255.9	1351.4 ± 146.1	1410.5 ± 115.3	1491.1 ± 185.7	ns
Year 3[b]	1055.3 ± 100.9	1487.2 ± 257.9	1268.3 ± 109.4	1270.1 ± 125.3	ns
Mg (mg kg^{-1})					
Year 1[b]	174.3 ± 30.4	137.6 ± 8.9	144.3 ± 12.5	163.0 ± 22.4	ns
Year 3[b]	164.7 ± 28.8	119.4 ± 10.03	131.4 ± 14.6	149.3 ± 17.2	ns
Na (mg kg^{-1})					
Year 1[c]	7.2 ± 0.32	6.2 ± 0.47	6.7 ± 0.98	7.1 ± 0.76	ns
Year 3[b]	15.7 ± 2.9	13.5 ± 2.1	12.3 ± 1.4	14.3 ± 1.9	ns
K (mg kg^{-1})					
Year 1[c]	403.6 ± 58.6	303.7 ± 37.2	360.3 ± 30.9	376.4 ± 39.8	ns
Year 3[b]	428.2 ± 38.8	343.4 ± 41.4	355.6 ± 63.5	347.6 ± 32.8	ns
P (mg kg^{-1})					
Year 1[b]	0.46 ± 0.04	0.48 ± 0.04	0.50 ± 0.04	0.48 ± 0.09	ns
Year 3[b]	1.66 ± 0.27	2.37 ± 0.46	1.7 ± 0.15	2.14 ± 0.28	ns
pH					
Year 1[b]	5.0 ± 0.10	5.1 ± 0.12	5.3 ± 0.07	5.4 ± 0.13	ns
Year 3[b]	4.7 ± 0.21	5.0 ± 0.10	5.1 ± 0.14	5.1 ± 0.08	ns

[a] p-Value: ns > 0.1.
[b] One-factor ANOVA.
[c] Blocked ANOVA.

significantly from the CONTROL, suggesting that substantial decomposition and settling of logging residues had occurred. These differences can be attributed primarily to combustion of, or addition to the O_i horizon, with only minor changes in the O_e and O_a horizons. Both BURN and THIN/BURN treatments resulted in significantly more exposed mineral soil relative to the other treatments during year 1. By year 3, these differences were no longer detectable, primarily as a result of new litter inputs. Increased soil exposure in these treatments might lead to increased erosion potential; however, this exposed area was a

Table 7
Soil physical characteristics (mean ± S.E., $n = 3$) in response to restoration cutting (THIN), burning (BURN) and restoration cutting followed by burning (THIN/BURN) at Lubrecht Experimental Forest, MT

	CONTROL	THIN	BURN	THIN/BURN	p[a]
O depth (cm)					
Year 1[b]	4.4 ± 0.5	5.0 ± 0.3	2.6 ± 0.5	2.5 ± 0.3	***
Year 3[b]	3.8 ± 0.4	3.5 ± 0.3	2.2 ± 0.4	1.6 ± 0.1	***
Db (g cm^{-3})					
Year 1[b]	0.91 ± 0.01	0.95 ± 0.05	0.90 ± 0.02	0.90 ± 0.04	ns
Year 3[b]	0.92 ± 0.04	0.98 ± 0.05	0.95 ± 0.04	0.96 ± 0.04	ns
Exposed soil (m^2)[c]					
Year 1[d]	0.05 ± 0.03	0.8 ± 0.29	2.6 ± 0.78	3.6 ± 0.04	**
Year 3[d]	0.04 ± 0.04	0.03 ± 0.02	0.5 ± 0.33	0.3 ± 0.20	ns

[a] p-value: ns > 0.1, *: <0.1, **: <0.05, ***: <0.01.
[b] One-factor ANOVA.
[c] Measurements were made within 1000 m^2 plots.
[d] Kruskal-Wallis.

very small fraction of each treatment unit area. We found no differences in soil bulk density among treatments. Higher bulk densities resulting from harvest operations in the THIN and THIN/BURN treatments were likely avoided because harvests were conducted on frozen and snow-covered soil using harvesting techniques designed to minimize soil compaction.

4.4. Prescribed burn severity

A unique aspect of this research is that treatments were both replicated and implemented at a scale more relevant than previous studies to real restoration projects. As a result, observed burn patterns and severities were more a function of factors such as fuel quantity and continuity, and weather conditions during the burn. In contrast, burn severities in studies using small plot sizes may not accurately reflect large scale operations because the entire plot may be effectively ignited, reducing the influence of weather and fuel distribution on burn severity. The scale and design used in this study allowed us to evaluate how variation in fire severity, expected in any large scale operation, was related to soil response variables. Most notably, we observed substantial variation in mean net mineralization and net nitrification in the BURN and THIN/BURN units, which we hypothesized was the result of fire severity. Correlation analysis revealed that net nitrification rate (Fig. 1) and net N mineralization (Fig. 2) showed strong positive correlations with the mean fine fuels consumed within each treatment unit. The mechanism responsible for these relationships could be the direct result of fire severity or the indirect result of soil climate conditions that likely co-vary as a result of fire severity. These relationships suggest that unavoidable variation in restoration treatments can have a substantial influence on mean soil N transformation. It is not clear whether the relationships between net nitrification and net N mineralization and fire severity remain linear beyond the fire severity experienced in this study.

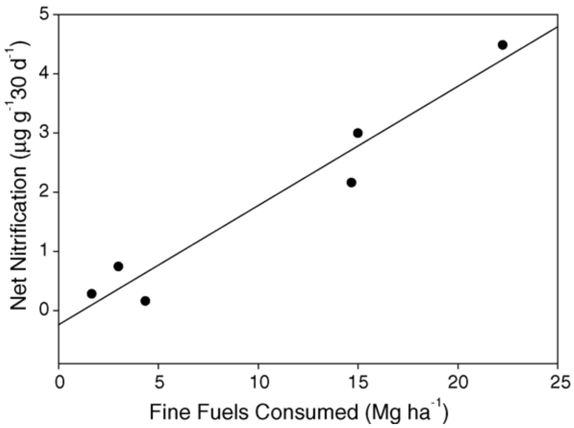

Fig. 1. The correlation between mean net nitrification against fine fuels consumed (diameter <7.6 cm) from six separate 9 ha prescribed burns at Lubrecht Experimental Forest, MT ($r^2 = 0.97$, $p = 0.001$).

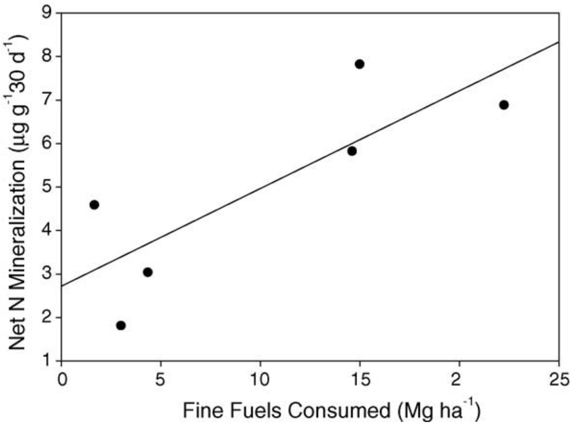

Fig. 2. The correlation between mean net N mineralization against fine fuels consumed (diameter <7.6 cm) from six separate 9 ha prescribed burns at Lubrecht Experimental Forest, MT ($r^2 = 0.814$, $p = 0.049$).

5. Conclusions

Numerous soil physical, chemical and biological properties differed among treatments. The most significant included net N mineralization, nitrification, NH_4^+ availability and decomposition rates, which were higher in both BURN and THIN/BURN treatments, with the most pronounced increase in the THIN/BURN treatment. Higher NO_3^- nitrate levels were also found in the THIN/BURN during weeks 4–5, whereas no other treatments resulted in elevated NO_3^- levels. Both BURN treatments also demonstrated a significant loss of the organic horizon, which resulted in reduced organic horizon C and a reduced C:N ratio. Very few differences in the soil microbial community were detected; however, the

THIN/BURN treatment resulted in a higher concentration of PLFA markers for actinomycetes 16–18 weeks after burning. The only differences found in the THIN treatment were a thicker O horizon and higher respiration rates than other treatments.

These differences in N cycling and availability among treatments may influence the composition of the biotic community that establishes following treatment. It is recognized that plant species possess different ecological strategies for regeneration and survival that involve numerous growth and allocation tradeoffs, of which a plant's N requirement is a central component. The importance of N as a structuring component of the plant community should be particularly strong in systems limited by N such as ponderosa pine ecosystems (Mandzak and Moore, 1994). The native grass species that reportedly dominated the understory of historical ponderosa pine forests likely relied on rapid nitrogen cycling that was promoted by periodic fire. Differences in short-term N cycling rates among restoration treatments may lead to substantial differences in site productivity and plant community composition. In addition to differences among restoration treatments, N cycling appears to have a positive linear relationship with fire severity within the severity range experienced in this study. This relationship, paired with a better understanding of the N strategies of target plant species, may allow land managers to more effectively use prescribed fire as a tool in restoring the ponderosa pine understory community.

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