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Initial effects of fire and mechanical thinning on soil enzyme activity and nitrogen transformations in eight North American forest ecosystems

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ABSTRACT

This study assessed the first-year effect of three ecosystem restoration treatments (prescribed fire, mechanical thinning, and their combination) on soil enzyme activity, soil N transformations, and C:N ratios of soil organic matter and mineral soil in eight North American forested ecosystems. The ecosystems we studied were part of the larger Fire and Fire Surrogate (FFS) network, and all had a history of frequent fire that has been altered by almost a century of organized fire suppression. Across all eight sites there were no statistically significant effects of the three manipulative treatments on phosphatase activity or chitinase activity; in contrast, at the network-scale phenol oxidase activity was reduced by fire alone, relative to the control. There was no significant network-scale effect of the three treatments on net N mineralization or net nitrification. Soil C:N ratio increased modestly after mechanical thinning, but not after prescribed fire or the combination of fire and thinning. There was a statistically significant reduction in forest floor C:N ratio as a result of all three treatments. Ordination of the differences between the treated and control areas indicated that fire alone resulted in greater changes in phenol oxidase activity and net nitrification than did the other two treatments. Large-scale restoration treatments such as those utilized in this study produce modest proximate effects on soil microbial activity and N transformations.

1. Introduction

Syntheses of the literature on the effects of fire on soil properties that developed over the last half century (e.g. Ice et al., 2004; Certini, 2005; Boerner, 2006) suggest that the effects of fire vary considerably among forest ecosystem types, in relation to fire severity, and over time. The diversity of ecosystem types, soil types, fires, response parameters, and experimental designs is, in fact, so daunting that developing generalizations that are useful at the local management scale is problematical.

This is also the case for restoration-oriented mechanical treatments (e.g. tree thinning or shrub layer manipulation). Although there exists a considerable literature on the impact of high intensity timber harvest (e.g. clear-cutting and whole-tree harvesting) on forest floor and soil properties (e.g. Matson and Vitousek, 1981; Rummer et al., 1997; Klepac et al., 1999), little is known of the effects of mechanical treatments at intensities useful for ecosystem restoration and wildfire hazard mitigation. The generalizations that have been developed from the clear-cutting literature seem unlikely to be applicable to the more modest mechanical treatments involved in restoration efforts.

The Fire and Fire Surrogate Network (FFS) project was established in 2000 to evaluate the efficacy of four alternative management strategies for simultaneously reducing wildfire hazards and increasing forest ecosystem sustainability, using a common experimental design in 12 forested ecosystems ranging from California and Washington in the west to Ohio and Florida in the east. All of the forested ecosystems represented in the FFS network shared a history of frequent, low severity fires over millennia, which was altered by the organized fire suppression that began in the early 20th century (Harmon, 1982; Sutherland, 1997). As such, the FFS network presented a unique opportunity to examine commonalities and differences in the effects of fire and mechanical treatments on forests that differ in vegetation, soil characteristics, and macroclimate (McIver et al., 2008). Using the common experimental design and suite of response variables of the Fire and Fire Surrogate Network project, we sought to test the following hypotheses: (1) fire will result in decreased forest floor C:N ratio as the result of combustion of the more recalcitrant components, but soil C:N ratio will change little. Any changes in soil microbial activity (measured as soil enzyme activity), N mineralization, or net nitrification will be the result of changes in microclimate, not soil organic matter quality. (2) Mechanical treatment will result in increased forest floor C:N ratio as the result of the deposition of logging slash. Despite the increase in forest floor C:N ratio, microbial activity and N mineralization in the soil will increase as the

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result of changes in surface microclimate following removal of parts of the tree and shrub canopies, and net nitrification will increase as the result of reduced plant demand for N. (3) The combination of fire and mechanical treatment will produce effects on C:N ratios that parallel those of fire alone. Microbial activity and N transformations will increase more from the combined treatment than from each of the treatments individually.

2. Methods

2.1. Study sites and sampling methods

This study employed eight of the twelve FFS study sites, ranging from California to South Carolina (Table 1). The eight sites were underlain by a range of soil types, of which Alfisols, Ultisols, and Inceptisols were the most prevalent (Table 1). Mollisols were present in one site and Entisols in two. Soil textures were dominated by loams and silt loams, though sands and fine sands were present in one site (Table 1). Complete descriptions of the vegetation, climate, and soils of the study sites are given by McIver et al. (2008).

Although the designated FFS experimental design was a randomized complete block with three blocks and four treatments (control, spring prescribed fire, mechanical treatment, and the combination of mechanical treatment and prescribed fire) allocated at random to those three blocks, two of the FFS sites used in this study (CaN and CaS) implemented completely randomized designs because of local logistics, and one site (OR) established four replicates of each treatment in a completely randomized design. CaS tested only the prescribed fire treatment as it was located in one of the U.S. National Parks, which do not permit mechanical treatments. We used change in aboveground biomass and surface fuels (downed woody debris + forest floor) to assess the impact of the three treatments at each site (Table 2).

Each treatment unit consisted of a minimum of 10 ha with a buffer zone of at least 4 ha surrounding it. Both the treatment unit and the buffer received the experimental treatment designated for that unit. Among the 12 FFS sites, the treatment units ranged in size from those approximating the minimum 14 ha to as large as 80 ha.

In the designated FFS design, each treatment unit was overlain with a 50 m grid and contained a minimum of 36 grid points. Ten 0.1-ha rectangular permanent sampling plots were located at random within each treatment unit, with one corner of each plot located at a grid point.

Vegetation components, soil, and fuels were sampled during the pre-treatment growing season and the growing season immediately following the completion of the treatment implementation. Two sites (CaN and OR) had incomplete pre-treatment sampling because their units and treatments had been installed before the designated FFS design was established, and logistic constraints resulted in pre-treatment sampling being incomplete in one additional site (CaS).

Soils were sampled either near the corners of the permanent sampling plots or in a subplot established within the permanent sampling plot. A range of 2–6 samples were taken in or around each permanent sampling plot, depending on site, yielding a total of 240–720 samples per site during the pre-treatment and post-treatment years. For the incubations used to measure N mineralization and net nitrification, samples were taken typically in June, whereas samples for enzyme activity were taken in August. Samples were kept refrigerated until analyzed, including during shipping from the field sites to the laboratory. All samples were analyzed within 5 days of arrival in the laboratory, and within 3 weeks of the sampling date, depending on site and shipping time.

The organic (O) horizon, if present, was removed prior to sampling the mineral soil. If no distinct boundary occurred between the Oa subordinate organic horizon (i.e. humic sub-horizon) and the A master horizon, the Oa was included in the sampling of the surface mineral soil. In sites where a distinct horizon boundary between the A and E occurred, samples were taken either for the full depth of the A horizon or to 15 cm, whichever was less.

Organic horizons (i.e. forest floors) were sampled by clearing the forest floor around an area of 0.25 m^2 and removing separately each discernable organic subordinate horizon (i.e. Oi, Oe, and Oa) in that exposed 0.25 m^2 area.

Net nitrogen (N) mineralization and net nitrification rates were estimated from 25 to 35 days *in situ* incubations utilizing either the buried polyethylene bag method (Eno, 1960) or paired, intact soil cores (Raison et al., 1987).

2.2. Laboratory methods

Subsamples were passed through a 2 mm sieve to remove stones and root fragments, extracted with 0.5 M K_2SO_4 or1.0 M KCl, then analyzed for NH_4^+ and NO_3^- using the microtiter methods of Sims et al. (1995). Total inorganic N (hereafter TIN) was defined as NH_4^+-N and NO_3^--N. Net N mineralization was defined as the difference in TIN between individual pre-incubation samples and TIN in either the corresponding post-incubation sample where $N = 1$ or the mean of the post-incubation samples where $N > 1$. Net nitrification was defined as the difference in NO_3^--N in pre-incubation and post-incubation samples. Proportional net nitrification was calculated by dividing net nitrification by the total NH_4^+-N available to be nitrified (initial NH_4^+-N + net N mineralized). Forest floor and soil organic carbon (C) and total N were analyzed by microDumas oxidation (Sollins et al., 1999).

For enzyme analysis, additional subsamples were passed through a 2 mm sieve to remove stones, root fragments, and particulate organic materials (i.e. remnants of the Oi, Oe), and then

Table 1
Geographic and edaphic information for the eight Fire and Fire Surrogate Network project study sites utilized in this study. Sites are ordered by longitude from west to east.

Study site	Location	Code	Soil orders	Predominant soil series	Soil Textural Class (es)
Southern Cascades Range, CA	Goosenest Adaptive Management Area (Klamath National Forest)	CA-N	Alfisols, Entisols	Belzar, Wintoner	Loam, silt loam
Central Sierra Nevada, CA	Sequoia-Kings Canyon National Park	CA-S	Inceptisols	Unknown	Loamy sand, sandy loam
Blue Mountains, OR	Hungry Bob (Wallowa-Whitman National Forest)	OR	Mollisols, Inceptisols	Fivebit, Melhorn, Blocker	Clay loam, loam, silt loam
Northern Rocky Mountains, MT	Lubrecht Experimental Forest	MT	Alfisols, Inceptisols	Winkler, Greenough, Tevis-Mitten	Silt loam, loam, sandy loam
Southwestern Plateau, AZ	Coconino and Kaibab National Forests	AZ	Alfisols, Mollisols	Unknown	Silty clay loam, clay loam, silty clay, clay
Central Appalachian Plateau, OH	Tar Hollow & Zaleski State Forests, Vinton Furnace Experimental Forest	OH	Alfisols, Inceptisols	Steinsburg, Gilpin, Shelocta	Silt loam, loam, sandy loam
Southeastern Piedmont, SC	Clemson Forest	SC	Ultisols, Inceptisols	Cecil, Madison, Pacolet	Sandy loam, clay loam
Southern Appalachians, NC	Green River Game Lands	NC	Ultisols, Inceptisols	Evard, Cowee, Cliffield	Loam, silt loam

Table 2
Mean net change in aboveground biomass carbon and surface fuel carbon (forest floor + downed woody debris) as the result of treatment with prescribed fire, mechanical treatment, or their combination in eight Fire and Fire Surrogate network sites. Data are from Boerner et al. (2008). n/a: data not available.

Site	Site code	Aboveground Biomass C			Surface Fuel C		
		Fire (%)	Mechanical (%)	Mechanical + fire (%)	Fire (%)	Mechanical (%)	Mechanical + fire (%)
Southern Cascades	Ca-N	−13.5	−29.4	−22.9	−74.4	n/a	n/a
Southern Sierra Nevada	Ca-S	−4.4	n/a	n/a	−73.7	n/a	n/a
Blue Mountains	OR	2.5	−28.3	−58.4	−73.5	−36.2	−62.9
Northern Rocky Mountains	MT	−6.5	−44.6	−57.0	−42.0	28.2	−24.9
Southwestern Plateau	AZ	0.3	−46.4	−45.7	−10.2	108.9	−24.5
Central Appalachian Plateau	OH	−0.7	−27.6	−22.5	−2.2	60.6	29.5
Southeastern Piedmont	SC	−9.9	−26.8	−42.0	−44.6	21.3	−16.0
Southern Appalachians	NC	−9.0	−4.4	−15.3	−35.4	15.4	−30.5
FFs Network Mean	FFS	−5.7	−27.4	−32.6	−38.3	19.8	7.2

analyzed for the activity of phosphatase, chitinase, and phenol oxidase. As all roots were removed prior to analysis, enzyme activities represent only microbial contributions.

Phosphatase (EC 3.1.3.1) was chosen as an indicator of overall microbial activity as phosphatase activity is strongly correlated with microbial biomass (Kandeler and Eder, 1993; Clarholm, 1993), fungal hyphal length (Häussling and Marschner, 1989) and N mineralization (Decker et al., 1999). Chitinases *sensu latu* are a series of bacterial enzymes that catalyze the breakdown of chitin, a by-product of the death of both fungi and arthropods, into carbohydrates and inorganic N. The specific member of this suite of enzymes we assayed was β-1,4-*N*-acetylglucosaminidase (EC 3.2.1.14). As chitin is intermediate in its resistance to microbial metabolism, its synthesis is only induced when other, more labile C and N sources are absent (Hanzlikova and Jandera, 1993). Chitinases are produced principally by bacteria; thus changes in chitinase activity relative to that of other enzymes give an indication both of changes in the relative contribution of chitinolytic bacteria to microbial activity as well as changes in organic matter along the gradient from labile to recalcitrant. Phenol oxidase (EC 1.14.18.1, 1.10.3.2) is produced primarily by white rot fungi, and is specific for highly recalcitrant organic matter, such as lignin (Carlile and Watkinson, 1994). Increases in phenol oxidase activity relative to other enzymes gives another indication of changes in the relative contribution of bacteria and fungi to microbial activity as well as an additional indication of the quality of the organic matter present. Thus, as a group these three enzymes supplied insight into changes in both the microbial community and the organic matter complex.

Enzyme activities were determined on field-moist soil using modifications of the standard methods developed by Tabatabai (1982). Sieved subsamples of fresh soil were suspended in 50 mM NaOAc buffer at pH 5.0 for the acidic soils of the eastern sites or $NaHCO_3$ buffer at pH 8.2 for the circumneutral soils of the western sites, and homogenized by rapid mechanical stirring. To minimize sand sedimentation, stirring was continued while aliquots were withdrawn for analysis.

For all sites except AZ and MT, phosphatase and chitinase activities in soil suspensions were determined using *p*-nitrophenol (*p*NP)-linked substrates. Following incubation, samples were centrifuged at 3000*g* for 3 min to precipitate particulates. An aliquot of 2.0 ml of the supernatant was transferred to a clean, sterile tube, and 0.1 ml of 1.0 M NaOH was added to halt enzymatic activity and facilitate color development. Prior to spectrophotometric analysis at 410 nm each sample of the supernatant was diluted with 8.0 ml of distilled, deionized water. Phosphatase and chitinase activities in samples from AZ and MT were measured in microplate wells using methlyumbelliferyl (MUB)-linked substrates. Excitation was measured at 360 nm and emission at 450 nm.

Phenol oxidase (EC 1.14.18.1, 1.10.3.2) activity in soil suspensions was measured by oxidation of L-DOPA (L-3,4-dihydroxyphenylalanine). In all sites except AZ and MT, 1 h incubations at 20–22 °C were followed by centrifugation as above and analyzed at 460 nm without dilution. Parallel oxidations using standard horseradish peroxidase (Sigma Chemical) were used to calculate the L-DOPA extinction coefficient. In MT and AZ, absorbance was determined at 460 nm every 5 min for 1 h to determine the rate of degradation of L-DOPA.

2.3. Data analysis

All response variables were normally distributed. As four of the eight sites utilized randomized complete block designs and four utilized completely randomized designs, pooled responses across the eight sites were analyzed by mixed model analysis of variance for a completely randomized design with sites, treatments, and units within treatments as main effects (SAS, 1995). For individual sites, the main effects were treatment, units within treatments, and plots within units. Treatment units were considered as the unit of replication, with $N = 3$ (4 for OR) per treatment per site. The criterion for significance was $p < 0.05$.

Although all sites were expected to take both pre-treatment and post-treatment samples, only four of the eight sites generated full pre-treatment data sets. To determine whether the lack of pre-treatment data was likely to produce type I errors, we did a preliminary analysis of the data from the four sites that did have complete pre-treatment data. This involved first analyzing the post-treatment responses at those four sites by analysis of variance, as indicated above, and then again by analysis of covariance with the pre-treatment conditions as covariates (Table 3). The magnitude and significance of the main treatment effects in the analyses with the pre-treatment conditions included as covariates (ANCOVAs) and those that included only the post-treatment data (ANOVAs) differed little, and <20% of the covariates were significant. Thus, the significance of the main post-treatment effects was relatively insensitive to the presence or absence of pre-treatment

Table 3
F statistic and associated probability of the treatment effect from mixed model analysis of variance (ANOVA), the treatment effect from analysis of covariance using pre-treatment conditions as the covariate (ANCOVA), and the covariate (COV) from the latter. Variance components significant at $p < 0.05$ are indicated by bold type.

Site	ANOVA	ANCOVA	COV
N Mineralization			
Sites pooled	**$F = 4.00, p < 0.008$**	**$F = 3.66, p < 0.013$**	$F = 1.02, p < 0.312$
AZ	$F = 1.34, p < 0.266$	$F = 1.34, p < 0.265$	$F = 0.23, p < 0.635$
OH	**$F = 6.45, p < 0.001$**	**$F = 6.21, p < 0.001$**	$F = 0.36, p < 0.552$
NC	**$F = 3.27, p < 0.024$**	**$F = 3.38, p < 0.021$**	$F = 0.41, p < 0.524$
SC	$F = 0.64, p < 0.594$	$F = 2.12, p < 0.103$	**$F = 13.71, p < 0.001$**
Forest Floor C:N			
Sites pooled	**$F = 38.92, p < 0.001$**	**$F = 29.64, p < 0.001$**	**$F = 4.17, p < 0.043$**
OH	**$F = 3.26, p < 0.025$**	**$F = 2.95, p < 0.037$**	$F = 1.59, p < 0.210$
NC	**$F = 61.16, p < 0.001$**	**$F = 14.63, p < 0.001$**	$F = 0.71, p < 0.400$
SC	**$F = 45.89, p < 0.001$**	**$F = 45.92, p < 0.001$**	$F = 0.67, p < 0.415$

Table 4
Mixed model analysis of variance of soil enzyme activity and N transformation rates among eight forest sites. The *F* statistic and associated probability for each variance component is given. Variance components significant at $p < 0.05$ are indicated in bold type.

Response	Full model	Treatment	Site	Units within treatments
Phosphatase activity	**$F = 12.38$, $p < 0.001$**	$F = 1.83$, $p < 0.206$	$F = 2.20$, $p < 0.143$	$F = 2.47$, $p < 0.060$
Chitinase activity	$F = 0.61$, $p < 0.889$	$F = 0.49$, $p < 0.699$	$F = 0.31$, $p < 0.862$	$F = 0.41$, $p < 0.987$
Phenol oxidase activity	**$F = 17.17$, $p < 0.001$**	**$F = 10.45$, $p < 0.006$**	**$F = 53.57$, $p < 0.001$**	$F = 2.22$, $p < 0.134$
Net N mineralization	**$F = 4.92$, $p < 0.001$**	$F = 0.57$, $p < 0.636$	**$F = 8.16$, $p < 0.001$**	**$F = 2.84$, $p < 0.001$**
Net nitrification	**$F = 8.33$, $p < 0.001$**	$F = 2.08$, $p < 0.101$	**$F = 6.67$, $p < 0.001$**	**$F = 3.56$, $p < 0.001$**
Soil C:N	**$F = 8.47$, $p < 0.001$**	**$F = 7.95$, $p < 0.001$**	**$F = 36.03$, $p < 0.001$**	**$F = 4.83$, $p < 0.001$**
Forest Floor C:N	**$F = 12.19$, $p < 0.001$**	**$F = 34.01$, $p < 0.001$**	**$F = 22.76$, $p < 0.001$**	**$F = 3.97$, $p < 0.001$**

data, at least for the four sites we could evaluate in this manner. In addition, meta-analysis of a broad range of pre-treatment soil parameters among all 12 FFS sites demonstrated no significant differences among treatment units within sites prior to treatment (Boerner et al., in press). This indicated to us that the lack of pre-treatment data from four of eight sites was not likely to lead to Type I errors.

3. Results

3.1. Soil enzyme activity

When the eight sites were pooled, there were no significant differences in phosphatase activity among treatments or sites (Table 4). In contrast, phosphatase activity was affected significantly by the treatments in five of the eight individual sites (Table 5). Among the five western sites, fire resulted in reduced phosphatase activity in six of eleven possible combinations of site and fire or fire + mechanical treatment, and in OR the fire and mechanical + fire treatments had lower phosphatase activity than did the mechanical treatment (Fig. 1). In addition, mechanical treatment alone resulted in reduced phosphatase activity at MT. Among the three eastern sites, only the mechanical + fire treatment in OH resulted in significantly reduced phosphatase activity (Fig. 1).

When the eight sites were pooled, there were no significant differences in chitinase activity among treatments or sites (Table 4). Chitinase activity was affected significantly by the treatments in four of eight individual sites (Table 5). Chitinase activity was reduced by all three manipulative treatments in CaN and OH, by fire (with or without mechanical treatment) in OR, and by the two individual treatments but not the combined treatment in NC (Fig. 2).

When the phenol oxidase activity of the soils of the eight sites was analyzed as a group, there were significant differences both among treatments and among sites (Table 4). Phenol oxidase activity was significantly lower in the prescribed burn units than in the units given the other three treatments (Fig. 3). Among the individual sites, phenol oxidase activity was affected significantly only in CaN, OR, and OH (Table 4). Phenol oxidase activity was reduced significantly by fire alone in CaN, by fire plus mechanical treatment in OH, and by mechanical treatment alone in OR (Fig. 3).

Pre-treatment and post-treatment phosphatase activities were significantly and positively correlated in soils from the control, prescribed fire, and mechanical treatment units, and marginally correlated in the mechanical + fire treatment units (Table 6). In contrast, pre- and post-treatment chitinase activity was only significantly correlated in the control and mechanical treatments (Table 6). There were no significant correlations between pre- and post-treatment phenol oxidase activity (Table 6).

3.1.1. N mineralization and net nitrification

Overall there were no significant effects of the manipulative treatments on net N mineralization (Table 4, Fig. 4) or net nitrification (Table 4, Fig. 5). There were significant differences in net N mineralization in only three of eight sites (Table 5). In MT, the combined mechanical + fire treatment produced significantly greater N mineralization rates than the control and in OH both the mechanical treatment alone and the combined treatment had significantly greater N mineralization than did the control (Fig. 4). In NC, fire alone resulted in significantly decreased N mineralization relative to the control (Fig. 4.)

The manipulative treatments resulted in significant effects on net nitrification in four of eight sites (Table 5). Net nitrification rates were enhanced by fire alone in CaS, and by fire combined with thinning in MT; in contrast, both fire treatments resulted in reduced net nitrification in OH (Fig. 5).

3.2. C:N ratios

Across the suite of eight sites, mechanical treatment resulted in a small, but statistically significant increase in soil C:N ratio (Table 4, Fig. 6). The overall relative difference between the mechanically treated units and the controls was approximately 7%. Five of the eight sites also exhibited significant effects of restoration treatments on soil C:N ratio (Table 5). In OR, SC, and NC the soil C:N ratio was significantly greater in the mechanical treatment than in the control. Fire alone resulted in increased soil C:N ratio in CaN and SC, but reduced soil C:N ratio in CaS. Again, these differences were small in absolute magnitude despite their strong statistical significance.

Over the eight sites, forest floor C:N ratio was reduced significantly by all three treatments, though once again the magnitude of the change was small (Table 4, Fig. 7). The relative difference between the controls and the three manipulative treatments averaged 8.5%. Relative to the controls, mechanical treatment

Table 5
Analysis of variance of soil enzyme activity and N transformation rates in eight forest sites. The *F* statistic and associated probability for the treatment are given, with those significant at $p < 0.05$ are indicated in bold type.

Site	Phosphatase	Chitinase	Phenol oxidase	N mineralization	Net nitrification	Soil C:N	Forest floor C:N
Ca-N	**$F = 14.47$, $p < 0.001$**	**$F = 9.33$, $p < 0.001$**	**$F = 4.76$, $p < 0.004$**	$F = 2.24$, $p < 0.088$	$F = 1.69$, $p < 0.174$	**$F = 10.49$, $p < 0.001$**	**$F = 55.29$, $p < 0.001$**
Ca-S	**$F = 23.72$, $p < 0.001$**	$F = 1.62$, $p < 0.207$	$F = 0.46$, $p < 0.500$	$F = 0.52$, $p < 0.472$	**$F = 6.70$, $p < 0.011$**	**$F = 8.98$, $p < 0.004$**	**$F = 8.12$, $p < 0.007$**
OR	**$F = 4.73$, $p < 0.005$**	**$F = 7.20$, $p < 0.001$**	**$F = 3.56$, $p < 0.018$**	$F = 1.71$, $p < 0.197$	$F = 0.17$, $p < 0.915$	**$F = 5.18$, $p < 0.003$**	**$F = 3.75$, $p < 0.016$**
MT	**$F = 7.14$, $p < 0.001$**	$F = 1.90$, $p < 0.134$	no data	**$F = 4.69$, $p < 0.005$**	**$F = 16.98$, $p < 001$**	$F = 0.44$, $p < 0.728$	**$F = 4.76$, $p < 0.004$**
AZ	$F = 1.89$, $p < 0.232$	$F = 0.17$, $p < 0.910$	$F = 1.35$, $p < 0.344$	$F = 1.34$, $p < 0.266$	$F = 1.71$, $p < 0.169$	$F = 2.48$, $p < 0.066$	**$F = 14.77$, $p < 0.001$**
OH	**$F = 7.21$, $p < 0.002$**	**$F = 2.64$, $p < 0.048$**	**$F = 2.81$, $p < 0.044$**	**$F = 6.45$, $p < 0.001$**	**$F = 5.89$, $p < 0.001$**	$F = 0.44$, $p < 0.722$	**$F = 3.26$, $p < 0.025$**
SC	$F = 0.83$, $p < 0.479$	$F = 0.91$, $p < 0.438$	$F = 0.93$, $p < 0.431$	$F = 0.64$, $p < 0.594$	$F = 1.29$, $p < 0.281$	**$F = 35.99$, $p < 0.001$**	**$F = 61.16$, $p < 0.001$**
NC	$F = 1.15$, $p < 0.329$	**$F = 3.98$, $p < 0.009$**	$F = 1.30$, $p < 0.276$	**$F = 3.27$, $p < 0.024$**	**$F = 3.51$, $p < 0.018$**	**$F = 11.98$, $p < 0.001$**	**$F = 5.89$, $p < 0.001$**

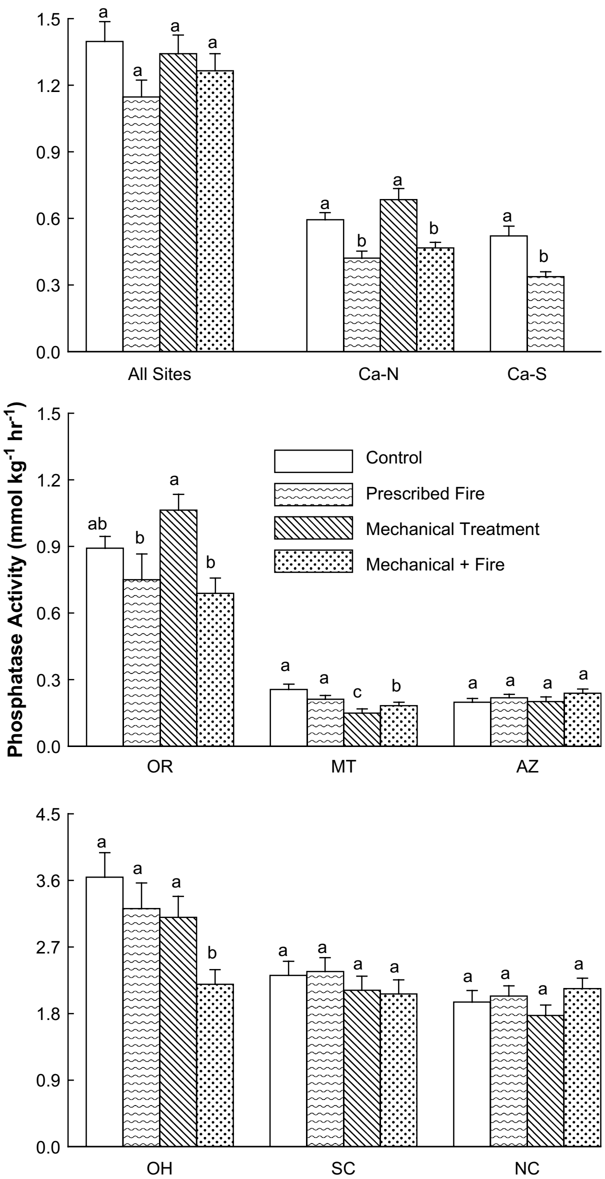

Fig. 1. Phosphatase activity in soils of eight Fire and Fire Surrogate Network sites in relation to three manipulative restoration treatments. Each histogram bar represents a mean of 3–4, except the All Sites bars which represent $N = 24–25$. Standard errors of the means are shown, and histogram bars labeled with the same lower case letter were not significantly different at $p < 0.05$. Site codes are: CaN = Southern Cascades Range, CA; CaS = Southern Sierra Nevada Range, CA; OR = Blue Mountains, OR; MT = Northern Rocky Mountains, MT; AZ = Southwestern Plateau, AZ; OH = Central Appalachian Plateau, OH; SC = Southeastern Piedmont, SC; and NC = Southern Appalachian Mountains, NC.

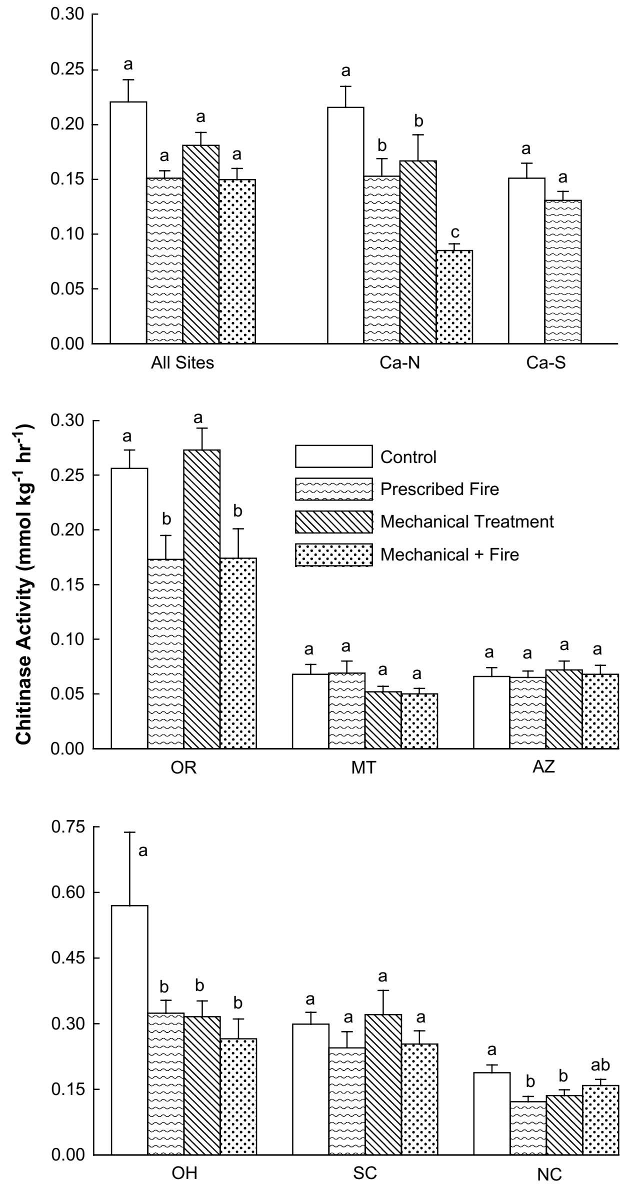

Fig. 2. Chitinase activity in soils of eight Fire and Fire Surrogate Network sites. Format follows Fig. 1.

resulted in increased forest floor C:N in only one site (SC). Fire resulted in reduced forest floor C:N in two sites (CaN and AZ) and increased C:N in one site (CaS) (Fig. 7). In six of the eight sites, the mechanical treatment resulted in significantly greater forest floor C:N than did the fire treatment (Fig. 7).

3.3. Ordination

NMS ordination of the differences between the post-treatment conditions in the control units and in the corresponding treated units in each site arrayed the site-treatment combinations along two axes which together accounted for >95% of the total variance in the matrix (Fig. 8). The large majority of the variance was represented by the first ordination axis, which was positively correlated with C:N ratios of soil and forest floor and negatively correlated with phosphatase activity, chitinase activity, and net nitrification (Fig. 8). The prescribed fire treatments were arrayed at the lower end of NMS Axis one, indicating that fire produced the greatest decreases in enzyme activity and net nitrification, relative to the corresponding controls. The mechanical and mechanical + fire units were arrayed at the center and upper portion of NMS axis one, indicating that these treatments produce greater increases in forest floor and soil C:N ratios than did the prescribed fire treatment. NMS axis two accounted for <10% of the variance and represented variance among sites within a treatment (Fig. 8).

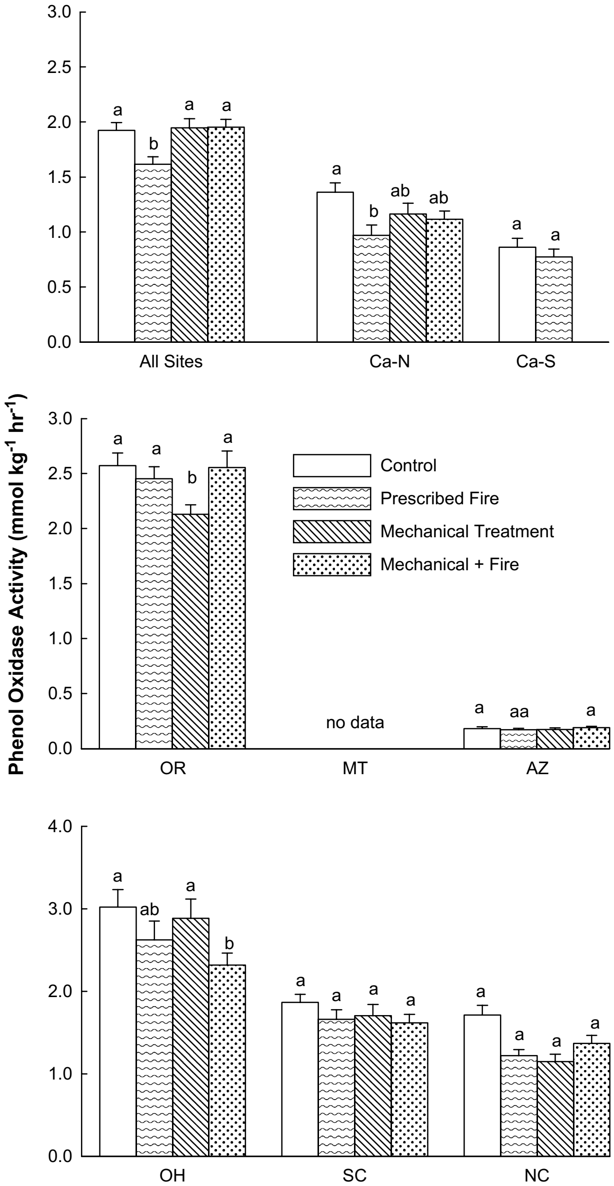

Fig. 3. Phenol oxidase activity in soils of eight Fire and Fire Surrogate Network sites. Format follows Fig. 1.

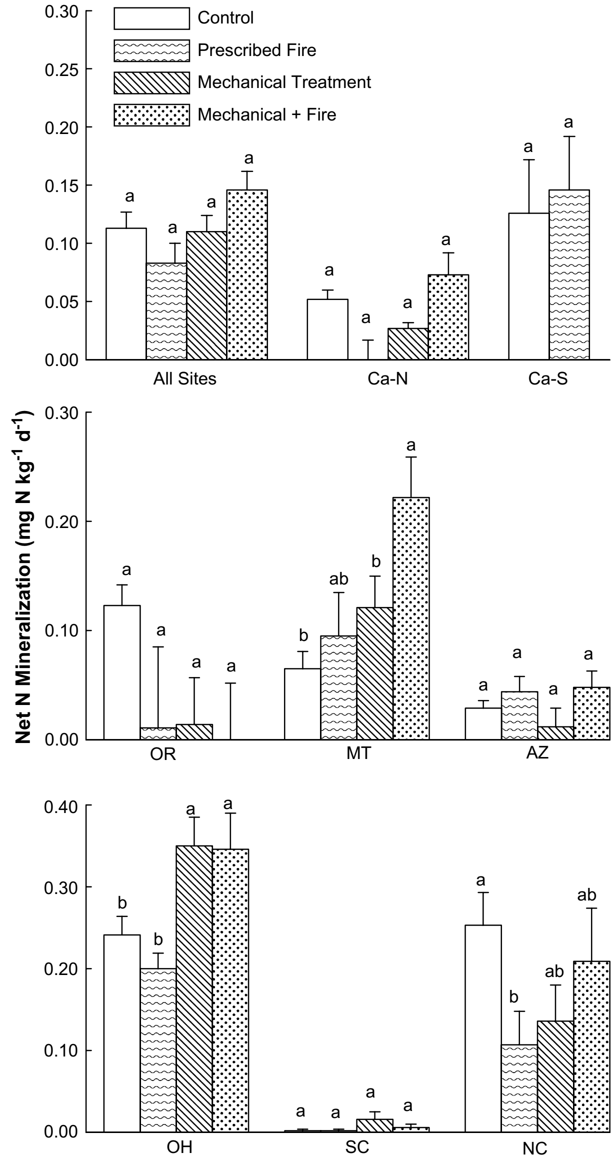

Fig. 4. Net N mineralization in soils of eight Fire and Fire Surrogate Network sites. Format follows Fig. 1.

4. Discussion

Soil microbes (*sensu latu*) release enzymes that metabolize the available soil organic matter. Some of these enzymes (e.g. phosphatase) are produced as long as the organism is metabolically active, whereas others (e.g. chitinases and phenol oxidase) are inducible and are only produced by certain microbial groups in response to the presence of specific substrates. We quantified activity rates of these three enzymes in order to gain insight into the microbial response to our restoration treatments.

When the eight study sites were considered as a group, phosphatase activity was not affected significantly by any of the three treatments; however, phosphatase activity was reduced significantly by treatments that included fire in four of the five western sites. Reductions in phosphatase activity by fire in dry coniferous forests have also been reported in *Pinus pinaster* and *Pinus sylvestris* stands in Spain (Saa et al., 1993). Among the eastern sites, phosphatase activity was reduced only by the combined treatment in the deciduous forests of the OH site. Although this result was consistent with prior studies in this particular site (Boerner and Brinkman, 2003; Boerner et al., 2004), there were no indications of significant reductions in phosphatase activity by any of the three treatments in the other two eastern sites.

Table 6
Correlations between pre-treatment and post-treatment enzyme activities in soils from eight Fire and Fire Surrogate Network sites. Correlation coefficients and associated probabilities are given.

Treatment	Phosphatase	Chitinase	Phenol oxidase
Control	0.796 ($p < 0.002$)	0.709 ($p < 0.010$)	0.230 ($p < 0.472$)
Prescribed fire	0.726 ($p < 0.008$)	0.070 ($p < 0.830$)	0.188 ($p < 0.559$)
Mechanical thinning	0.799 ($p < 0.002$)	0.584 ($p < 0.047$)	0.396 ($p < 0.202$)
Mechanical + fire	0.560 ($p < 0.059$)	0.467 ($p < 0.127$)	0.170 ($p < 0.597$)

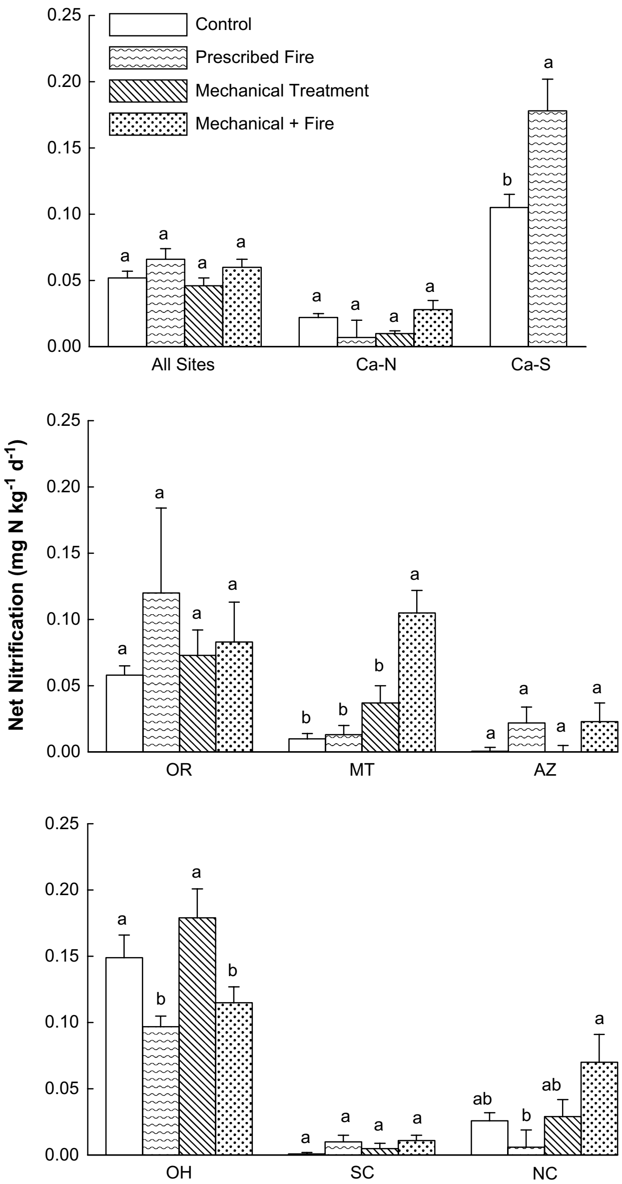

Fig. 5. Net nitrification in soils of eight Fire and Fire Surrogate Network sites. Format follows Fig. 1.

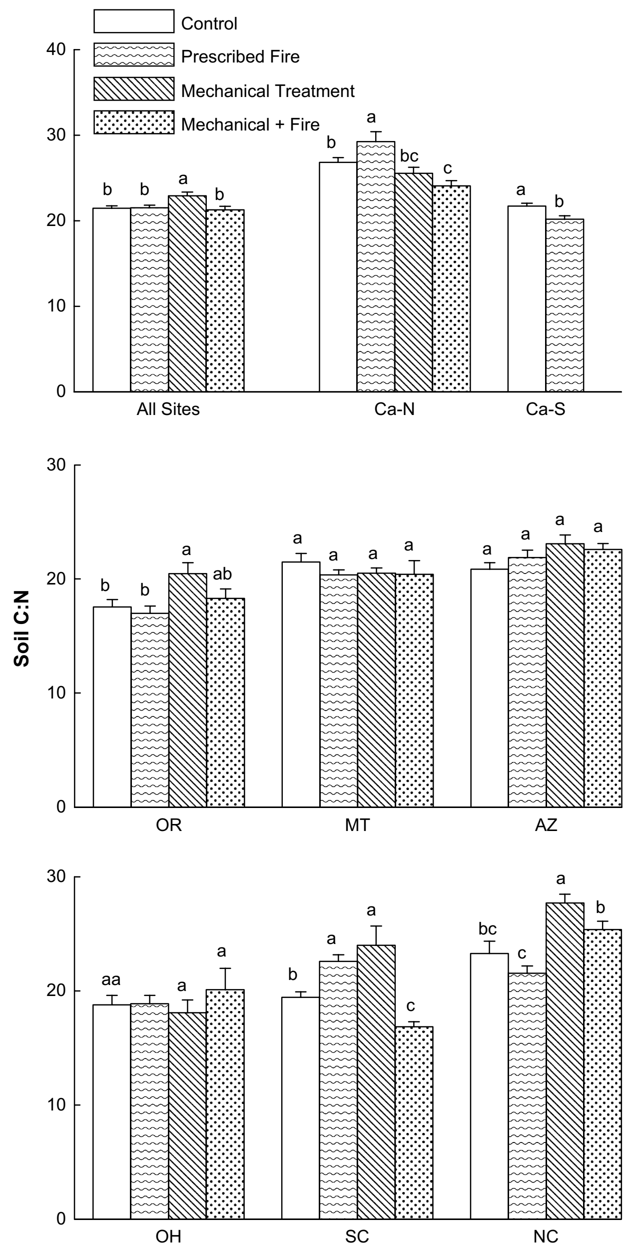

Fig. 6. C:N ratio in soils of eight Fire and Fire Surrogate Network sites. Format follows Fig. 1.

As was the case for phosphatase, there were no significant overall effects of the three treatments on chitinase activity. In four of the eight sites chitinase activity was not significantly affected by any of the three manipulative treatments, whereas in the other four either the two treatments involving fire or all three treatments exhibited reduced chitinase activity. There was no geographic pattern to the effects on chitinase: there were two eastern and two western sites among the four in which treatments affected chitinase activity. Similarly, the sites in which chitinase activity was reduced included deciduous and coniferous forests, relatively dry and relatively humid sites, and sites with relatively low and high soil organic matter (McIver et al., 2008; Boerner et al., 2008).

Phenol oxidase activity varied greatly among sites. The soils of the OR and OH sites supported phenol oxidase activity ~10- to 15-fold greater than did the soils of the AZ site. Overall, fire alone resulted in reduced phenol oxidase activity, though this difference was driven primarily by strong reductions after fire in CaN and after the combined mechanical + fire treatment in OH. We could find no previous studies that documented phenol oxidase activity in western coniferous forests following fire and/or harvesting, and prior studies of phenol oxidase activity in eastern forests have produced conflicting results (Boerner and Brinkman, 2003; Boerner et al., 2004, 2007).

Examining the correlations in the pre- and post-treatment activity of each enzyme produced several interesting contrasts. Phosphatase activity is controlled primarily by environmental factors, including temperature, moisture, and N availability. Pre- and post-treatment phosphatase activity were strongly and positively correlated in the control, prescribed fire, and mechanical treatment units, but only weakly (and not statistically significantly) correlated in the mechanical + fire plots. This suggests that the

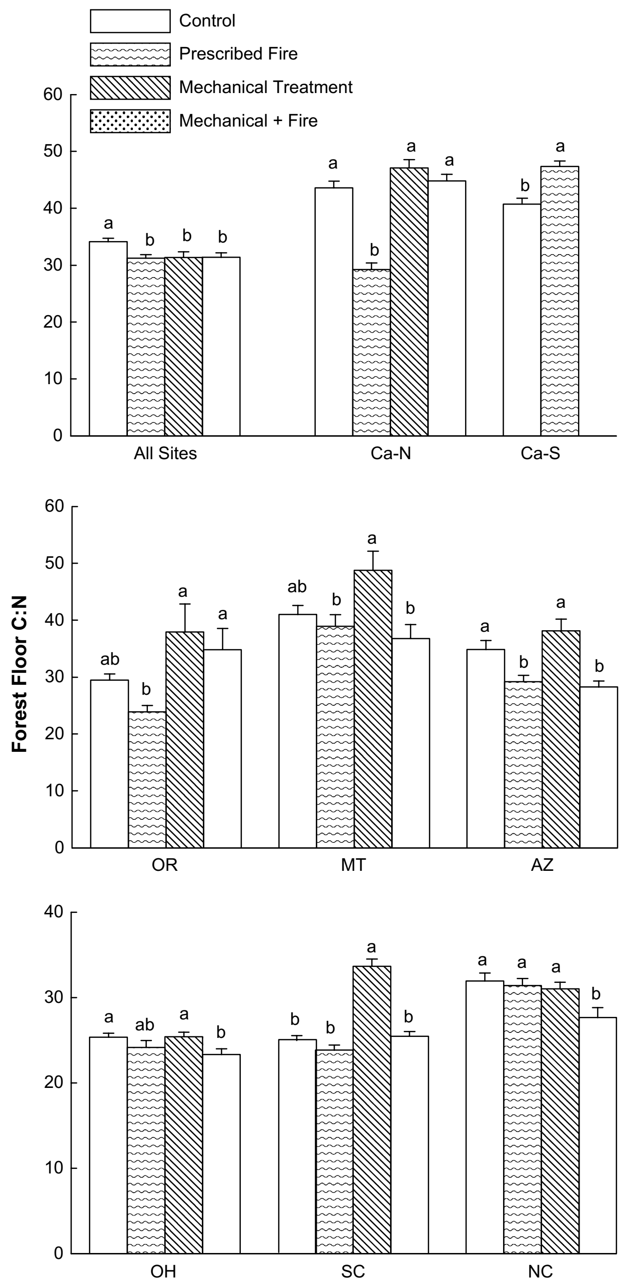

Fig. 7. C:N ratio in forest floors of eight Fire and Fire Surrogate Network sites. Format follows Fig. 1.

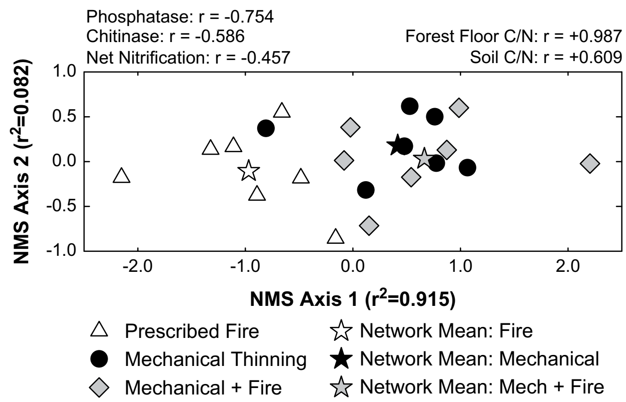

Fig. 8. NMS ordination of the difference in soil factors of sets of treatment units given one of three manipulative treatments, in relation to the corresponding control units in eight Fire and Fire Surrogate Network sites.

impact of the combined treatment on the soil microclimate was considerably greater than that of the two individual treatments. In contrast, pre- and post-treatment chitinase activities were positively correlated only in the control and mechanical treatments. As induction of chitinase activity occurs primarily when substrates more easily metabolized than chitin are absent (Hanzlikova and Jandera, 1993), the reductions in chitinase activity we observed in the fire and mechanical + fire treatments in four of the sites may have been the result of the deposition of more labile, partially combusted organic matter following fire. Pre- and post-treatment phenol oxidase activity were uncorrelated, both on a treatment basis and overall. This suggests to us that interannual variations in phenol oxidase activity may often be larger than treatment effects, and this may be the cause of the conflicting effects of fire on phenol oxidase activity in previous studies (Boerner and Brinkman, 2003; Boerner et al., 2004, 2007).

Neither net N mineralization nor net nitrification was affected by any of the treatments over all eight sites, and there was no consistent pattern among the relatively few within-site differences. Furthermore, variability in N transformations among plots within treatments was considerably greater than were variations in enzyme activity. Similarly, Knoepp and Swank (1993) monitored N mineralization rates after clear-cutting of a mixed oak–pine stand in Tennessee and found that N mineralization was both greater and more variable in the harvested sites. In addition, the variation about the mean was considerably greater in the western sites than the eastern sites despite similar sampling intensity. This suggests that the interactions between spatial heterogeneity in fire severity and sampling design may have been more important in western coniferous forests than eastern forests, at least in this study.

Our results may, at first glance, seem to be in contradiction with the many previous studies that have demonstrated increases in N mineralization and net nitrification after single fires (Wagle and Kitchen, 1972; reviews by Raison, 1979; Wan et al., 2001; Boerner, 2006); however, when the results of the meta-analysis done by Wan et al. (2001) were stratified by fire intensity and ecosystem, they concluded that high intensity wildfires and slash fires in conifer forests resulted in increased N turnover whereas prescribed burning and other fires in hardwood forests did not. Whether this difference is driven by fire intensity or ecosystem type is unclear, as most of the western coniferous forest fires in that data set were wildfires and most of the fires in the eastern deciduous forest were planned, low intensity prescribed fires. The lack of impact of a single prescribed fire on N turnover in eastern forests is further supported by studies that postdate the meta-analysis of Wan et al. (2001). For example, in an analysis of the initial effects of the FFS treatments in the OH site Boerner et al. (2000) found no significant effect of a single fire on N mineralization in an Ohio mixed-oak forest, and a similar lack of fire effect on N mineralization has been reported for oak-pine forests in Georgia and Tennessee (Hubbard et al., 2004) and oak–pine stands in North Carolina (Knoepp et al., 2004).

It is important to note that the results of single fires or relatively short term studies may not scale linearly across longer time periods. Vance and Henderson (1984) measured rates of N mineralization in a Missouri oak flatwoods that had been burned either annually or periodically (3–4 year rotation) for approximately 30 years, and found that N mineralization was reduced by long-term burning. They concluded that this change was a consequence of a change in organic matter quality (measured as C:N ratio), not quantity. Similarly, Eivasi and Bayan (1996) resampled the same Missouri oak flatwoods a decade later, and concluded that microbial biomass and enzyme activity had been reduced in proportion to fire frequency even though the amount of soil organic matter present had not been significantly affected. This would be consistent with what one would expect if long-term burning results in an accumulation of recalcitrant C forms, including black carbon, over time (Ponomarenko and Anderson, 2001).

Changes in soil N transformations following pre-commercial thinning and other partial harvest practices may be the result of additions of logging residues, which may include both relatively low C:N ratio leaf material and relatively high C:N ratio woody residues. In addition, opening of the canopy may produce changes in forest floor and soil microclimate, as well as reductions in plant N uptake resulting from the removal of tree basal area (Johnson and Curtis, 2001). For example, clear-cutting in a Virginia hardwood forest resulted in reduced plant N uptake and in increased microbial biomass and N mineralization rate (Johnson et al., 1985). Similarly, Frazer et al. (1990) reported N mineralization and net nitrification rates in clearcuts in CA mixed conifer forests 4-fold and 2-fold greater, respectively, than in uncut stands.

A number of mechanisms may underlie the lack of apparent effect of the FFS mechanical treatments on N turnover: (1) the harvests that removed only 25–33% of the aboveground biomass that characterized the FFS mechanical treatments were insufficient to produce changes in soil microclimate large enough to affect microbial activity and N uptake, (2) the mix of logging residues was sufficiently heterogeneous to result in no net change in organic matter quality, and (3) spatial heterogeneity of canopy opening and/or logging slash may produce increases in variance without changes in mean rates.

When all eight sites in this study were pooled, the C:N ratio of both soil and forest floor was affected significantly by the treatments, though the mean differences among treatments were $<$10% in both cases. Fire resulted in increased soil C:N in two sites (CaN and SC) and decreased soil C:N in another (CaS), whereas five sites exhibited no significant effect. Results of previous studies of the effects of a single fire on soil C:N have been equally mixed. In western coniferous forests Black and Harden (1995) documented a small but significant increase in C:N ratio after fire while Antos et al. (2003) found a significant decrease.

Forest floor C:N decreased after fire, with or without mechanical treatment, in five of eight sites. This is a result that has been commonly reported in the literature, and is primarily the result of partial combustion removing higher C:N ratio residues from the forest floor mix. For example, Vose and Swank (1993) reported a reduction in forest floor C:N ratio of 10–20% following fire in an eastern mixed forest. Similarly, Antos et al. (2003) observed a decrease of $\sim$30% in forest floor C:N ratio after prescribed fire in a western coniferous forest.

Mechanical treatment resulted in increased soil C:N overall and in three of the eight individual sites. Black and Harden (1995) noted that soil C:N in sites clearcut 2 years prior had C:N ratio of 26–29, compared with an average C:N of 22 in uncut sites. The primary mechanism at work here would appear to be the mixing of forest floor material into the mineral soil as the result of vehicle traffic or other logging activities.

Woody residues remaining after logging typically have high C:N ratios, and therefore we had hypothesized widespread effect of partial harvesting on forest floor C:N ratio; thus, the observation that the FFS mechanical treatments resulted in increased forest floor C:N in only one site (SC) was unexpected. The mechanical treatments were designed to be consistent with established commercial harvesting practices at the various sites. Thus, the suite of mechanical treatments applied across the network varied both in the proportion of basal area removed, and perhaps more importantly, in the way the logging residues were treated. Some of the sites removed logging residues from the site, some left the residues in place, and others chopped the residues and mixed them with the forest floor. The variations in the intensity of harvesting and in residue treatment may well have obscured the somewhat higher C:N ratio of the initial logging residues. Even in sites where residues were left in place, the mix of foliar and woody residues may have varied spatially, adding a strong element of spatial heterogeneity and thereby preventing statistically significant mean effects from occurring. For example, Olsson et al. (1996) compared coniferous forest logging residues that were dominated by foliar materials to those comprised of a mix of foliage and branches. The C:N ratio of the former was 44–55 whereas the latter had C:N ratio of 74–136.

The ordination approach we used clearly separated the prescribed fire treatment from the mechanical and mechanical + fire treatment. The former had relatively greater (negative) effects on three indicators of microbial activity (phosphatase activity, chitinase activity, and net nitrification) whereas the latter two treatments produced greater increases in soil and forest floor C:N ratio. Thus, the prescribed fire treatment seemed to result in a proximate reduction in microbial activity, whereas the two mechanical treatments produced changes in the organic matter complex that had potentially more persistent inhibitory effects on microbial activity.

Only repeated sampling of these sites over time and through several fire cycles will allow us to determine if these first-year trends persist. As management strategies and decisions are designed to maximize outcomes over meaningful periods of time, so must experiments be designed to inform such decisions.

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