RESTORING MIXED-CONIFER FORESTS WITH FIRE AND MECHANICAL THINNING: EFFECTS ON SOIL PROPERTIES AND MATURE CONIFER FOLIAGE

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ABSTRACT

The forests of northern California experienced frequent, low-intensity fire prior to Euro-American settlement, but more than a century of grazing, logging and fire suppression has resulted in changes in tree community structure that contribute to infrequent, high-intensity fires in these forests today. Although ecosystem restoration for reduction of wildfire hazard has received substantial attention in recent years, many ecological questions remain unanswered. For example, it is not yet clear how large-scale forest manipulations, such as reduction of tree density via forest thinning or prescribed fire, differentially affect soil fertility, nor how impacts on soil nutrient availability in turn affect forest productivity. My research in the Klamath National Forest of northern California investigates the impacts of experimental restoration treatments (prescribed fire, mechanical thinning, and their combination) on soil physical, chemical and microbial parameters and forest floor C and N content, and the time lag and duration of response of leaf nutrient concentrations of two dominant tree species to each treatment. Results showed that significant differences existed among treatments in terms of soil nutrient status and microbial activity, with the effect of fire either mediated or enhanced by thinning; however, for most variables the magnitude of effect was small. Prescribed fire had different effects on soil nutrients and microbial activity in unthinned areas than in areas that had been mechanically thinned prior to fire, and the species composition of
trees that remain following thinning significantly affected soil nutrient availability and forest floor C and N content. Thinning also affected conifer needle nutrient concentration and size whereas fire alone does not, and the time since treatment as well as the magnitude and direction of response differed between tree species and among treatments. These results provide an intermediate-term evaluation of the effects of fire and thinning on soil and vegetation, and increase understanding of the link between the above- and belowground components of a mixed-conifer ecosystem. This study contributes to an ecosystem-level understanding of forest restoration strategies, and provides information that is directly applicable to fire and forest management policies in the western United States.
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CHAPTER 1
INTRODUCTION

Fire has been an important process in determining vegetation structure and composition of ecosystems throughout North American history. Prior to Euro-American settlement, low-intensity fires in western mixed-conifer forests occurred as frequently as every 2-15 years due to lightning strikes, volcanic activity, or seasonal ignitions by indigenous peoples (Agee 1993). Historically frequent fires limited growth of shrubs and small trees in the forest understory and facilitated dominance of thick-barked, shade-intolerant tree species such as Pinus ponderosa (ponderosa pine).

Today’s forests differ substantially from historic conditions in characteristics such as stand density, species composition, frequency of disease and insect outbreaks, and nutrient cycling. These changes are due in part to more than a century of grazing, logging and aggressive fire suppression policies (Agee 1993). For example, forests that were historically described as open, park-like stands of large trees now contain a dense understory of young, shade-tolerant trees (Covington and Moore 1994), which contribute to the development of fires of far greater intensity than historical fires, as seen by the occurrence of large, catastrophic wildfires in California in recent years. These
catastrophic fires in turn impact human and economic systems via the high costs of continued fire suppression, particularly in areas of wildland-urban interface, and the loss of homes and forest resources such as timber.

Although management activities such as forest thinning or prescribed fire may restore forests to approximate historic conditions, the ecological effects of these activities on critical components of soil productivity, such as nutrient status and microbial activity, are not well understood. Furthermore, although thinning and burning are each known to alter the belowground ecosystem, comparisons of the magnitude and duration of these effects within a suite of long-term restoration treatments have not been well investigated.

Evaluating the effects of forest restoration treatments on soils in conjunction with the nutrient content of plant leaves provides important insight into both the short- and long-term sustainability of a forest ecosystem. For example, the availability of essential plant nutrients in soil, such as nitrogen (N) and phosphorus (P), influences the health and growth of vegetation, suggesting that changes in forest soils may serve as an early indicator of treatment effects on vegetation and, ultimately, the forest ecosystem. Previous studies have reported that forest management activities influence the size (McDonald et al. 1992) and N and P concentrations (Feeney et al. 1998) of conifer needles, and soil nutrients have been shown to correlate with needle nutrient content (Wang and Klinka 1997, Amponsah et al. 2005) and, therefore the potential for photosynthesis, a key driver of ecosystem productivity.

This study is a component of the long-term, national Fire and Fire Surrogates (FFS) network study, which was initiated in 2000 as a multi-institutional collaboration
among academic and federal researchers. The national FFS study was designed to evaluate the long-term ecological effects of thinning and prescribed fire in forests that historically (pre-1900s) experienced frequent, low-intensity fire. The Klamath National Forest of northern California was selected for the southern Cascades FFS study site, representing one of the 12 FFS network sites; and serves as the location for the dissertation presented here.

The national FFS study used a common experimental design (treatments, replication, plot size, and response variables) across sites to facilitate broad integration and applicability of results (Weatherspoon 2000). Although the FFS treatments were “restorative” in that thinning and prescribed fire help approximate historic forest structure or ecosystem function, each non-control treatment was guided by a desired future condition (DFC) designed “…to achieve stand and fuel conditions such that, if impacted by a head fire under 80th percentile weather conditions, at least 80 percent of the basal area of overstory (dominant and codominant) trees will survive” (Weatherspoon 2000). The FFS treatments included thinning, prescribed fire, the combination of thinning and prescribed fire, and an untreated control.

Due to a variety of logistical constraints, rather than being implemented as an independent study, in 2002 the southern Cascades FFS study was overlain on an existing long-term ecological study (the Little Horse Peak Interdisciplinary Study) located in the Goosenest Adaptive Management Area (GAMA) in the Klamath National Forest in northern California. The Little Horse Peak Interdisciplinary Study (LHPIS) was initiated
in 1998 to investigate the effects of mechanical treatment and prescribed fire designed to accelerate the development of late-successional stand characteristics in a mixed-conifer forest (Ritchie 2005).

The LHPIS study consisted of 4 treatments (two different thinning treatments, the combination of thinning and prescribed fire, and an untreated control), each replicated five times. Three of the five LHPIS replicates were selected from the thinning+fire treatment, one of the thinning treatments, and the untreated control to serve as FFS treatments; the first three units of the thinning+burning and thinning treatments that had been thinned in the LHPIS study were selected for the FFS study, whereas the three Control units were randomly selected. Because the LHPIS did not include the use of fire in the absence of thinning, three additional treatment units were established in 2002 in untreated areas similar in stand structure and species composition to the LHPIS controls, and treated with prescribed fire in Autumn 2002. Thus, the full suite of experimental treatments used in my study consisted of LHPIS and FFS treatments as follows:

**Pine-preference Thinning:** Reduced total number of trees, and selectively removed shade-tolerant species such as *Abies concolor* (white fir). The restoration goal was to attain a pine-dominated forest, with a diversity of age classes. Thinning was done during summers of 1998 and 1999.

**Size-preference Thinning:** Thinned with a restoration goal to remove small to medium-sized trees of all species to maximize growth of the larger remaining individuals, regardless of species. Thinned was conducted concurrently with Pine-preference units.
**Thinning plus Burning:** Thinned following Pine-preference protocol, followed by a late-autumn prescribed fire.

**Burning:** Consisted of a late-autumn prescribed fire only.

**Control:** No intentional thinning or burning

My objectives were to evaluate the effects of thinning and prescribed fire in a northern California mixed-conifer forest on (1) soil physical and chemical properties and microbial activity, and (2) the response of mature conifers to these treatments via nutrient concentrations in needle cohorts formed over the course of the experimental period. Although the FFS study was designed primarily as an exploratory study (Weatherspoon 2000), I evaluated the hypothesis that different management strategies (thinning, burning, the combination of thinning and burning, and an untreated control) result in measurable differences in soil and forest floor characteristics.

In Chapter 2, I present results of my investigation of the effects of FFS treatments on soil physical, chemical and microbial properties, as well as on the C and N content of forest floor material. In Chapter 3, I describe the short-term effects of prescribed fire on soils in thinned and unthinned forest stands. In Chapter 4, I investigate the effects of differences in thinning prescription by describing differences in soil and forest floor characteristics in stands that were thinned to either restore dominance to *P. ponderosa*, or to restore dominance to large trees, regardless of species. In Chapter 5, I evaluate the response of mature *P. ponderosa* and *A. concolor* to thinning and prescribed fire via
needle N and P concentration in live needles formed in each year over the course of the experimental period. In Chapter 6, I present conclusions from this study and recommendations for further study.

Within the larger, long-term FFS study as well as within the extant body of scientific literature, this study is unique in that it addresses the full cycle of interaction among ecosystem components: from initial changes in above-ground vegetation structure, to changes in below-ground soil resources, to the timing and duration of changes in foliar characteristics of vegetation. This study therefore strengthens our understanding of the linkages between above- and belowground components of a forested ecosystem, as influenced by large-scale experimental restoration treatments.
CHAPTER 2

BELOW-GROUND EFFECTS OF FIRE AND FIRE SURROGATE TREATMENTS IN A NORTHERN CALIFORNIA MIXED-CONIFER FOREST

Introduction

Descriptions of the pre-settlement mixed-conifer forests of northern California and southern Oregon describe open, park-like stands of trees, with *Pinus ponderosa* P. & C. Lawson (ponderosa pine) the most abundant tree species (Laudenslayer & Darr 1990; Covington & Moore 1994). In contrast, the California mixed-conifer forests of today often differ substantially from historic conditions in many characteristics, and livestock grazing, logging and aggressive fire suppression policies have all contributed to post-settlement changes in stand composition and structure (Weaver 1951; Agee 1993). Forests that were historically dominated by Ponderosa pine now contain a large percentage of *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir) and other shade-tolerant species. Stem density in these stands is much greater today than at the time of European settlement (Zack et al. 1999; Taylor 2004; Ritchie and Harcksen 2005), and accumulations of both surface and vertical fuels have produced conditions conducive to the development of fires with intensity far greater than the historical condition.

The logging of the late 1800s or early 1900s had a particularly strong impact on the large, old tree component, and dense stands of small, young trees that established...
following logging now occupy areas that once supported open, multiple-aged stands (Zack et al. 1999; Taylor 2004; Ritchie and Harcksen 2005). Today these forests have a paucity of the large woody stems (live or dead) that are considered important to many wildlife species (Thomas 2002), and large snags and downed logs will remain limited in these systems until a significant component of large trees can be grown to produce them. The high density of the present stands makes it unlikely that the large tree component will be restored without management intervention (Dolph et al. 1995), and these dense, young stands are likely to promote high intensity fires (Agee and Skinner 2005) that will further lengthen the time necessary to restore the large tree component.

The problem of hazardous fuel conditions in forests has received substantial attention in recent years as land managers attempt to reduce the threat of catastrophic fires. Reduction of fuel loads, especially in areas of wildland-urban interface, has been conducted primarily via mechanical thinning from below, although prescribed burning or combinations of thinning and burning have also been used. Although such stand manipulations may be able to return forests to a condition resembling (to some degree) the historic structure, the ecological effects of these manipulations, such as on the properties of forest soils and forest floor layers, are not well understood (SNEP1996).

The availability of nutrients (especially N and P) in the soil and the accumulation of organic matter in the forest floor and mineral soil determine the potential of a site for tree seedling establishment, tree growth and ecological functioning. Soil nutrient status is affected by the nutrient content of the litter produced by the plants (Ferrari 1999; Prescott
2002), as well as local soil type. Harvesting methods (Thiffault et al. 2006) and spatial arrangement of tree stems on the landscape (Parsons et al. 1994; Bauhus and Barthel 1995) can also influence soil nutrient availability.

Decomposition of that litter and release of nutrients for subsequent plant uptake and growth are influenced both by the site microclimate (Hart & Firestone 1992) and by the nutrient content of the litter (Boerner 1984). Thus, the effects of forest management strategies on the nature and decomposition of forest floor organic matter, and the subsequent nutrient characteristics of the forest soil may vary according to stand structure and composition, the inherent variability of soil properties across a landscape, and the mechanical disturbance caused by forest management activities (Stone 1975). Consequently, seemingly minor differences in management activities may result in significant ecological differences between stands across a landscape.

The interdisciplinary national Fire and Fire Surrogate (FFS) network study was initiated in 2000 and was designed to evaluate long-term ecological effects of thinning and prescribed fire in forests that historically experienced frequent, low-intensity fire. The Klamath National Forest of northern California represents one of the 12 network sites, and serves as the location for the study presented here. In this mixed-conifer ecosystem, we hypothesized that differences in restoration strategies (thinning, burning, and the combination of thinning and burning) would result in measurable differences in
soil nutrients, nutrient cycling and microbial activity, and in the nutrient status of forest floor material. Here, we present first and third year post-treatment effects of FFS treatments on soil and forest floor characteristics in the Klamath National Forest of northern California.

**Methods**

*Study Site*

This study took place in the Goosenest Adaptive Management Area (GAMA) of the Klamath National Forest in Siskiyou County, California (lat 41°35′N, long 121°53′W). The forests of GAMA were logged between 1900 and 1920, and all merchantable trees were removed over large areas. The gentle, dissected landscape of GAMA is the result of recent volcanic activity. Slopes are generally <10% but can locally be >50%, with elevation ranging from 1500 to 2000 m. *Pinus ponderosa* P. & C. Lawson (ponderosa pine) and *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir) are dominant in the forest canopy, together typically comprising >90% of the basal area. *P. lambertiana* Dougl. (sugar pine), *Calocedrus decurrens* (Torr.) Florin (incense cedar), *Abies magnifica* A. Murr. var. *shastensis* Lemmon (Shasta red fir), and *P. contorta* Dougl. ex Loud. var. *murrayana* (Grev. & Balf) Englem. (Sierra lodgepole pine) are also present at low density. The shrub layer is sparse, ranging in cover from 0.0 to 5.4% of the ground area. Shrubs present include *Ceanothus* spp. (ceanothus), *Arctostaphylos* spp. (manzanita), *Purshia tridentata* (Pursh) DC. (antelope bitterbrush), *Cercocarpus ledifolius* Nutt. (curl-leaf mountain mahogany), *Chrysothamnus* spp.
(rabbitbrush), and Artemisia spp. (sagebrush) (USDA Forest Service 1996). Forb and grass cover ranged from 3.2 to 18.3%, and averaged 8.5% among our treatment units.

The historical fire regimes of the southern Cascade range were characterized by frequent, low-intensity fires in the low to middle elevations and mixed-intensity fires in the upper montane (Taylor 2000; Skinner and Taylor 2006; Taylor et al. 2008). Fire has largely been excluded from the forests since the logging that occurred in the early 1900s, and this has likely intensified the alteration of stand structure through eliminating the thinning effect of fire on developing stands.

The soils of the experimental area are dominated by the Belzar–Wintoner complex of inceptisols and alfisols (USDA Forest Service 1982). The Belzar series of loamy-skeletal, mixed, frigid Andic Xerochrepts covers the great majority of the study area. Interspersed within the matrix of Belzar series soils are areas of somewhat thinner pumice deposits in which the Wintoner series (pumice overburden phase) of fine-loamy, mixed, frigid Ultic Haploxeralfs are mapped. Both of these soil types have high silt and sand content, drain rapidly, have relatively low water-holding capacity, and are relatively low in nutrient availability. The climate is Mediterranean-type, and the study site receives most of the 25–100 cm annual precipitation as winter snowfall (USDA Forest Service 1996).

Experimental Design

The GAMA Fire and Fire Surrogate study (FFS) is a completely randomized design consisting of 4 treatments each replicated 3 times (Figure 2. 1). The treatment
units of this study were overlaid on existing research plots of the Little Horse Peak Interdisciplinary Study (LHPIS) that was established in 1998 to accelerate the development of late-successional characteristics of eastside pine forests (Zack et al. 1999, Ritchie 2005). An untreated Control (Figure 2. 2), a mechanical thinning treatment (thinning from below; hereafter Thin) (Figure 2. 3), and the combination of mechanical treatment and prescribed fire (hereafter Thin+Burn) (Figure 2. 4) was replicated in 5 experimental units for the LHPIS study; in 2000, the first three units that had been thinned were selected from both of the treatments that involved thinning, and three Control units were selected randomly for this FFS study. Treatment units for FFS Burn-only treatments (hereafter Burn) (Figure 2. 5) were interspersed among the Little Horse Peak in 2002. In each 10-ha FFS treatment unit ten 20m x 50m (0.1-ha) random, permanent sampling plots were systematically established from a randomly-selected initial point on a 50-m grid, and the corners marked with permanent posts.

Whole-tree harvesting methods were applied to Thin and Thin+Burn treatments and processing followed standard harvesting procedure for forests in this region. Whole trees were transported to central processing landings where all boles, limbs, and tops of trees 10.2-45.7 cm dbh were removed and logs cut to appropriate length for hauling to processing plants. Limbs and tops of trees were sorted and either chipped at landings and shipped for pulp, or shipped for electricity generation; thus, all the slash generated by the thinning was removed from the units. All damaged trees were removed. Sub-merchantable understory trees were hand-cleared from both treatments within one year after larger trees were thinned from below; this material was scattered on site. The
thinning was completed during the growing seasons of 1998-2000. A more thorough discussion of thinning treatment prescription and pre- and post-treatment stand conditions is provided by Ritchie (2005).

A late fall prescribed fire was conducted in the Thin+Burn treatment in 2001. Stand structure in the Burn treatment was not modified mechanically prior to burning, and a late fall prescribed burn was conducted in this treatment in 2002. Firing techniques used in the prescribed burns in the Thin+Burn and Burn treatments were strip-head firing and tree-centered spot ignition (Weatherspoon et al. 1989). Weather and fuel moisture conditions (air temperature burn-only 6 ± 5 ºC [mean ± standard deviation], thin+burn 12 ± 5 ºC ; relative humidity burn-only 24 ± 13%, thin+burn 32 ± 16 %; wind speed burn-only 1.7 ± 1.3 km/hr, thin+burn 2.6 ± 1.6 km/hr) combined with the ignition pattern to produce a low-intensity, surface fire (flame length burn-only 24 ± 11 cm, thin+burn 40 ± 18 cm).

Soil Sampling and Laboratory Analysis

Four sample points were located at each of the corners of the FFS 0.1-ha plots, and 1 sample point was located at the midpoint of each of the long sides of the 0.1-ha plots. In June - August of 2002-2004 soil samples to 10 cm depth were taken from those 6 points in each sample plot as follows: Control (two treatment units), Thin, and Thin+Burn (post-fire) 2002, Burn (post-fire) 2003, and Control, Thin, Burn, and Thin+Burn 2004. In addition, one of the three FFS Control units was sampled in 2001 and not in 2002; however, because data analysis showed that, in general, soil variables
did not differ significantly between years within the same unit and that soil variables did not differ among Control units in 2004, we considered the Control unit sampled in 2001 and the Control units sampled in 2002 to represent Year 1 data. Samples taken in 2001-2003 therefore represent the first year of observations following implementation of the full suite of FFS treatments, and are hereafter referred to as Year 1 data; samples taken in 2004 represent the third post-FFS study year for all treatments except the Burn treatment, and are hereafter referred to as Year 3 data. Soil samples on successive dates in each treatment unit were taken within 1.0 m of those from the previous year. All samples were returned to the laboratory under refrigeration. As this study was initiated in 2001 and no belowground component existed in the original Little Horse Peak study that began in 1998, no pre-treatment soil sampling was done.

During each summer, a transect was established along the long axis of each 0.1 ha plot. Twenty random points were selected along each transect, at distances of 1-3 m. At each point, soil disturbance was recorded via estimating exposed soil surface area in a 1 m² circular plot, using the following scale: 0=undisturbed/natural; 1=virtually undisturbed, organic layer intact; 3=organic layer only partially intact, soil puddled or compacted in part; 4=surface soils partially removed or mixed with subsoil, organic layer gone, signs of physical disruption; 5=subsoil exposed, compacted, or removed, hydrology affected. Soil strength at 90 mm and 150 mm was also measured with a soil penetrometer at each of the sampling points in Thin and Control treatments in 2002, and
in all treatments in 2004. We used soil strength as a measure of mechanical impedance of soil because the fine texture and lack of structure in these soils prevented accurate sampling of soil cores for bulk density measurements.

To evaluate soil chemical characteristics, each sample was allowed to air dry and was then passed through a 5-mm sieve to remove stones and root fragments. Sieved, air-dried soil samples were extracted with 0.5 M K$_2$SO$_4$ for NO$_3^−$, NH$_4^+$, and P; NO$_3^−$ and NH$_4^+$ were analyzed using the microtiter methods of Hamilton & Sims (1995), and P was analyzed by the stannous chloride/molybdate colorimetric method (Olsen & Sommers 1982). Sieved, air-dried soil samples were also extracted for Ca and K with 1.0 M NaOAc, and the concentration of Ca and K was determined with ion-specific electrodes. Soil pH was determined in a 1:2 mass:volume solution of 0.01 M CaCl$_2$. Organic carbon (C) and total N were determined by oxidation/fluorescence on a Carlo-Erba CN analyzer after grinding air-dried soil samples to pass through a 0.32-mm mesh screen.

Estimation of N mineralization and nitrification for all study plots was done using aerobic, in situ incubations following the method of Raison et al. (1987). Groups of three 10-cm deep PVC soil cores were taken at each of the 6 sampling points around each permanent sampling plot (N = 720). One was returned to the lab immediately whereas the remaining two incubated in situ for 20-30 days. One of the in situ cores was covered with a PVC cap while the other remained open. As the results from capped and uncapped cores were not significantly different, they were pooled for later data analysis. All 3 cores from a given sampling point were extracted and analyzed for inorganic N as indicated above. Net N mineralization was calculated as the difference in total inorganic N (NO$_3^−$ +
NH$_4^+$ concentration between the initial samples and those that incubated for 20-30 days. Net nitrification was calculated as the difference in NO$_3^-$ N in the incubated and initial samples. The rate of N mineralization and nitrification were calculated by dividing net values by the number of days between sampling of initial and in situ cores.

To measure the activity of microbes important in decomposition, we measured the microbial exoenzymes acid phosphatase (produced by microbes and roots), chitinase (produced by a guild of specialist bacteria), and phenol oxidase (produced primarily by white rot fungi). As our samples were sieved to remove roots prior to analysis, enzyme activities represent microbial activity only. Samples for analysis of these enzyme activities were taken from randomly-located gridpoints (N=240).

Enzyme activities were analyzed using methods developed by Tabatabai (1982), as modified by Sinsabaugh (Sinsabaugh et al. 1993; Sinsabaugh & Findlay 1995). Acid phosphatase (EC 3.1.3.2) and chitinase (EC 3.2.1.14) activities were determined using $p$-nitrophenol ($p$NP)–linked substrates: $p$NP-phosphate for acid phosphatase and $p$NP-glucosaminide for chitinase. Phenol oxidase (EC 1.14.18.1, 1.10.3.2) activity was measured by oxidation of $\alpha$-DOPA (1,3,4-dihydroxyphenylalanine), and parallel oxidations using standard horseradish peroxidase (Sigma Chemical, St. Louis, MO) were used to calculate the $\alpha$-DOPA extinction coefficient.

Forest floor samples for analysis of C and N concentration were taken from 6 locations within each of the 0.1-ha plots in 2001-2003. Forest floor sampling was also planned for 2004, but did not occur until 2005. Unconsolidated litter and fragmented
layers were sampled as a single unit. Forest floor samples were ground in a Wiley mill, and subsamples were dried at 70°C before analysis for C and N using a Carlo-Erba CN analyzer.

Data Analysis

The Year 1 variables Ca, K, acid phosphatase, chitinase, phenol oxidase, and forest floor C:N were log-transformed to achieve normality, and data for soil C and N were converted to normality using a square root transformation. Forest floor N concentration was normally distributed, whereas soil pH, available P, TIN, N mineralization, net nitrification, soil C:N, forest floor C concentration, and soil strength at 90 mm and 150 mm were ranked prior to analysis. The Year 3 variables soil Ca, K, net nitrification and soil C concentration were normally distributed, whereas pH, available P, TIN, soil C:N, and all three microbial exoenzymes were converted to normality using a log transformation. Year 3 N mineralization, forest floor C, N, C:N, and soil strength at 90 mm and 150 mm were ranked before analysis.

Log-normal distributions are common with soil nutrient and microbial activity data, and using log or square root transformations to normalize distributions is common (e.g. Thiet et al. 2005). We performed a one-way analysis of covariance (PROC GLM, SAS 2004) on the variables listed above, using sample plot elevation as a covariate; variance was partitioned among treatments and units within treatments. Each year was analyzed separately. Among-treatment differences in soil surface disturbance class were
determined at using chi-square analysis, using df=3 and a chi-square critical value of 7.815; significant among-treatment tests were followed by pairwise chi-square tests, using df=1 and a critical value of 3.841.

The unit of replication for this experiment was the treatment unit (N=3 for each treatment), with three treatment units within each treatment. For all treatments, we had 120 samples of soil and 60 forest floor samples per treatment unit. The Ryan-Einot-Gabriel-Welsch Multiple Range test was used for means separation, as this approach minimizes the risk of Type I errors (SAS 2004). Statistical significance is reported at \( p=0.05 \) unless otherwise indicated.

*Elevation Transects*

Because early data analyses suggested that soil nutrients increased with elevation, in 2005 I sampled soil in untreated forest along two transects that spanned the elevation gradient present in the LHPIS study area (1480-1790 m). I sampled soil and forest floor material at 10m elevation increments along each transect (N=52). I performed linear regression to determine the effect of elevation on the soil nutrients NH\(_4\), NO\(_3\), TIN, PO\(_3\), C, total N, and C:N ratio, and on forest floor C, N and C:N ratio. Linear regression was performed on the log of NH\(_4\), NO\(_3\), TIN, PO\(_3\), soil C and total N, and on forest floor C:N; soil C:N and forest floor C were ranked prior to analysis, and forest floor N was normally distributed.
To visualize how FFS treatments affected the full suite of soil and forest floor parameters simultaneously, we used Non-metric Multidimensional Scaling (NMS) ordination (Kruskal 1964, Mather 1976). Analysis was done using PC-ORD for Windows, version 4.0 (McCune and Mefford 1999). We used the Sorenson (Bray-Curtis) distance measure and relativized each parameter to prevent weighting of the variables relative to each other. The initial run used 4-dimensional space, the Sorenson (Bray-Curtis) distance measure and 100 iterations with random starting configuration. Plots of stress versus iteration were examined to determine the optimal number of dimensions, below which reductions in stress resulting from the addition of axes were minimal (McCune and Grace 2002). A final run of 67 iterations was made using 2 dimensions, and the stress in 15 runs of real data was compared with the stress in 30 runs of randomized data (Monte Carlo test, data shuffled within columns).

**Results**

**Soil Physical Characteristics**

There was no significant difference in soil strength at 90 mm or at 150 mm between Thin and Control treatments in Year 1 whereas significant differences in soil strength were evident in Year 3 (Table 2. 1, Figure 2. 6, Figure 2. 7). In Year 3, soil strength at 90 mm was reduced by thinning alone and by burning alone, but not by the combination of thinning and burning. The use of fire alone reduced soil strength at 90 mm by 19% relative to the control, whereas thinning alone resulted in a relative reduction
of 5% (Figure 2.6). Soil strength at 150 mm was significantly reduced by the use of fire alone in Year 3, and the relative difference between the Burn and Control treatments was 20% (Figure 2.7).

There were no differences among treatments in soil disturbance, averaged across all disturbance classes (Table 2.2, Figure 2.8); however, significant differences among treatments were evident when the proportional frequencies of low (classes 0 and 1) and high (classes 4 and 5) were calculated (Table 2.3). The Control had the greatest proportion of low disturbance (35% and 16% for Years 1 and 3, respectively) and the lowest proportion of high disturbance classes (36% and 45% for Years 1 and 3, respectively) (Table 2.3, Figure 2.9, Figure 2.10). In contrast, the Thin+Burn treatment had the lowest proportion of low disturbance (0%) and the greatest proportion of high disturbance classes in Year 3 (93%) (Table 2.3, Figure 2.9, Figure 2.10). The Thin treatment had a greater proportional frequency of low disturbance in Year 3 than did the Control; however, the frequency of high disturbance classes did not differ statistically between the Control and Thin treatments (Table 2.3, Figure 2.9, Figure 2.10).

**Soil Nutrients and Chemical Measures**

Soil organic C (SOC) concentration was significantly reduced by the use of fire alone in Year 1, and this effect persisted in Year 3 (Table 2.1). Relative to the Control, SOC in the Burn treatment was reduced by 40% in Year 1 and by 36% in Year 3. There was no difference in SOC among the Control, Thin, or Thin+Burn treatments in either year (Table 2.1, Figure 2.11). Similarly, burning reduced total soil N concentration by
40% in Year 1 and by 29% in Year 3 relative to the Control, and there were no statistical differences among Thin, Thin+Burn and Control means (Table 2.1, Figure 2.12). Across all treatments, soil C:N ratio was greatest in the Burn treatment and lowest in the Thin+Burn treatment in Year 1 (Table 2.1, Figure 2.13). Soil C:N in the Thin+Burn treatment was 10% lower than the Control, and 16% lower than the Burn treatment in Year 1. Burn treatment soil C:N was 13% greater than the Thin treatment, and neither the Burn nor Thin treatments differed significantly from the Control during the first measurement period (Table 2.1, Figure 2.13). In Year 3, soil C:N in the Control was 18% greater than in the Thin treatment, and this was the only statistically significant difference among treatment means (Table 2.1, Figure 2.13).

Total inorganic N (TIN) was greater in all of the three manipulative treatments than in the Control in Year 1 (Table 2.1, Figure 2.14). Relative to the Control, TIN was increased by 43% by thinning alone, 195% by burning alone, and 101% by the combination of thinning and burning. Burning, alone or in combination with thinning, also increased Year 1 TIN relative to thinning alone (105% and 85% for Burn and Thin+Burn, respectively) (Table 2.1, Figure 2.14). In contrast, TIN in Year 3 was reduced by burning alone (19%) and in combination with thinning (21%), relative to the Control. Soil TIN in the Thin treatment did not differ significantly from any treatment in Year 3. (Table 2.1, Figure 2.14).

In Year 1, the N mineralization rate was greater in the Control and Thin+Burn treatments than in the Thin or Burn treatments. Relative to the Control, N mineralization rate was decreased by 48% in the Thin treatment, and by 49% in the Burn treatment.
(Table 2. 1, Figure 2. 15). The effects on the rate of net nitrification in Year 1 followed a similar pattern; net nitrification rate was reduced by 48%, relative to the Control, and the Control and Thin+Burn treatments did not differ significantly from each other (Table 2. 1, Figure 2. 16).

In Year 3, there were no differences in the rates of N mineralization or net nitrification among the Control, Thin, or Burn treatments, and the Thin+Burn treatment exhibited the greatest N mineralization and net nitrification rates (5200% and 5000% greater than the Control for N mineralization and net nitrification, respectively) (Table 2. 1, Figure 2. 15, Figure 2. 16).

There were no differences in soil available P among treatments in either of the two measurement periods (Table 2. 1, Figure 2. 17). Soil pH was increased by treatments that involved fire alone and in combination with thinning, and the results observed in Year 1 persisted in Year 3 (Table 2. 1, Figure 2. 18). Soil Ca did not differ between any treatment and the Control in Year 1; however, both treatments that involved burning exhibited greater soil Ca than the Thin treatment, with relative differences of 27% and 22% for Burn and Thin+Burn, respectively (Table 2. 1, Figure 2. 19). There were no differences in soil Ca among treatments in Year 3 (Table 2. 1, Figure 2. 19). Similarly, there were no differences in soil K in Year 1; in Year 3, however, soil K was greater in the Burn treatment than in all other treatments, and the difference relative to the Control was 20% (Table 2. 1, Figure 2. 20).
Soil Microbial Exoenzymes

Acid phosphatase was reduced by both treatments that involved fire in Year 1, and by all treatments in Year 3 (Table 2.1, Figure 2.21). Relative to the Control in Year 1, acid phosphatase was reduced by 33% in the Burn treatment, and by 22% in the Thin+Burn treatment. In Year 3, acid phosphatase was reduced by 31% by thinning alone, 53% by burning alone, and 61% by the combination of thinning and burning, relative to the Control (Figure 2.21). Similarly, chitinase was reduced by all treatments in Year 3; however, there were no differences among treatments in Year 1 (Table 2.1, Figure 2.22). Relative to the Control, in Year 3 chitinase was reduced by 35% by thinning alone, 44% by burning alone, and 59% by the combination of thinning and burning (Figure 2.22). Phenol oxidase was reduced by 20% by burning alone in Year 1, relative to the Control; however, there was no difference between the Burn or Thin treatments, or among the Control, Thin, and Thin+Burn treatments (Table 2.1, Figure 2.23). In Year 3, phenol oxidase activity was reduced in the Thin and Burn treatments (by 23% and 29%, respectively, relative to the Control), and the Thin+Burn treatment did not differ from any other treatment (Table 2.1, Figure 2.23).

Forest Floor

There was no forest floor material present in Burn treatment units in the first year following the prescribed fire (Figure 2.24, Figure 2.25, and Figure 2.26). Forest floor C concentration was 4% greater in the Thin and the Thin+Burn treatments than in the Control in Year 1, and did not differ among treatments in Year 3 (Table 2.1, Figure 2.26).
There were no differences in forest floor N concentration among treatments in Year 1, and all treatments exhibited a $\geq 63\%$ increase in forest floor N relative to the Control in Year 3 (Table 2.1, Figure 2.25). Similarly, there were no differences in forest floor C:N ratio in Year 1, whereas all treatments reduced soil C:N by $\geq 25\%$ in Year 3, relative to the Control (Table 2.1, Figure 2.26).

**Elevation Transects**

Elevation was a significant predictor of NO$_3$ ($p<0.05$), TIN ($p<0.05$), and total N ($p=0.02$), and was marginally significant for NH$_4$ ($p=0.05$); however, the $R^2$ for each significant regression was very weak, indicating that elevation explains $<10\%$ of the variation in these soil nutrients (Table 2.4). It is, however, interesting to note that elevation predicted N-based nutrients only.

**NMS Ordination**

The NMS ordination arrayed the treatment units along 2 axes, which together accounted for 94.0% of the variation (Figure 2.27). Because NMS does not arrange axes in order of importance, axis numbers were assigned arbitrarily. The final stress of the ordination was 10.9 (67 iterations).

Axis 1 explained the largest proportion of the variation and was negatively correlated with soil strength at 90 mm and 150 mm, soil C and N, and forest floor C, and positively correlated with soil pH and K (Table 2.5). Axis 2 was negatively correlated with soil strength at 90 mm and 150 mm, available P, Ca, and phenol oxidase activity.
Year 1 units were arrayed in the lower left-hand corner of the ordination space, indicating greater soil strength, soil C and N, forest floor C, and phenol oxidase activity, relative to the majority of Year 3 units (Figure 2.27). With the exception of Thin units, there was little separation among treatments or among units within treatments in Year 1. The majority of Year 3 treatment units were arrayed slightly above and to the right of Year 1 units in ordination space, indicating relatively greater pH and K, and lower soil Ca, available P, and soil strength (Figure 2.27). Further, the locations of Year 3 treatments as well as units within treatments were more dispersed in the ordination space than were Year 1 treatment units, indicating relatively greater variation among units in Year 3. Two Year 3 Burn units were arrayed to the right of all other treatment units, indicating greater soil K, and pH relative to other treatment units.

The average change in treatment unit placement along Axis 1 between Years 1 and 3 was greater for the Burn treatment (change in Axis 1 score = 1.79±0.57 s.e.) than for the Thin+Burn treatment (change in Axis 1 score = 0.23±0.30 s.e.), and the change in placement of the Control and Thin treatment units (0.56±0.32 s.e. and 0.74±0.90 s.e., respectively) did not differ significantly from each other or from the change in Burn or Thin+Burn units (p<0.048). There was no difference in the change in Axis 2 placement among treatments (p=0.060).

Discussion

Although forest management strategies designed to reduce accumulated fuel in western mixed-conifer forests may be effective in reducing fire severity (Agee & Skinner
and mechanical approaches may successfully restore pre-settlement tree species composition, size distributions, and spatial patterns, such management interventions have the potential to influence long-term forest health and sustainability via effects on the soil and forest floor. Thus, the objective of this study was to evaluate the response of soil and forest floor characteristics to a suite of alternative forest management strategies in a northern California mixed-conifer ecosystem. We hypothesized that different management strategies (thinning, burning, the combination of thinning and burning, and the absence of active management) would result in measurable differences in soil and forest floor characteristics.

We found that soil strength was reduced by thinning alone and burning alone at 90 mm, and by burning alone at 150 mm. Fire may reduce soil strength by causing the abundant pumice that is present in the soils at this site to expand, or by consuming fine roots and fungal hyphae that provide structural stability. When fire is applied to these forests, the pumice in the soil expands, and appears to “pop” similar to popcorn. Where a log burns out for extended time, the expansion can be considerable; however, the expanded pumice is very fragile and may disintegrate rapidly due to weathering (USDA Forest Service Pacific Southwest Research Station, C. Skinner, personal communication).

Because the fires conducted for this study were allowed to burn to extinction, there was no post-fire “mop-up” activity such as raking that would have physically reduced soil strength in burned treatments. Visual observations of disturbed soil in thinned treatments suggest that the physical effects of harvesting on these pumice-rich soils resulted in greatly loosened, rather than compacted, soil. It is unclear why the
disturbance effects of thinning and burning are not additive when used in combination, as the Thin+Burn treatment did not differ from the Control in Year 3 at either depth. Although Gomez et al. (2002) reported that compaction of sandy loam soils had a positive effect on growth of young ponderosa pine, whereas compaction on finer textured soils produced the opposite effect, it is unclear what effect a <20% reduction in soil strength in the coarse-textured soils at this FFS site will have on seedling establishment or growth of existing trees.

Relative to the Control, all treatments increased the frequency of high soil surface disturbance classes. For this parameter, it appears that fire exacerbates the effects of thinning, as the frequency of high disturbance classes observed in the Burn treatment was intermediate between the frequencies observed in the Thin and Thin+Burn treatments.

Soil organic C and total N concentrations were reduced by the use of fire alone in both years, and were not affected by thinning or the combination of thinning and fire. Similarly, burning resulted in the lowest quality soil organic matter (highest soil C:N) in Year 1, relative to the Thin and Thin+Burn treatments; however, this difference did not persist in Year 3, and there was no difference between the Control and Burn in either year.

Other studies have reported increases in soil C after logging in coniferous forests. For example, a review by Johnson (1992) reported increases in mineral soil C content of 18% and 23% in mixed conifer forests after whole-tree harvesting and 6 years after a clearcut harvest, respectively; however, if thinning activities increased the concentration of soil C, we would expect to see greater soil C in the Thin treatment than in the Control
or Thin+Burn in Year 1, and this is not the case. Thus, it does not appear that harvesting activities significantly increased the concentration of soil organic C at this study site. It is, however, important to emphasize that the data presented here represent C concentrations, rather than total pool size (content) of soil C.

An earlier study at this site suggested that high pre-burn soil C concentration coupled with low fire severity in the Thin+Burn treatment may explain the difference in post-burn soil C levels between the Burn and Thin+Burn treatments (Miesel et al. 2007); however, it is important to note that relatively low levels of soil C existed in the Burn treatment prior to the fire. Thus, although fire significantly reduced soil C in the Burn treatment (Miesel et al. 2007), the magnitude of difference among Year 1 treatments may be due in part to low pre-burn soil C levels, and not to the effect of fire alone.

Fire-induced losses of soil organic matter are largely dependent upon the temperature and intensity of a fire (Ahlgren and Ahlgren 1960); prescribed burning generally results in increased soil C near the soil surface, but higher-severity fires have been shown to decrease soil C (Johnson 1992). Carbon can also be added to the soil when charcoal from burned forest floor material is transported into the soil, and this can result in overly conservative estimates of the loss of soil organic C during fire (Johnson and Curtis 2001). The relatively lower concentration of soil organic C in the Burn treatment could have been due either to loss via combustion during the fire or to increased microbial mineralization of organic matter after the fire; however, our assays of microbial enzymes indicate a reduction of microbial activity in all treatments. Thus, the more likely explanation appears to be greater consumption of organic matter by fire in the Burn
treatment than in the Thin+Burn treatment. Although fire weather and flame lengths were similar during the fires in the burn-only and thin+burn treatments, flame length (fire intensity) is not directly correlated with fire severity (loss of forest floor organic matter). For example, a slow-moving fire with low flame lengths may sustain greater soil heating and organic matter combustion than a relatively faster-moving fire with greater flame lengths, and vice versa.

Similar to the effects we observed at the GAMA FFS site, Moghaddas and Stephens (2007) reported that significant reductions in the concentration of soil C occurred only in the Burn treatment, relative to the Control, in the central Sierra Nevada FFS site; however, the meta-analysis of ecosystem C dynamics by Boerner et al. (2008) showed that although total mineral soil C stocks (Mg/ha for 0-30 cm depth) were reduced by fire alone at the GAMA FFS site in the first post-treatment sampling year, this effect did not persist, and the 95% confidence interval around the mean network-wide effect for both FFS sampling periods overlapped zero.

Fire increased TIN in the Burn and Thin+Burn treatments in Year 1, although this effect did not persist in Year 3. This short-term, temporary increase in inorganic N is a typical pattern following fire (Raison 1979, Monleon et al. 1997, DeLuca and Zouhar 2000). In contrast to the effects on TIN, the use of thinning or fire alone, but not in combination, reduced the rates of N mineralization and net nitrification in Year 1, whereas the combination of fire and thinning increased the rates of both N mineralization and net nitrification in Year 3 only. Monleon et al. (1997) also reported reductions in net annual N mineralization following prescribed fire, and DeLuca and Zouhar (2000) found
that prescribed fire reduced potentially mineralizable N relative to a control at 1-11 years post-burn. Although we expected that the effect of fire on N mineralization and net nitrification rates would be similar between the two treatments that involved prescribed fire, this was not the response shown by our data. It is possible that the combination of an opened canopy, reduced stem density, and increased N availability in the Thin+Burn treatment may have increased N cycling in this treatment, whereas the increased temperature and therefore reduced soil moisture in the Thin treatment may have reduced the activity of the soil organisms involved in these processes. Our results of acid phosphatase (an exoenzyme correlated with N mineralization; Decker et al. 1999), however, do not support this, and the specific cause of these effects remains unclear.

Relative to the Control, none of the treatments affected soil available P or Ca; however, both of the treatments that involved fire had greater soil Ca than did the Thin treatment in Year 1, and this is likely due to the cations deposited in ash produced by the combustion of plant material (Raison 1979). Ash deposition also increases soil pH, and our results are consistent with this pattern in both years. Potassium (K) is also present in ash and was increased by the use of fire alone, although this effect was evident only in Year 3.

Because plant growth is strongly influenced by nutrient availability, it may be expected that differences in essential plant nutrients such as TIN and available P would produce among-treatment differences in tree growth over time; however, our results indicate that no differences in these nutrients exist among FFS treatments by Year 3, and that the increases in cations we observed are minor. It is possible that the increased TIN
observed in Burn and Thin+Burn units in Year 1 was rapidly taken up by plants during the growing season following the burns, immobilized by microbes, or was leached through the soil by rain or snowmelt (Raison 1979) by Year 3.

It is possible that differences in tree growth may become evident over time, due to reduced competition for nutrients and water. For example, Parsons et al. (1994) showed that soil NO₃⁻ was increased in experimentally created gaps of 15 or 30 trees in a 95-yr-old *Pinus contorta* (lodgepole pine) stand in Wyoming relative to control areas; however, the authors reported that small gaps (1-5 trees) did not produce the same effect, and there were no corresponding increases in NH₄⁺. In our northern California FFS site, however, we observed an increase in TIN, relative to the Control, in the Thin treatment in Year 1 only, and no difference between the Thin and Control treatments in Year 3. Because Year 1 data were taken 3-4 years after thinning operations were completed in the Thin treatment, it is possible that increases in TIN due to reduced competition do not persist beyond this time frame. Over longer periods of time, however, nutrients stored in decaying stumps of cut trees in the Thin and Thin+Burn treatments and in stumps and stems of fire-killed trees in the Burn treatment will also become available for uptake by remaining live trees.

The suite of three exoenzymes we assayed gives an indication of changes in the activity of several components of the microbial community (Hanzlikova & Jandera 1993). We chose acid phosphatase as an indicator of overall microbial activity, as the activity of this enzyme is often strongly correlated with microbial biomass (Kandeler & Eder 1993), microbial biomass N (Clarholm 1993), fungal hyphal length (Häussling &
Marschner 2005), and N mineralization (Decker et al. 1999). Chitinase is produced primarily by bacteria, and as chitin is intermediate in its resistance to microbial metabolism, synthesis of chitinase is induced only when other, more labile C and N sources are absent (Hanzlikova & Jandera 1993). Finally, the index of fungal activity we used was phenol oxidase, an enzyme produced primarily by white rot fungi, which is specific for highly recalcitrant organic matter such as lignin (Carlile & Watkinson 1994). Although phenol oxidase activity should not be considered a proxy for the activity of all fungi, it is a useful indicator of those that specialize on the breakdown of wood, bark, and other lignin-rich substrates (Carlile & Watkinson 1994).

In general, soil microbial activity, as measured by the enzymes acid phosphatase, chitinase and phenol oxidase, was reduced by FFS treatments. Acid phosphatase and phenol oxidase were reduced by treatments in both years, whereas effects on chitinase activity were evident only in Year 3. Phenol oxidase was reduced by both thinning alone and burning alone, but not by their combination, in Year 3.

Other studies have shown substantial decreases in acid phosphatase levels following fire. For example, Saa et al. (1993) reported 80-90% decreases in acid phosphatase levels after fire in gorse (Ulex europaea) shrublands and pine plantations in Spain, and Boerner et al. (2000) reported decreases of similar magnitude to those we report here in their study of fire in mixed-oak (Quercus spp.) forests. Acid phosphatase activity may remain low for as long as 4 years after burning, at least in the jack pine (Pinus banksiana) forests of Ontario studied by Staddon et al. (1998).
Effects on chitinase activity were not evident until Year 3, when the activity of this enzyme was reduced in all treatments, relative to the Control. Chitinase activity reflects the use of chitin (the detrital remains of arthropods and fungi) as a source of both C and N by bacteria and, in some ecosystems, actinomycetes. Chitin is intermediate in its susceptibility to microbial attack, and becomes a preferred source of carbohydrates and/or N only when high quality organic matter is lacking (Hanzlikova and Jandera 1993). A decrease in chitinase activity, which we observed in all treatments relative to the Control in Year 3, should indicate a reduction in bacterial abundance, a reduction in the importance of chitin as a source of C and N, or both.

The index of fungal activity we used was phenol oxidase, an enzyme involved in the metabolism of particularly recalcitrant compounds (e.g. lignin, suberin). Based on this parameter, fungal activity was reduced in the Burn treatment in both years, and by the Thin treatment in Year 3; however, the activity of this enzyme did not differ significantly between the Control and the Thin+Burn treatment in either year. If treatments altered the quality of soil organic matter in a way that affected the relative availability of labile to recalcitrant organic matter, one might expect to see decreases as well as increases in microbial activity across the suite of enzymes we assayed. For example, if an increase in organic matter quality of the magnitude we observed was important for microbial activity in these treatments, one might expect acid phosphatase, and possibly chitinase to increase in Year 3; however, our data show no instances in which microbial activity was increased relative to the Control.
Soil microbial activity can be reduced following fire if the heat produced by the fire reaches lethal temperatures, or if the organic substrates required for metabolism are destroyed. For example, microbial biomass has been shown to decrease in organic soil following clear-cut harvesting, with or without fire (Entry et al, 1986, Pietikainen and Fritze 1995), and similar effects may or may not occur in mineral soil, depending on the temperature and severity of the burn (Busse and DeBano 2005). Even though the fires conducted for this study were low-intensity prescribed burns, temperatures as low as 60-100°C are sufficient to denature proteins or to kill fungi and bacteria (DeBano 1991). Although no measurements of heat transfer to the soil were taken during the prescribed burns, the slow-moving fires may have produced enough sustained heating to transfer a sufficient amount of heat into the upper mineral soil to result in the reduction of microbial activity we observed.

The concentration of C in forest floor organic matter was increased by thinning alone and in combination with fire in Year 1, whereas the quality of that organic matter was increased by all of the manipulative treatments in Year 3, relative to the Control, as a result of the much greater forest floor N concentration. Although the nutrient concentration of litter from young trees has been shown to be greater than that of older trees of the same species (Wang & Klinka 1997), thinning, burning and their combination all greatly reduced the young tree component of these stands relative to the Control (Ritchie 2005, Skinner, unpublished data). Thus, it is possible that each of the restoration treatments increased nutrient concentration in the litter via increased N uptake by the trees that remained. For example, foliar nutrition of conifers has been positively
correlated with soil nutrients (Wang and Klinka 1997), and foliar N concentration in conifers has been shown to exhibit significant increases following thinning or prescribed fire (Miller et al. 1976, Feeney et al. 1998, Amponsah et al. 2005).

As a reservoir of nutrients, the forest floor provides an indication of future nutrient supply to plants. Over the longer term, the higher-N forest floor material in the restoration treatments would be expected to decompose at a faster rate than the material in the Control, and would thus supply nutrients to the available soil pools at greater rates. From an ecosystem restoration standpoint, the current conditions of these fire-suppressed stands not only contribute to the potential for catastrophic fires, but hold a significant quantity of nutrients in the live biomass of young trees and may greatly retard nutrient cycling due to the poor quality of forest floor material. It is, however, important to note that the difference in the quality of forest floor organic matter that we observed occurred in Year 3 only; it is not clear whether this difference will persist, or whether patterns of relative quality will continue to vary among years.

Although our early analyses suggested that soil C increased with elevation, elevation was a significant covariate for soil C, in Year 1 only; elevation was not a significant covariate for the other soil variables we measured in the FFS plots. Further, linear regression using soil nutrients from samples collected across the full elevation gradient present at the GAMA showed that elevation was a significant predictor of soil inorganic and total N only. The disagreement between these results is likely due to tree species composition: *Abies concolor* increase in dominance with elevation, and the litter of this species is of greater N concentration than *Pinus ponderosa* litter (J. Miesel,
unpublished data). Because the elevation transects spanned a greater elevation gradient at the GAMA than did the FFS units, it is likely that the effect of *A. concolor* that is present at higher elevation is not evident at the lower end of the elevation gradient, at which the FFS units are located.

Non-metric multidimensional scaling ordination of the 24 unit-treatment-year combinations arrayed Year 3 units slightly above and to the right of Year 1 units in the ordination space, indicating greater soil K, pH, C:N, N mineralization, and forest floor N, and somewhat lesser soil C, N, TIN, net nitrification, chitinase activity, and forest floor C and C:N. Consistent with analyses performed on individual variables, the increased dispersion of Year 3 units relative to Year 1 suggests that treatment effects are delayed and become more pronounced over time, at least for this early and relatively short-term study.

In general, these results indicate that fire, alone as well as in combination with thinning, produce the greatest effects on soil, among the suite of FFS treatments. Thinning may either mediate or enhance the effect of fire, when fire and thinning are combined. Although effects on some soil and forest floor characteristics occurred in the first observation period only, others persisted into the second; still other effects were delayed and were evident in Year 3 only.

Because a century of fire suppression has dramatically altered the structure, species composition and fire regime of northern California mixed conifer forests from their historical conditions, these FFS treatments provide a relatively early view of the ecological effects of restorative forest management strategies. As comparisons with
undisturbed forests are complicated by the rarity of such forests as well as differences in soil type, species composition, or location, we are unable to determine the similarity between post-FFS treatment soils and their historical or undisturbed counterparts, nor to accurately predict the long-term effects of the differences among approaches that were conducted in this site. This and the full FFS network study therefore provide a valuable opportunity to observe the relative differences among a suite of alternative forest management strategies. This study in the Klamath National Forest provides a short-term comparison of the effects of thinning and prescribed fire on soil and forest floor in a northern California mixed-conifer ecosystem, and will serve as an important benchmark for long term investigations.
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Table 2. 1. ANCOVA of soil and forest floor characteristics in Fire and Fire Surrogate treatments at the Goosenest Adaptive Management Area, Klamath National Forest, California. Main effects of the model were treatment and units within treatments; all analyses were performed with elevation as the covariate. F statistics for all parameters are given, with significance indicated as * p<0.05, ** p<0.01, *** p<0.001.
Table 2.1., Continued

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Soil Microbial Exoenzymes

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‡ Statistical results for soil disturbance are reported in the text
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<th>df</th>
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<tbody>
<tr>
<td>Mean Disturbance</td>
<td>1</td>
<td>0.46</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.68</td>
<td>3</td>
</tr>
<tr>
<td>Frequency of Disturbance Classes 0+1</td>
<td>1</td>
<td>17.38*</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>35.85*</td>
<td>3</td>
</tr>
<tr>
<td>Frequency of Disturbance Classes 4+5</td>
<td>1</td>
<td>15.12*</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>68.22*</td>
<td>3</td>
</tr>
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Table 2. Chi-square test statistics for soil disturbance in Fire and Fire Surrogate treatments at the Goosenest Adaptive Management Area, Klamath National Forest, California. Differences among treatments (N=4) were determined at P<0.05, using df=3 and a critical chi-square statistic = 7.815. Significant differences among treatments are indicated by *. See text for disturbance class definitions.
<table>
<thead>
<tr>
<th>Variable</th>
<th>Treatments</th>
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<tr>
<td>Mean Disturbance</td>
<td>Control</td>
<td>Thin</td>
<td>Burn</td>
<td>Thin+Burn</td>
</tr>
<tr>
<td>Control</td>
<td>--</td>
<td>0.11</td>
<td>0.11</td>
<td>0.57</td>
</tr>
<tr>
<td>Thin</td>
<td>0.11</td>
<td>--</td>
<td>0.22</td>
<td>0.57</td>
</tr>
<tr>
<td>Burn</td>
<td>0.11</td>
<td>0.22</td>
<td>--</td>
<td>0.57</td>
</tr>
</tbody>
</table>

Frequency of Disturbance Classes 0+1

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>Thin</th>
<th>Burn</th>
<th>Thin+Burn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>--</td>
<td>12.38*</td>
<td>7.64*</td>
<td>28.21*</td>
</tr>
<tr>
<td>Thin</td>
<td>12.38*</td>
<td>--</td>
<td>20.02*</td>
<td>28.21*</td>
</tr>
<tr>
<td>Burn</td>
<td>7.64*</td>
<td>20.02*</td>
<td>--</td>
<td>23.48*</td>
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</tbody>
</table>

Frequency of Disturbance Classes 4+5

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>Thin</th>
<th>Burn</th>
<th>Thin+Burn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>--</td>
<td>3.46</td>
<td>15.16*</td>
<td>53.06*</td>
</tr>
<tr>
<td>Thin</td>
<td>3.46</td>
<td>--</td>
<td>18.62*</td>
<td>53.06*</td>
</tr>
<tr>
<td>Burn</td>
<td>15.16*</td>
<td>18.62*</td>
<td>--</td>
<td>64.76*</td>
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</table>

Table 2. Chi-square test statistics for pairwise comparisons between treatments for soil disturbance in Fire and Fire Surrogate treatments at the Goosenest Adaptive Management Area, Klamath National Forest, California. Differences between treatments were determined at P<0.05, using df=1 and a critical chi-square statistic = 3.841. Significant differences are indicated by *. See text for disturbance class definitions.
<table>
<thead>
<tr>
<th>Variable</th>
<th>Model F</th>
<th>Elevation (s.e.)</th>
<th>Intercept (s.e.)</th>
<th>Adj. R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>NH₄</td>
<td>3.89†</td>
<td>0.002 (0.001)</td>
<td>-2.50 (1.70)</td>
<td>0.06</td>
</tr>
<tr>
<td>NO₃</td>
<td>4.10*</td>
<td>0.002 (0.001)</td>
<td>-2.05 (1.73)</td>
<td>0.06</td>
</tr>
<tr>
<td>TIN</td>
<td>4.25*</td>
<td>0.002 (0.001)</td>
<td>-1.50 (1.65)</td>
<td>0.06</td>
</tr>
<tr>
<td>Soil N</td>
<td>5.72*</td>
<td>0.004 (0.002)</td>
<td>-3.78 (2.72)</td>
<td>0.09</td>
</tr>
</tbody>
</table>

† marginally significant (p=0.054)  
* significant at p<0.05

Table 2. 4. Significant regression equations of elevation on soil nutrients obtained along an elevation gradient in untreated forest within the LHPIS study area. Shown are model F statistics, elevation (s.e.= standard error), intercept (s.e.) and adjusted $R^2$. 
<table>
<thead>
<tr>
<th>Variable</th>
<th>Axis 1</th>
<th>Axis 2</th>
</tr>
</thead>
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<tr>
<td>Soil Strength (90 mm)</td>
<td>-0.934*</td>
<td>-0.666*</td>
</tr>
<tr>
<td>Soil Strength (150 mm)</td>
<td>-0.773*</td>
<td>-0.821*</td>
</tr>
<tr>
<td>Disturbance Classes 4 &amp; 5</td>
<td>0.109</td>
<td>-0.168</td>
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<tr>
<td>Soil C</td>
<td>-0.557*</td>
<td>-0.126</td>
</tr>
<tr>
<td>Soil N</td>
<td>-0.543*</td>
<td>-0.058</td>
</tr>
<tr>
<td>Soil C:N</td>
<td>0.217</td>
<td>-0.101</td>
</tr>
<tr>
<td>TIN</td>
<td>-0.358</td>
<td>-0.353</td>
</tr>
<tr>
<td>N Mineralization</td>
<td>0.045</td>
<td>0.303</td>
</tr>
<tr>
<td>Net Nitrification</td>
<td>-0.053</td>
<td>0.014</td>
</tr>
<tr>
<td>Available P</td>
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<td>-0.599*</td>
</tr>
<tr>
<td>Ca</td>
<td>0.384</td>
<td>-0.554*</td>
</tr>
<tr>
<td>K</td>
<td>0.451*</td>
<td>-0.239</td>
</tr>
<tr>
<td>pH</td>
<td>0.554*</td>
<td>0.019</td>
</tr>
<tr>
<td>Acid Phosphatase</td>
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<td>0.226</td>
</tr>
<tr>
<td>Chitinase</td>
<td>-0.244</td>
<td>0.184</td>
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<tr>
<td>Phenol Oxidase</td>
<td>-0.260</td>
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</tr>
<tr>
<td>Forest Floor C</td>
<td>-0.564*</td>
<td>-0.345</td>
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<tr>
<td>Forest Floor C:N</td>
<td>-0.344</td>
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</tr>
<tr>
<td>Forest Floor N</td>
<td>0.149</td>
<td>0.090</td>
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<tr>
<td>Elevation</td>
<td>-0.373</td>
<td>0.270</td>
</tr>
</tbody>
</table>

Table 2.5. Correlation coefficients of soil and forest floor variables and elevation with axes determined by NMS ordination of 20 variables in 2-dimensional ordination space. Correlation coefficients significant at p<0.05 are indicated by *.
Figure 2. 1. Map of the Goosenest Adaptive Management Area in northern California showing the placement of treatment units for the Little Horse Peak study. Units used for the Fire and Fire Surrogate study were Control units 4, 10, and 18, Thin units 5, 9, and 12, Burn units F1, F2, and F3, and Thin+Burn units 6, 13, and 15. Darker lines represent logging roads and lighter lines represent 50 m elevation contours.
Figure 2.2. Fire and Fire Surrogate Control treatment at the Goosenest Adaptive Management Area, Klamath National Forest, CA, showing conditions of uncut and unburned forest. Photos taken in 2004 by J.R. Miesel.
Figure 2.3. Fire and Fire Surrogate Thin treatment at the Goosenest Adaptive Management Area, Klamath National Forest, CA. Thinning was conducted between 1998-1999. Photos taken in 2004 by J.R. Miesel.
Figure 2.4. Fire and Fire Surrogate Thin+Burn treatment at the Goosenest Adaptive Management Area, Klamath National Forest, CA. Thinning was conducted between 1998-1999, and was followed by a single, low-intensity prescribed fire in October 2001. Photo in the upper right was taken from a clearing and facing the treated area, and shows the height of branches killed by the prescribed fire. Photos taken in 2004 by J.R. Miesel.
Figure 2.5.  Fire and Fire Surrogate Burn treatment at the Goosenest Adaptive Management Area, Klamath National Forest, CA. A single, low-intensity prescribed fire was conducted in October 2002. Photos taken in 2004 by J.R. Miesel.
Figure 2. Soil strength (kPa) at 90 mm in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2.7. Soil strength (kPa) at 150 mm in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2.8. Mean soil surface disturbance class in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. See text for disturbance class definitions.
Figure 2.9. Average proportional frequency of low (0+1) disturbance classes in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05. See text for disturbance class definitions.
Figure 2. Average proportional frequency of high (4+5) disturbance classes in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05. See text for disturbance class definitions.
Figure 2. Mean soil organic carbon (C) concentration (g/kg soil) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean total soil N concentration (g/kg soil) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean soil C:N ratio in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean soil total inorganic nitrogen (TIN) concentration (mg/kg soil) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean N mineralization rate (mg/kg soil/dy) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean net nitrification rate (mg/kg soil/d) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean soil available P (µg/kg soil) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment.
Figure 2.18. Mean soil pH in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean soil available Ca (mg/kg soil) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean soil K (mg/kg soil) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean acid phosphatase activity (mmol/kg soil/hr) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean chitinase activity (mmol/kg soil/hr) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean phenol oxidase activity (mmol/kg soil/hr) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean forest floor organic C concentration (g/kg) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. Mean forest floor N concentration (g/kg) in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. 26. Mean forest floor C:N ratio in Fire and Fire Surrogate treatments in the Klamath National Forest, California. Histogram bars represent means ± standard errors of N=3 units for each treatment. Letters indicate significant differences within years, determined at p<0.05.
Figure 2. 27. NMS ordination of 20 soil and forest floor properties among 24 treatment-unit-year combinations representing four Fire and Fire Surrogate treatments. The proportion of total variance in the parameter matrix represented by each axis is indicated in parentheses. Linear correlations between axis scores and variables significant at p<0.05 are indicated in order of strength of correlation; correlation values for each variable are provided in Table 2. 5. Definitions for abbreviations used here not given in the text include: SS90, SS150 = soil strength at 90 and 150 mm, respectively; FFC = forest floor C; PhenOx = phenol oxidase.
CHAPTER 3

IMPACT OF FIRE ON SOIL RESOURCES
IN A NORTHERN CALIFORNIA MONTANE ECOSYSTEM

Introduction

Fire has been an important process in determining vegetation structure and composition of ecosystems throughout North American history. In western North America pre-settlement *Pinus ponderosa* (ponderosa pine) (nomenclature follows Hickman 1993) forests experienced fire return intervals as frequent as 2 to 15 years (Agee 1993, Weaver 1951). These fires resulted from both natural causes, such as lightning strikes or volcanic activity, and anthropogenic ignitions, such as seasonal burns set by Native American peoples (Weaver 1951, Agee 1993). The historic pattern of frequent, low-intensity fires limited understory growth and selected for resistant, thick-barked, shade-intolerant tree species such as ponderosa pine. Reports of pre-settlement forests describe open, park-like stands of trees (Laudenslayer and Darr 1990, Covington and Moore 1994), and detailed dendrochronological analysis of forests dominated by ponderosa pine and *P. jeffreyi* (Jeffrey pine) in the Cascade Range and Sierra Nevada of California and Oregon profile a pine-dominated forest that was originally moderately open, uneven-aged, large-tree dominated, and shaped by frequent low intensity fires (Agee 1993, Skinner and Chang 1996; Taylor 2000).
Today’s forests differ substantially from historic conditions in several characteristics, including stand density, species composition, presence of disease, and nutrient cycling, among others. Grazing, logging, and aggressive fire suppression policies have contributed to these post-settlement changes in stand composition and structure (Weaver 1951, Agee 1993). Forests that were historically dominated by a low density of large pines now include large numbers of *Abies concolor* (white fir) and other shade-tolerant species, and stem density in these stands has increased dramatically since European settlement. The combination of fire suppression and higher stem density has led to the accumulation of both surface and vertical fuels such that conditions are now conducive to the development of fires with intensity far greater than the historical condition. Large, catastrophic wildfires in California during the summers of 1977, 1987, 1990, 1992, 1999, 2001, and 2003 provide stark evidence of the potential of existing forest conditions for extensive and severe fires.

The problem of hazardous fuel conditions in forests has received substantial attention in recent years as land managers attempt to reduce the threat of catastrophic fires. Reduction of fuel loads, especially in areas of wildland-urban interface, has been conducted primarily via mechanical treatment (usually thinning from below), although prescribed burning or combinations of thinning and burning are also used. Although such stand manipulations may be able to return forests to approximate historic structural conditions, many questions about the ecological consequences of these fire surrogate
treatments remain unanswered (SNEP 1996). For example, the question of the effects of structural and functional manipulations on soil fertility, microbial ecology, and nutrient cycling has only recently begun to attract scientific attention (e.g. DeLuca and Zouhar 2000).

This study details one portion of the National Fire and Fire Surrogate Network study, which was designed to evaluate the efficacy of alternative management strategies for the mitigation of the current wildfire hazard and for the improvement of forest ecosystem sustainability and health on a national scale. Our site in the southern Cascades Range of northern California is one of twelve in which a common experimental design is employed to determine whether prescribed fire, mechanical treatment (usually thinning from below), or a combination of the two could best (1) minimize the hazard of catastrophic fire, and (2) accelerate and sustain the development of a large-tree dominated, late-successional pine forest similar to those originally created and sustained by the historical fire regime. Within that context, we present here the results of a study designed to determine the belowground impacts of prescribed fire and thinning, both alone and in combination.

**Methods**

*Study Area*

This study took place in the Goosenest Adaptive Management Area (GAMA) of the Klamath National Forest in Siskiyou County, CA (lat 41°35’N, long 121°53’W). The forests of GAMA were logged between 1900 and 1920. The gentle, dissected landscape
of the GAMA is the result of recent volcanic activity. Slopes are generally <10% but can locally be >50%, with elevation ranging from 1500 to 2000 m asl. White fir and ponderosa pine are dominant in the forest canopy, with *P. lambertiana* (sugar pine), *Calocedrus decurrens* (incense cedar), *Abies magnifica* var. *shastensis* (Shasta red fir), and *P. contorta* var. *murrayana* (lodgepole pine) common. Shrubs include *Ceanothus* spp., *Arctostaphylos* spp., *Purshia tridentata*, *Cercocarpus ledifolius*, *Chrysothamnus* spp., and *Artemesia* spp.

The soils of the experimental area are entisols mixed with lesser cover of alfisols of the Belzar-Wintoner complex (USDA Forest Service 1982). The Belzar family consists of loamy-skeletal, mixed, frigid Andic Xerochrepts. The Wintoner family, pumice overburden phase, consists of fine-loamy, mixed, frigid Ultic Haploxeralfs. These sand and sandy loam soils drain rapidly and have relatively low water-holding capacity. The climate is Mediterranean-type and the study site receives most of the 25-100 cm annual precipitation as winter snowfall.

**Study Design and Field Methods**

The GAMA Fire and Fire Surrogate study (FFS) is a completely randomized design consisting of 4 treatments each replicated 3 times. The treatment units of this study were overlaid on existing research plots of the Little Horse Peak Interdisciplinary Study (LHPIS) that was established in 1998 to accelerate the development of late-successional characteristics of eastside pine forests (Zack et al. 1999, Ritchie 2005). The combination of mechanical treatment (thinning from below) and prescribed fire (hereafter...
thin+burn) was replicated in 5 experimental units for the LHPIS study, and the first 3 units that had been thinned in the LHPIS study were selected in 2000 for this FFS study. Treatment units for FFS Burn-only treatments (hereafter burn-only) were interspersed among the Little Horse Peak in 2002. In each 10-ha FFS treatment unit ten 20m x 50m (0.1-ha) random, permanent sampling plots were established on a 50-m grid and the corners marked with permanent posts.

The thinning of the thin+burn units involved thinning from below combined with selection cutting that focused on removing shade tolerant species such as white fir. An average of 34% of the basal area was removed as mean basal area was reduced from 36.5 m²/ha to 24.1 m²/ha. Processing consisted of removing whole trees to central processing landings where limbs and tops were removed from larger trees and logs cut to appropriate length for hauling to processing plants. Limbs and tops were chipped at the landings and removed; sub-merchantable understory trees were hand-cleared within one year after larger trees were thinned from below, and this material was scattered on site. This is standard procedure in this region. Thinning was done during the summers of 1998 and 1999, and was followed by a prescribed fire in the late fall of 2001; a more thorough discussion of thinning treatment prescription and pre- and post-treatment stand conditions is given by Ritchie (2005).

The burn-only treatment consisted of a late fall prescribed burn in 2002. Stand structure was not modified mechanically prior to burning in the burn-only units. Firing
techniques used in the prescribed burning were strip-head firing and tree-centered spot ignition (Weatherspoon et al. 1989). Weather conditions and flame lengths are given in Table 3.1.

**Soil Sampling and Laboratory Analysis**

Four sample points were located at each of the corners of the 0.1-ha plot, and 1 sample point was located at the midpoint of each of the long sides of the 0.1-ha plot. In June - August of 2001-2003 soil samples to 10 cm depth were taken from those 6 points in each sample plot as follows: thin+burn pre-fire 2001 (after thinning was completed), thin+burn post-fire 2002, burn-only pre-fire 2002, and burn-only post-fire 2003. Soil samples on successive dates in each treatment unit were taken within 1.0 m of those from the previous year. All samples were returned to the laboratory under refrigeration. Each sample was passed through a 5-mm sieve to remove stones and root fragments.

Organic C and total N were determined by oxidation/fluorescence on a Carlo-Erba CN analyzer after grinding to pass an 80-mesh screen. Soil samples were extracted with 0.5M K₂SO₄ for NO₃⁻, NH₄⁺ (Olsen and Sommers 1982), and analyzed using the microtiter methods of Hamilton and Sims (1995).

Estimation of N mineralization and nitrification for all study plots was done using aerobic, *in situ* incubations following the method of Raison et al. (1987). Groups of three 10-cm deep PVC soil cores were taken at each of the 6 sampling points around each permanent sampling plot (N = 720). One was returned to the lab immediately whereas the remaining two incubated *in situ* for 20-30 days. One of the *in situ* cores was covered
with a PVC cap while the other remained open. As the results from capped and uncapped cores were not significantly different, they were pooled for later data analysis. All 3 cores from a given sampling point were extracted and analyzed for inorganic N as indicated above. Net N mineralization was calculated as the difference in total inorganic N (NO$_3^-$ + NH$_4^+$) concentration between the initial samples and those that incubated for 20-30 days. Net nitrification was calculated as the difference in NO$_3^-$ N in the incubated and initial samples. Proportional nitrification was estimated by dividing the net NO$_3^-$ accumulation due to nitrification by total amount NH$_4^+$ available to be nitrified (initial NH$_4^+$ + net N mineralization)

Two samples for analysis of acid phosphatase, chitinase, and phenol oxidase activity were taken during each sampling year (N = 240). Acid phosphatase was chosen as an indicator of overall microbial activity, and acid phosphatase activity often varies in parallel with other important soil microbial processes, such as N mineralization (Decker et al. 1999). Chitinase is a bacterial enzyme that catalyzes the breakdown of chitin, a by-product of both fungi and arthropods, into carbohydrates and N. As chitin is intermediate in its resistance to microbial metabolism and is produced only by bacteria, changes in chitinase activity relative to that of the other enzymes we assayed gives an indication both of changes in the relative contribution of bacteria to microbial activity and changes in organic matter along the gradient from labile to recalcitrant. Phenol oxidase is produced primarily by white rot fungi, and is specific for highly recalcitrant organic matter, such as lignin. Increases in phenol oxidase activity relative to the other enzymes we assayed gives another indication of changes in the relative contribution of bacteria vs.
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 give us considerable insight into changes in both the microbial community and the organic matter complex.

The enzyme activities were analyzed using methods developed by Tabatabai (1982), as modified by Sinsabaugh (Sinsabaugh et al., 1993; Sinsabaugh and Findlay, 1995). Subsamples of approximately 10 g of fresh soil were suspended in 120 ml of 50 mM NaOAc buffer (pH 5.0) and homogenized by rapid mechanical stirring for 90 s. To minimize sand sedimentation, stirring was continued while aliquots were withdrawn for analysis.

Acid phosphatase (EC 3.1.3.1) and chitinase (EC 3.2.1.14) activities were determined using p-nitrophenol (pNP) linked substrates: pNP-phosphate for acid phosphatase and pNP-glucosaminide for chitinase. Samples were incubated for 1 h (acid phosphatase) or 2 h (chitinase) at 20-22°C with constant mixing. Following incubation, samples were centrifuged at 3,000 X 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.

Phenol oxidase (EC 1.14.18.1, 1.10.3.2) activity was measured by oxidation of L-DOPA (L-3,4-dihydroxyphenylalanine) during 1 hr incubations at 20-22°C. Following
incubation, samples were centrifuged as above and analyzed at 460 nm without dilution. Parallel oxidations using standard horseradish peroxidase (Sigma Chemical) were used to calculate the 1-DOPA extinction coefficient.

Data Analysis

All response variables were either normally distributed or could be transformed to normality with a square root transformation. As the prescribed fires applied to the burn-only and thin+burn treatments occurred in successive growing seasons, this experiment was not a two-by-two factorial design with years and fire as main effects. Instead, we treated it as a completely randomized design, and evaluated the effect of fire on the burn and thin+burn units as independent 1-way analyses of variance (SAS 1995). Statistical significance is reported at $P = 0.05$.

Results

Fire significantly reduced soil organic C in the burn-only treatment ($P < 0.001$) but not in the thin+burn treatment ($P < 0.188$) (Figure 3. 1). Fire reduced soil organic C in the burn-only treatment by an average of 29%. Similarly, fire significantly affected soil C:N ratio in the burn-only ($P < 0.001$) but not the thin+burn treatment ($P < 0.266$) (Figure 3. 1). In the burn only treatment, soil C:N ratio increased by 18%. Thus, fire significantly reduced both organic matter quantity and quality in units that had not been mechanically thinned, but not in units that had been thinned prior to burning.
In the burn-only units there was no significant effect of fire on either net N mineralization rate ($P < 0.527$) or net nitrification ($P < 0.973$) (Figure 3. 2). In contrast, in the treatment units that were mechanically thinned prior to burning, fire resulted in a significant reduction in net nitrification and net N mineralization ($P < 0.001$ for both) (Figure 3. 2). The reduction in net nitrification rate due to burning in the thin+burn units was 24%, and the reduction in net N mineralization was 22%. Total inorganic N in the soil solution (TIN) increased significantly as a result of fire in both the burn-only and the thin+burn treatments ($P < 0.001$ in both) (Figure 3. 2).

Acid phosphatase activity was significantly reduced by fire in both treatments ($P < 0.001$ burn-only; $P < 0.013$ thin+burn) (Figure 3. 3). Acid phosphatase activity was reduced by an average of 42% in the burn-only treatment but only an average of 17% in the thin+burn treatment. Chitinase activity was reduced significantly by fire in the thin+burn ($P < 0.028$), but not in the burn-only treatment ($P < 0.116$) (Figure 3. 3). Phenol oxidase activity was not significantly affected by fire in either treatment ($P < 0.103$ burn-only; $P < 0.137$ thin+burn) (Figure 3. 3).

**Discussion**

The primary objective of this study was to assess initial below-ground responses to restoration treatments that involved fire, alone and in combination with a mechanical thinning treatment. Although the National Fire and Fire Surrogate Study was designed to be a long term analysis of the efficacy of these treatments in reducing wildfire hazard and improving ecosystem sustainability, we present here an assessment of the proximate
effects of these treatments in the southern Cascades FFS study site both as a benchmark against which to evaluate longer term ecosystem responses and for comparison with the existing fire effects literature, most of which focuses on first year effects.

Fire reduced soil organic matter quantity in the burn-only treatment, but not in the treatment units that had been mechanically thinned prior to burning. High pre-burn soil C content coupled with low fire severity may explain the lack of significant change in organic matter quantity in units that received thinning prior to prescribed fire. Other studies of mechanically thinned coniferous forests have also noted high soil C after logging. For example, a review by Johnson (1992) reports increases in mineral soil C of 18% and 23% in mixed conifer forests after whole-tree harvesting and 6 years after a clearcut harvest, respectively.

The loss of soil organic matter is largely dependent upon the temperature and intensity of a fire (Ahlgren and Ahlgren 1960); prescribed burning generally results in increased soil C near the soil surface, but higher-severity fires have been shown to decrease soil C (Johnson 1992). Carbon can also be added to the soil when charcoal from burned forest floor material is transported into the soil, and this can result in overly conservative estimates of the loss of soil organic C during fire (Johnson and Curtis 2001). The significant loss of organic matter in the burn-only treatment could have been due either to loss via combustion during the fire or to increased microbial mineralization of organic matter after the fire. As our microbial activity estimates do not support the latter, the more likely explanation appears to be greater consumption of organic matter by fire in the burn-only treatment than in the thin+burn treatment. Although fire weather and flame
lengths were similar during the fires in the burn-only and thin+burn treatments, flame length (fire intensity) is not directly correlated with fire severity (loss of forest floor organic matter). For example, a slow-moving fire with low flame lengths may sustain greater soil heating and organic matter combustion than a relatively faster-moving fire with greater flame lengths, and vice versa.

More important to the difference in organic matter loss may have been the spatial continuity of the fuel bed. It is possible that the activities associated with the thinning may have resulted in some mixing of litter, duff, and mineral soil. This, in turn, would result in a reduction of the exposure of that organic matter to direct combustion, thus preventing the prescribed fire from having as significant an effect in the thin+burn treatment as it did in the burn-only treatment. Furthermore, although total pre-burn fine and coarse woody debris loads in the thin+burn treatment were equal to that of the burn-only treatment (7.42 Mg ha⁻¹), fuels were not as continuous in the thin+burn as in the burn-only treatment (Schmidt 2005).

We observed an increase in C:N ratio (indicating a reduction of organic matter quality) in the burn-only treatment but no corresponding difference in the thin+burn treatment. In the burn-only treatment, the quality of soil organic matter was likely decreased by the combination of an addition of partially combusted woody material with high C:N ratio and a loss of relatively C:N ratio organic matter to direct combustion. The lack of a similar effect on C:N ratio in the thin+burn treatment again supports the notion of lower fire severity in these treatment units.
The rates of N mineralization and nitrification were reduced significantly in the thin+burn treatment but not in the burn-only treatment. Although the processes of N mineralization are accomplished by a wide variety of soil organisms, including bacteria, fungi, and nematodes, nitrification is accomplished primarily by a specialist guild of bacteria. Thus, modification of the chemical and biochemical conditions in the soil is more likely to affect the latter more than the former (Raison 1979); however, we observed a similar magnitude of decrease for both N mineralization and net nitrification in the thin+burn treatment.

It was initially unclear to us why there was a lack of change in N mineralization in the burn-only units, as many studies have demonstrated increases in N mineralization after single fires (reviews by Raison 1979, Boerner 1982, Wan et al. 2001). Such increases are often attributed to the alteration of organic matter by fire in such a manner as to render it more susceptible to microbial attack, to increases in microbial activity, and to changes in microclimate. Our results rule out an increase in microbial activity and the increase we observed in C:N ratio suggests that susceptibility to microbial attack would have been reduced rather than enhanced by fire in this site. Given the paucity of growing season precipitation in this region, changes in microclimate during the parts of the year that are otherwise suitable for mineralization may not have been sufficient to overcome the lack of rainfall.

TIN increased as a result of fire in both treatments, although thin+burn plots exhibited a four-fold increase in TIN from pre-fire to post-fire years while levels in burn-only plots merely doubled. The difference in the magnitude of the increase in TIN is
consistent with studies that report that thinning and the creation of canopy gaps as small as 0.07 ha in forests create areas of greater N availability (Prescott et al. 1992, Bauhus and Barthel 1995, Parsons et al. 1994).

This increase in mineral N was expected, as Wan et al. (2001) concluded from their meta-analysis of fire effects on N that TIN generally increases in coniferous forests during the initial post-fire growing season. The difference in magnitude of increase observed for TIN between the two treatments may be explained by difference in fires severity, as lower intensity fires transfer larger amounts of NH$_4^+$ to the soil than more severe fires, during which a greater amount of soil N is volatized (DeBano 1991).

Mineral soil N may increase after fire due to transport of N from the forest floor (Wells et al. 1979), as well as from the release of NH$_4^+$ from soil minerals and clay-organic complexes during combustion, and both may be followed by conversion of NH$_4^+$ to NO$_3^-$ due to nitrification (Russell et al. 1974, Raison 1979). However, such increases in available N are typically transitory and are likely to dissipate by the end of the second post-fire growing season (Wan et al. 2001).

We used acid phosphatase activity as an index of overall microbial activity, as this enzyme is released into the soil by bacteria, fungi, and other soil organisms as they metabolize relatively labile, high quality organic matter. Acid phosphatase activity was reduced significantly by both treatments. Similarly, Saa et al. (1993) reported 80-90% decreases in acid phosphatase levels after fire in gorse (Ulex europaea) shrublands and pine plantations in Spain, and Boerner et al. (2000) reported decreases of similar magnitude to those we report here in their study of fire in mixed-oak (Quercus spp.)
forests. Acid phosphatase activity may remain low for as long as 4 years after burning, at least in the jack pine (Pinus banksiana) forests of Ontario studied by Staddon et al. (1998).

In our study, acid phosphatase activity was reduced considerably more by the burn-only treatment (42%) than by the thin+burn treatment (16%), and this may reflect a greater fire severity in the burn-only than thin+burn treatment (Eivazi and Bayan 1996, Staddon et al. 1998).

Chitinase activity reflects the use of chitin (the detrital remains of arthropods and fungi) as a source of both C and N by bacteria and, in some ecosystems, actinomycetes. Chitin is intermediate in its susceptibility to microbial attack, and becomes a preferred source of carbohydrates and/or N only when high quality organic matter is lacking (Hanzlikova and Jandera 1993). Chitinase activity decreased as a result of the thin+burn treatment but not as a result of fire alone.

A decrease in chitinase activity should indicate a reduction in bacterial abundance, a reduction in the importance of chitin as a source of C and N, or both. As our results indicate that organic matter quality and quantity decreased following the burn-only treatment but not the thin+burn treatment, one would anticipate that chitinase activity would increase in the burn-only treatment and remain unchanged in the thin+burn treatment. This is the opposite of what we actually observed. We currently have no explanation for this apparent contradiction.

It should be noted, however, that the degree of variability present in our pre-burn data for the burn-only treatment was 3-4 fold greater than was the case in any other
enzyme-treatment-year combination. This variability was the reason that the difference between pre-burn and post-burn years was not statistically significant in the burn-only treatment, despite similar absolute (0.03 mmol/g/h for both) and relative (16% and 20%) decreases in chitinase activity in the burn-only and thin+burn treatments. Whether this greater variability was a reflection of a difference in spatial heterogeneity between treatment units or an aberration in sampling and/or analysis is unclear.

The index of fungal activity we used was phenol oxidase, an enzyme involved in the metabolism of particularly recalcitrant compounds (e.g. lignin, suberin). Based on this parameter, fungal activity was not affected by burning, alone or in combination with mechanical thinning. Given the preponderance of relatively recalcitrant materials in the forest floor and soils of this (and most other) coniferous forests and the relatively low severity of the fires, the lack of response by organisms that specialize on low quality organic matter is not a surprising result.

Taken together, the results of our analysis of these three soil enzymes indicate that overall microbial activity was reduced by fire, whether thinned prior to fire or not. Furthermore, as fungal activity was relatively unchanged by fire, we attribute the bulk of this result to a reduction in the activity of organisms other than fungi. As chitinase activity was also reduced by fire, at least in the thin+burn treatment, some of that reduction must represent a loss of bacterial activity. Thus, our results suggest that the impact of fire may differ among types of soil organisms associated with decomposition, and those effects may be influenced by treatment type.
Management Implications and Conclusions

This study demonstrates that fire has short-term effects on soil ecological properties including soil organic matter, N turnover and availability, and microbial functional community structure, and that the combination of mechanical thinning and fire may have different effects than fire alone. Fire alone resulted in reduced soil organic matter quality and quantity, whereas the combination of a mechanical thinning treatment and burning did not affect soil organic matter. In general, the higher relative fuel loads in more dense forest stands will support fires of higher severity than fires in open stands, and activities associated with thinning may mix litter, duff, and mineral soil materials in such a manner as to make the organic matter less susceptible to combustion. The more continuous ground fuels and lower relative humidity in the burn-only treatment may have contributed to greater fire severity and thereby to comparatively greater volatilization of nutrients during the fires.

Soil organic matter is important to a productive forest ecosystem because of its role in stabilizing soil, maintaining soil conditions suitable for seedling establishment and growth, supplying nutrient storage and water holding capacity. Thus, managers should be aware not only of the effect that management activities may have on soil organic matter but also the strong interactions that exist among stand density, fuel loading, fire behavior, and soil organic matter.

Our results also show that burning influences nitrification and available inorganic N in the soil, and that those effects differed between burn-only and thin+burn treatments.
Based on prior studies in coniferous forests, the increases we observed in available N (TIN) are likely to be transitory, and further study is required to determine if there will be longer term effects of these treatments on the supply of N to trees.

Overall microbial activity was decreased by fire, both with and without mechanical thinning, and the patterns of variation in the three soil enzymes we quantified suggested that there was also a decrease in the activity of microbes that rely on easily digested organic matter (such as bacteria) but not in those that specialize on recalcitrant organic compounds (such as wood rotting fungi). If this change in functional microbial community structure were to persist, it could affect the rate at which nutrients are recycled from detritus for use by vegetation. We assume that this effect will dissipate as soon as new litterfall restores the supply of relatively higher quality organic materials and as microbial populations rebound from fire.

The thin+burn treatment resulted in a greater impact on N turnover and soil enzyme activity, both of which are indicative of biological activity in the soil. Thus, for our mixed conifer site in northern California, the application of prescribed fire to mechanically thinned stands has a greater impact on soil biological processes one year after burning, whereas soil C and organic matter quality is impacted more by fire in stands that were not mechanically thinned prior to burning. Furthermore, the post-burn forest floor is much more shaded in burn-only treatment than the thin+burn treatment due to the persistence of standing dead white fir understory in the former; a cooler and more moist soil environment may facilitate more rapid recolonization of soil microbes in the year following a fire.
Fire effects are strongly dependent upon fire severity, which is in turn influenced by fuel loading, stand characteristics, and weather. Our data indicate that stand characteristics contribute significantly to below-ground fire effects. This study provides information useful for predicting the short term, ecosystem-level effects of different forest restoration and wildfire hazard reduction techniques in the widespread ponderosa pine ecosystem type.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Burn-only</th>
<th>Thin + burn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature (°C)</td>
<td>6 ± 5</td>
<td>12 ± 5</td>
</tr>
<tr>
<td>Relative Humidity (%)</td>
<td>24 ± 13</td>
<td>32 ± 16</td>
</tr>
<tr>
<td>Wind speed (km h⁻¹)</td>
<td>1.7 ± 1.3</td>
<td>2.6 ± 1.6</td>
</tr>
<tr>
<td>Flame length (cm)</td>
<td>24 ± 11</td>
<td>40 ± 18</td>
</tr>
</tbody>
</table>

Table 3.1. Fire weather and behavior characteristics for prescribed fires in the burn-only and thin + burn treatment areas of the Goosenest Adaptive Management Area, northern California. Means ± standard deviations are given. Data are from USDA Forest Service, Pacific Southwest Research Station, Redding, California.
Figure 3.1. Soil organic C and C:N before and one year after fire (2001 and 2002 for thin+burn treatment; 2002 and 2003 for burn-only treatment) at the Goosenest Adaptive Management Area in northern California. Histogram bars denote means with standard errors of the means; significant differences at $P = 0.05$ are indicated by *.
Figure 3.2. Net N mineralization rate, net nitrification rate, and total inorganic N (mg TIN/kg soil) before and one year after fire (2001 and 2002 for thin+burn treatment; 2002 and 2003 for burn-only treatment) at the Goosenest Adaptive Management Area in northern California. Histogram bars denote means with standard errors of the means; significant differences at $P = 0.05$ are indicated by *.
Figure 3. Activity of acid phosphatase, chitinase, and phenol oxidase before and one year after fire (2001 and 2002 for thin+burn treatment; 2002 and 2003 for burn-only treatment) at the Goosenest Adaptive Management Area in northern California. Histogram bars denote means with standard errors of the means; significant differences at $P = 0.05$ are indicated by *.
CHAPTER 4
MECHANICAL RESTORATION OF CALIFORNIA MIXED-CONIFER FORESTS: DOES IT MATTER WHICH TREES ARE CUT?

Introduction

Descriptions of the pre-settlement mixed-conifer forests of northern California and southern Oregon describe open, park-like stands of trees, with Pinus ponderosa P. & C. Lawson (Ponderosa pine) the most abundant tree species (Laudenslayer & Darr 1990; Covington & Moore 1994). In contrast, the California mixed-conifer forests of today often differ substantially from historic conditions in many characteristics, and livestock grazing, logging and aggressive fire suppression policies have all contributed to post-settlement changes in stand composition and structure (Weaver 1951; Agee 1993). Forests that were historically dominated by Ponderosa pine now contain a large percentage of Abies concolor (Gord. & Glend.) Lindl. ex Hildebr. (White fir) and other shade-tolerant species. Stem density in these stands is much greater today than at the time of European settlement (Zack et al. 1999; Taylor 2004; Ritchie and Harcksen 2005), and accumulations of both surface and vertical fuels have produced conditions conducive to the development of fires with intensity far greater than the historical condition.

The logging of the late 1800s or early 1900s had a particularly strong impact on the large, old tree component, and dense stands of small, young trees that established
following logging now occupy areas that once supported open, multiple-aged stands (Zack et al. 1999; Taylor 2004; Ritchie and Harcksen 2005). Today these forests have a paucity of the large woody stems (live or dead) that are considered important to many wildlife species (Thomas 2002), and large snags and downed logs will remain limited in these systems until a significant component of large trees can be grown to produce them. The high density of the present stands makes it unlikely that the large tree component will be restored without management intervention (Dolph et al. 1995), and these dense, young stands are likely to promote high intensity fires (Agee and Skinner 2005) that will further lengthen the time necessary to restore the large tree component.

The problem of hazardous fuel conditions in forests has received substantial attention in recent years as land managers attempt to reduce the threat of catastrophic fires. Reduction of fuel loads, especially in areas of wildland-urban interface, has been conducted primarily via mechanical thinning from below, although prescribed burning or combinations of thinning and burning have also been used. Although such stand manipulations may be able to return forests to a condition resembling (to some degree) the historic structure, the ecological effects of these manipulations on the properties of forest soils and forest floor layers are not well understood (SNEP 1996).

The availability of nutrients (especially N and P) in the soil and the accumulation of organic matter in the forest floor and mineral soil determine the potential of a site for tree seedling establishment, tree growth and ecological functioning. Soil nutrient status is affected by the nutrient content of the litter produced by the plants (Ferrari 1999; Prescott 2002), which varies among plant species and stand ages (Alban 1969; Vitousek 1982;
Gholz et al. 1985; Hart & Firestone 1991; Grulke & Retzlaff 2001), as well as local soil type. For example, Alway et al. (1933) demonstrated species-specific differences of coniferous and deciduous trees on forest floor and soil nutrient availability in Minnesota. Harvesting methods (Thiffault et al. 2006) and spatial arrangement of tree stems on the landscape (Parsons et al. 1994; Bauhus & Barthel 1995) can also influence soil nutrient availability and leaf production and nutrient content.

Decomposition of that litter and release of nutrients for subsequent plant uptake and growth are influenced both by the site microclimate (Hart & Firestone 1992) and by the nutrient content of the litter (Boerner 1984). Thus, the effects of forest thinning strategies on the nature and decomposition of forest floor organic matter, and the subsequent nutrient characteristics of the forest soil may vary according to species composition of remaining trees, the inherent variability of soil properties across a landscape, and the mechanical disturbance caused by forest management activities (Stone 1975). Consequently, seemingly minor differences in management activities may result in significant ecological differences between stands across a landscape.

The USDA Forest Service initiated a long-term study of the effects of experimental forest management practices in the Klamath National Forest of northern California in 1998, and conducted two alternative thinning prescriptions in order to evaluate long-term ecosystem responses to mechanical reductions of stand density as a structural restoration method. The objective of one treatment was to restore dominance
of Ponderosa pine by thinning from below to achieve an 80% composition of ponderosa pine by basal area, whereas the objective of the other was to maximize individual tree growth of the largest trees, regardless of species.

Because efforts to reduce fuel and return western mixed-conifer forests to historical stand structure also have the potential to affect belowground processes, we hypothesized that differences in thinning prescriptions would result in ecologically important differences in the forest floor and soil; however, to date no direct comparisons of soil and forest floor between two different thinning prescriptions have been reported. The primary objective of this study was to compare forest floor and soil nutrient content and soil microbial activity at 5-6 years following a mechanical thinning treatment that emphasized retention of ponderosa pine with one that emphasized retention of large trees regardless of species.

Methods

Study Site

This study took place in the Goosenest Adaptive Management Area (GAMA) of the Klamath National Forest in Siskiyou County, California (lat 41°35′N, long 121°53′W). The forests of GAMA were logged between 1900 and 1920, and all merchantable trees were removed over large areas. The gentle, dissected landscape of GAMA is the result of recent volcanic activity. Slopes are generally <10% but can locally be >50%, with elevation ranging from 1500 to 2000 m. *Pinus ponderosa* P. & C. Lawson (ponderosa pine) and *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white
fir) are dominant in the forest canopy, together typically comprising >90% of the basal area. *P. lambertiana* Dougl. (sugar pine), *Calocedrus decurrens* (Torr.) Florin (incense cedar), *Abies magnifica* A. Murr. var. *shastensis* Lemmon (Shasta red fir), and *P. contorta* Dougl. ex Loud. var. *murrayana* (Grev. & Balf) Englem. (Sierra lodgepole pine) are also present at low density. The shrub layer is sparse, ranging in cover from 0.0 to 5.4% of the ground area. Shrubs present include *Ceanothus* spp. (ceanothus), *Arctostaphylos* spp. (manzanita), *Purshia tridentata* (Pursh) DC. (antelope bitterbrush), *Cercocarpus ledifolius* Nutt. (curl-leaf mountain mahogany), *Chrysothamnus* spp. (Rabbitbrush), and *Artemisia* spp. (sagebrush) (USDA Forest Service 1996). Forb and grass cover ranged from 3.2 to 18.3%, and averaged 8.5% among our treatment units.

The historical fire regimes of the southern Cascade range were characterized by frequent, low-intensity fires in the low to middle elevations and mixed-intensity fires in the upper montane (Taylor 2000; Skinner and Taylor 2006; Taylor et al. 2008). Fire has largely been excluded from the forests since the early logging. This has likely intensified the alteration of stand structure through eliminating the thinning effect of fire on developing stands.

The soils of the experimental area are dominated by the Belzar–Wintoner complex of inceptisols and alfisols (USDA Forest Service 1982). The Belzar series of loamy-skeletal, mixed, frigid Andic Xerochrepts covers the great majority of the study area. Interspersed within the matrix of Belzar series soils are areas of somewhat thinner pumice deposits in which the Wintoner series (pumice overburden phase) of fine-loamy, mixed, frigid Ultic Haploxeralfs are mapped. Both of these soil types have high silt and
sand content, drain rapidly, have relatively low water-holding capacity, and are relatively low in nutrient availability. The climate is Mediterranean-type, and the study site receives most of the 25–100 cm annual precipitation as winter snowfall (USDA Forest Service 1996).

Experimental Design

The Pine-preference and Size-preference treatments and the untreated Controls are part of the Little Horse Peak Interdisciplinary Study, a long-term ecological study initiated in 1998. Each of the treatments was randomly assigned to 5 replicate 100-ha units, each of which contains a 100-m permanent grid (Figure 4. 1, Figure 4. 2), and 3 of these 5 units were selected for the study presented here. All units were located on a predominantly northwestern aspect. Elevation ranges among units within each treatment were: Control, 1560–1692 m, Size-preference 1485–1578 m, and Pine-preference 1560–1666 m (Figure 4. 1).

Whole-tree harvesting methods were applied to both Pine-preference and Size-preference treatments and processing followed standard harvesting procedure for forests in this region (Table 4. 1). Whole trees were transported to central processing landings where all boles, limbs, and tops of trees 10.2-45.7 cm dbh were removed and logs cut to appropriate length for hauling to processing plants. Limbs and tops of trees were sorted and either chipped at landings and shipped for pulp, or shipped for electricity generation; thus, all the slash generated by the thinning was removed from the units. All damaged trees were removed. Sub-merchantable understory trees were hand-cleared from both
treatments within one year after larger trees were thinned from below; this material was scattered on site. The thinning was completed during the growing seasons of 1998-2000; a more detailed description of thinning operations is provided by Ritchie (2005).

As we wished to evaluate whether the two alternative thinning treatments would produce changes in the soil that would persist long enough to have meaningful effects on future forest condition, we sampled one treatment unit from each of the two thinning treatments in the sixth growing season following thinning and two from each of the thinning treatments in the fifth growing season following treatment.

Pre-treatment basal area and density was greater in Pine-preference than Size-preference, while the quadratic mean diameter (QMD) was the reverse. The proportion of basal area of fir (Abies spp.) was similar in the two manipulated treatments (Table 4.2). After the restoration thinning treatments, the Pine-preference units supported a slightly greater total basal area and total tree density, density of Ponderosa pine, and density of small trees than did the Size-preference units (Table 4.2). The QMD, proportion of basal area represented by fir, and density of larger trees were similar for both thinning treatments (Table 4.2). A more thorough discussion of treatment prescription and pre- and post-treatment stand conditions is given by Ritchie (2005).

Soil Sampling and Laboratory Analysis

Soil samples were taken from randomly-selected locations in each of the Pine-preference and Control units in June-August 2004 (N=180) and from each of the Size-preference treatment units in October 2004 (N=90). Given that <1.0 cm of precipitation
fell during the month prior to sampling or during the period during June - October, no appreciable effect of the difference in sampling time was likely. As this study was initiated in 2004 and no belowground component existed in the original Little Horse Peak study that began in 1998, no pre-treatment soil sampling was done. However, in addition to our 2004 samples, samples were taken from the Control units in 2001 and 2002, and those results were included in the multivariate analysis presented here.

Samples were taken to a depth of 10 cm and returned to the laboratory under refrigeration. Each sample was passed through a 5-mm sieve to remove stones and root fragments. Sieved, air-dried soil samples were extracted with 0.5 M K$_2$SO$_4$ for NO$_3^-$, NH$_4^+$ and P (Olsen & Sommers 1982); NO$_3^-$ and NH$_4^+$ were analyzed using the microtiter methods of Hamilton & Sims (1995) and P was analyzed by the stannous chloride/molybdate colorimetric method. Organic carbon (C) and total N were determined by oxidation/fluorescence on a Carlo-Erba CN analyzer after grinding air-dried soil samples to pass through a 0.32-mm mesh screen.

In order to measure the activity of microbes important in decomposition, we measured the microbial exoenzymes acid phosphatase (produced by microbes and roots), chitinase (produced by a guild of specialist bacteria), and phenol oxidase (produced primarily by white rot fungi). As our samples were sieved to remove roots prior to analysis, enzyme activities represent microbial activity only. Samples for analysis of these enzyme activities were taken from randomly-located gridpoints ($n$=240 for Control and Pine-preference, $n$=90 for Size-preference).
Enzyme activities were analyzed using methods developed by Tabatabai (1982), as modified by Sinsabaugh (Sinsabaugh et al. 1993; Sinsabaugh & Findlay 1995). Acid phosphatase (EC 3.1.3.2) and chitinase (EC 3.2.1.14) activities were determined using p-nitrophenol (pNP)–linked substrates: pNP-phosphate for acid phosphatase and pNP-glucosaminide for chitinase. Phenol oxidase (EC 1.14.18.1, 1.10.3.2) activity was measured by oxidation of L-DOPA (L-3,4-dihydroxyphenylalanine), and parallel oxidations using standard horseradish peroxidase (Sigma Chemical, St. Louis, MO) were used to calculate the L-DOPA extinction coefficient.

Forest floor samples for analysis of C and N concentration were taken from randomly located gridpoints in each of the Control and Pine-preference treatment units \( (n=60) \) and Size-preference units \( (n=90) \) in 2005. Unconsolidated litter and fragmented layers were sampled as a single unit. Although sampling designed to estimate the total mass of forest floor material in each unit was anticipated, mass samples were actually taken for the Control and Pine-preference units only. Therefore, our results are limited to C and N concentrations in forest floor material and cannot be extrapolated to the total C and N forest floor pool sizes. Forest floor samples were ground in a Wiley mill, and subsamples were dried at 70°C before analysis for C and N as above.

**Data Analysis**

Seven of the twelve soil and forest floor properties were normally distributed. Available P, total inorganic N, forest floor N, acid phosphatase and chitinase activity were log-normally distributed and were log transformed prior to further analysis. Log-
normal distributions are common with soil nutrient and microbial activity data, and using log or square root transformations to normalize distributions is common (e.g. Thiet et al. 2005). We performed a one-way analysis of covariance (PROC GLM, SAS 2004) using sample plot elevation as a covariate. As we sampled units that were in their fifth and sixth growing seasons since treatment, we also evaluated time since treatment as a covariate, and eliminated it from further analysis when it failed to produce significant covariance effects.

The unit of replication for this experiment was the treatment unit \( n=3 \) for each treatment), with three units within each treatment. In the Pine-preference treatment and Control we had 120 samples of soil and 60 forest floor samples per treatment unit, whereas in the Size-preference treatment \( n=90 \) for both soil and forest floor. The Ryan-Einot-Gabriel-Welsch Multiple Range test was used for means separation, as this approach minimizes the risk of Type I errors (SAS 2004). Statistical significance is reported at \( p=0.05 \) unless otherwise indicated.

Although the primary analysis of covariance was designed to assess differences among the three treatments, a primary objective of this study was to compare the two thinning treatments to each other. To this end, we also performed pair-wise comparisons of the two thinning treatments and present those results within the context of the larger analysis.

To visualize how the two thinning treatments affected the full suite of soil and forest floor parameters simultaneously, we used Non-metric Multidimensional Scaling
(NMS) ordination (McCune and Mefford 1999). We used the Sorenson (Bray-Curtis) distance measure and relativized each parameter to prevent weighting of the variables relative to each other.

**Results**

*Soil Nutrient Status*

Total inorganic N (hereafter TIN) was significantly greater in soils of the Size-preference treatment than in those of the Pine-preference treatment and Control, although there was no significant difference in TIN between the latter two (Table 4.3; Figure 4.3). The relative difference between the two thinning treatments was approximately 4-fold. Similarly, soil pH was significantly greater in Pine-preference and Control than Size-preference, and did not differ between Pine-preference and Control. Although soil pH differed only by 0.3 pH units between treatments, the difference was statistically significant at \( p=0.0008 \) (Table 4.3; Figure 4.3). There was no effect of treatment on available P; however, analysis of variance indicated that variation in available P was greater among units within a treatment than among treatments (Table 4.3).

*Soil C, N and Microbial Activity*

There was no difference in soil organic C or total soil N concentrations among the three treatments (Table 4.3, Figure 4.4), though pairwise comparison of the two thinning treatments indicated significantly greater soil organic C in Size-preference than Pine-preference \( (p<0.01) \) (Figure 4.4). Variation in soil organic C among units within
treatments was greater than the variation among treatments (Table 4.3). Soil C:N ratio was significantly greater in the Control than in the two thinning treatments, but there were no significant differences between Pine-preference and Soil-preference in soil C:N ratio (Table 4.3; Figure 4.4).

There were no significant differences in acid phosphatase and chitinase activity between the two thinning treatments, although both exhibited significantly lower levels of both enzymes than the Control (Table 4.3; Figure 4.5). Phenol oxidase activity did not vary significantly among the three treatments (Table 4.3), but pairwise comparison of the two thinning treatments indicated that Size-preference soils supported significantly greater phenol oxidase activity (by an average of 51.3%) than did Pine-preference soils (Figure 4.5). Phenol oxidase activity was the only variable for which elevation was a significant covariate (Table 4.3).

Forest Floor C and N Concentrations

Forest floor organic C concentration did not differ among treatments (Table 4.3; Figure 4.6). In contrast, total N concentration and C:N ratio did differ significantly among treatments (Table 4.3, Figure 4.6). Total N concentration in the forest floor differed between treatments in the order Pine-preference>Control>Size-preference, and the relative difference between the Pine-preference treatment and the Size-preference and Control were 179 and 125%, respectively. In contrast, the Size-preference and Control differed from each other by 19% (Figure 4.6). As a result of the larger difference in forest floor N concentration than C concentration, the forest floor C:N ratio differed
among treatments in the order Size-preference>Control>Pine-preference, with a relative difference between the two thinning treatments of 91% (Table 4.3; Figure 4.6). Thus, the forest floor organic material in the Pine-preference treatment was of significantly greater overall quality (as indicated by total N concentration and C:N ratio) than the forest floor material in the Size-preference or Control treatments.

*NMS Ordination*

NMS ordination arrayed the six manipulated treatment units and the eight control unit-year combinations along two axes which together explained 96.7% of the variance in the data matrix (Figure 4.7). Axis 1 was negatively correlated with soil organic C and total soil N. Axis 2, which explained most of the variation, was positively correlated with TIN, and negatively correlated with soil pH and acid phosphatase activity (Figure 4.7). The three Size-preference units were arrayed in the upper left corner of the ordination, indicating relatively high soil organic C, total soil N, and TIN and low microbial activity, relative to the Pine-preference and Control units. The three Pine-preference units fell well within the range of Control points, and therefore within the spatial and temporal range of variation in Control soils. In particular, the Pine-preference and Control units differed little in their placement along Axis 2, which explained most of the variation in the data matrix (Figure 4.7).
Discussion

Although forest management strategies designed to reduce accumulated fuel in western mixed-conifer forests may be effective in reducing fire severity (Agee & Skinner 2005), and mechanical approaches may successfully restore pre-settlement tree species composition, size distributions, and spatial patterns, such management interventions have the potential to influence long-term forest health and sustainability via effects on the soil and forest floor. The primary objective of this study was to investigate the magnitude of difference in forest floor and soil nutrient properties and soil microbial activities between two alternative thinning prescriptions that were conducted on sites with similar initial forest composition and soil conditions. Our data were collected between 5-6 years following the thinning treatments, and as such provide a comparison of the persistent, intermediate-term differences between two experimental forest management techniques, rather than a measurement of more transient, short-term post-disturbance effects.

We observed lower soil pH and greater TIN in the Size-preference treatment than in the Pine-preference treatment. Although various harvesting methods (e.g. whole-tree v. stem-only) have different effects on soil pH and N status (Staaf & Olsson 1991; Nykvist & Rosén 1985; Thiffault et al. 2006), both the Size- and Pine-preference treatments involved whole-tree harvest of a similar proportion of the basal area; thus, we do not feel that differences in the harvesting process were likely responsible for differences in pH and nutrient status. Plant roots may also either acidify or alkalinize the rhizosphere, depending on the species’ preference for NH₄⁺ versus NO₃⁻, as well as by products of root respiration (Hinsinger 2001). As these two thinning prescriptions left
behind quite different tree species assemblages, the species composition of the remaining tree stratum is more likely to have been a cause of the differences we observed in soil pH and N availability.

Total inorganic N was considerably greater in the Size-preference treatment than in the Pine-preference treatment (and the Control), and this difference may have been the result of post-treatment differences in N uptake, N mineralization, N fixation, or the post-treatment spatial arrangement of trees. Differences in N uptake rates between Ponderosa pine and White fir may affect soil N status, as Ponderosa pine is considered superior in obtaining nutrients from nutrient-poor soils that limit growth of other species (Oliver and Ryker 1990). Thus, it is possible that the fir component in the Size-preference assemblages took up less inorganic N than did the Ponderosa pines in the post-treatment assemblages, resulting in greater residual inorganic N in the soils of the Size-preference treatment. We analyzed N concentrations in age-specific needle classes of both White fir and Ponderosa pine in an effort to test this, and results are presented in Chapter 5.

In addition to trees, soil microbes take up considerable inorganic N; thus, reduced microbial activity in the Size-preference treatment could account to some extent for greater N availability. Our data do not, however, support this hypothesis, as our measures of acid phosphatase and chitinase suggest no difference among the two thinning treatments, and phenol oxidase activity was greater in Size-preference than Pine-preference.

Inorganic N is released to the soil solution as the product of the mineralization of N-containing organic matter by a diverse assemblage of soil microbes and microfauna.
Although it is reasonable to hypothesize that the differences in TIN among treatments were the result of differences in N mineralization rates, two years of in situ N mineralization measurements in the Control and Pine-preference treatments do not support this hypothesis (2002: Control 0.024±0.05 v. Pine-preference 0.025±0.06; 2004: Control 0.001±0.005 v. Pine-preference 0.004±0.006; J. Miesel, unpublished data).

It is also reasonable to hypothesize that soil pH and TIN might have been influenced by the spatial distribution of trees following the two thinning prescriptions. For example, soil NO$_3^-$ concentrations in experimentally created gaps in a 95-yr-old Pinus contorta (lodgepole pine) stand in Wyoming were greater in gaps created by removing at least fifteen trees than in uncut areas, and was greatest in gaps created by removing thirty trees (Parsons et al. 1994). Gap size did not affect NH$_4^+$, and concentrations of NO$_3^-$ in gaps of one or five trees did not differ from controls (Parsons et al. 1994).

Ritchie (2005) notes that the thinning criteria gave tree size or species precedence over tree spacing; thus, a patchy distribution of remaining live trees could have resulted from either or both of the two thinning treatments. If large gaps between dense tree patches were produced, those areas might be more susceptible to losses of available N by leaching than areas of more even tree distributions (Parsons et al. 1994). Although we did observe lower levels of TIN in Pine-preference than Size-preference, we have no quantitative measure of stem spatial distribution following thinning, and are unable to
determine whether the Pine-preference treatment contains more or larger regions of heavier thinning that do in fact exhibit greater losses of inorganic N, and consequently contribute to lower TIN.

The suite of three exoenzymes we assayed gives an indication of changes in the activity of several components of the microbial community (Hanzlikova & Jandera 1993). We chose acid phosphatase as an indicator of overall microbial activity, as the activity of this enzyme is often strongly correlated with microbial biomass (Kandeler & Eder 1993), microbial biomass N (Clarholm 1993), fungal hyphal length (Häussling & Marschner 2005), and N mineralization (Decker et al. 1999). Chitinase is produced primarily by bacteria, and as chitin is intermediate in its resistance to microbial metabolism, synthesis of chitinase is induced only when other, more labile C and N sources are absent (Hanzlikova & Jandera 1993). Finally, the index of fungal activity we used was phenol oxidase, an enzyme produced primarily by white rot fungi, which is specific for highly recalcitrant organic matter such as lignin (Carlile & Watkinson 1994). Although phenol oxidase activity should not be considered a proxy for the activity of all fungi, it is a useful indicator of those that specialize on the breakdown of wood, bark, and other lignin-rich substrates (Carlile & Watkinson 1994).

We observed no significant differences in acid phosphatase or chitinase between the two thinning treatments, though the controls had significantly greater acid phosphatase and chitinase activity than did either of the thinning treatments. Acid phosphatase production by roots and microorganisms is greatest when P is the most limiting nutrient for plant growth (McGill and Cole 1981); however, we observed no
significant differences between the two thinning treatments in either P availability or acid phosphatase activity, suggesting that variations in P availability between treatments may not be ecologically important in limiting tree growth.

There was, however, more than two-fold variation in phenol oxidase activity among the nine treatment units. The NMS ordination arrayed the Pine-preference units at the lower end of the phenol oxidase/soil organic C gradient and the Size-preference units at the upper end of that gradient. In contrast, the three control units spanned most of that gradient. If one were to compare the two thinning treatments, phenol oxidase activity and soil organic C concentration would be significantly greater (by averages of approximately 50 and 43%, respectively) in the Size-preference than the Pine-preference treatment. As our primary objective was to assess the differences, if any, in the impact of the two alternative thinning treatments, we conclude from this that the soils of Size-preference have more soil organic matter and greater fungal activity than do soils of Pine-preference. Although it is the case that including the unthinned Controls renders these differences between thinning treatments statistically insignificant relative to the difference between thinned and unthinned areas, this comparison was not our primary objective.

In spite of similar forest floor C concentrations among treatments, the forest floor C:N ratio of Size-preference was nearly double that of Pine-preference, and this was the result of high and highly variable forest floor N concentrations in Pine-preference. The 95% probability limits indicate that Unit 12, one of the three Pine-preference treatment units, contains a relatively large number of forest floor N concentrations at the extreme upper end of the distribution. Unit 12 mean forest floor N concentration was 46.8 ± 3.9
SE g/kg, a mean that was 267% of the average of the other two Pine-preference units. It is interesting to note that plant available P in the soil in Unit 12 was >3-fold greater than in the other two Pine-preference units as well (Unit 12: 188.6 ± 1.3 SE mg/kg, Unit 5: 66.9 ± 1.4 SE mg/kg, Unit 9: 55.2 ± 1.6 SE mg/kg). However, the presence of this somewhat anomalous unit did not substantially affect the statistical analysis of forest floor N concentration we presented, as analyses of covariance performed both with and without Unit 12 did not differ in their determination of the statistical significance of the treatment effect.

Forest floor N concentrations of the magnitude we observed in unit 12 would not be surprising in an area that had received direct applications of fertilizer or significant inputs from N-fixation. A chi-square analysis of ground surface cover of the N-fixing shrubs *Ceonothus* spp. (the only common N-fixing plant in this ecosystem) showed that unit 12 had significantly greater cover of *Ceonothus* spp. (11.6% average ground surface area) than did the other two Pine-preference units (<1.0% average ground surface area, difference between unit 12 and units 5+9, p<0.001).

Although we know of no among-unit differences in grazing animal use or stand history that might have contributed to this difference in forest floor N concentration, a somewhat greater density of trees <10 cm dbh in Unit 12 may have been a contributing factor. Litter from younger trees may contribute to the higher N in Pine-preference forest floor, since the foliage of younger trees may have greater nutrient concentrations than older trees of the same species (Wang & Klinka 1997).
As a reservoir of nutrients, the forest floor provides an indication of future nutrient supply to plants. In contrast to the current soil nutrient availability patterns (i.e. Size-preference > Pine-preference), the concentration of N in forest floor material was greater and the C:N ratio lower in Pine-preference than in Size-preference. If the change in forest floor mass caused by the harvesting activities was similar, and we have no reason to postulate otherwise, the differences in total C and N content will parallel those in C and N concentration. Over the longer term, the higher-N forest floor material in the Pine-preference treatment would then be expected to decompose at a faster rate than the material in Size-preference, and would thus supply nutrients to the available soil pools at greater rates in the Pine- than Size-preference treatment over time. Consequently, over time there may be a change in the relative soil nutrient availability between treatments, with Pine-preference becoming more nutrient-rich than Size-preference in the long term. It is clear, then, that the interplay between short- and long-term treatment effects will affect the success of forest management efforts over lengthy periods of time.

**Conclusions**

Our results suggest that thinning with an emphasis on retaining large trees (regardless of species) in northern California mixed-conifer forests may initially result in greater N availability, and therefore, a short-term increase in productivity and tree growth. Although no difference between the quality of soil organic matter was detected, the higher quality forest floor organic matter of the Pine-preference treatment indicates
greater potential for future nutrient availability. Thus, as these materials are decomposed, available nutrients for plants in the Pine-preference treatment may increase in the long term, relative to the Size-preference treatment.

This study demonstrates that differences in forest floor and soil nutrient content and organic matter are significant 5-6 years following two alternative restoration thinning treatments, and shows that differences in thinning prescription, when conducted in a mixed-conifer forest on a single soil type, result in significant differences in forest floor and soil nutrient content. Whether these results persist over decadal time periods and/or prove to be ecologically significant for long-term forest health and sustainability will be understood only with continued studies.
<table>
<thead>
<tr>
<th></th>
<th>Pine-preference</th>
<th>Size-preference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Treatment objectives</strong></td>
<td>To re-establish dominance by ponderosa pine (<em>Pinus ponderosa</em>) by thinning from below to achieve an 80% composition of Ponderosa pine by basal area.</td>
<td>To maximize individual tree growth of the largest trees, regardless of species, and minimize the number and size of forest openings for a 50-year period.</td>
</tr>
<tr>
<td><strong>Mandatory retention trees</strong></td>
<td>Retained trees included all white fir (<em>Abies concolor</em>) &gt;76 cm dbh, all dominant and codominant ponderosa pine &gt;31 cm dbh, all sugar pine (<em>Pinus lambertiana</em>), all incense-cedar (<em>Calocedrus decurrens</em>) &gt;25 cm dbh, all Douglas-fir (<em>Pseudotsuga menziesii</em>), trees similar in size to, and within 0.61 m of, mandatory retention trees (to minimize windthrow), all snags &gt;38 cm dbh.</td>
<td>Retained all trees &gt;76 cm dbh.</td>
</tr>
<tr>
<td><strong>Spacing criteria</strong></td>
<td>Determined based on the diameter of the larger tree, according to the function ( S = 5 + dbh ) where ( S ) = spacing in feet and ( dbh ) is determined in inches; however, mandatory tree retention criteria was given priority over tree spacing guidelines.</td>
<td>Applied only to trees &lt;76.2 cm dbh; specific criteria were to leave the largest dominant and codominant trees at 5.5- to 7.6-m spacing, regardless of species, to retain the tree with the greatest live crown ratio, and to leave trees similar in size and within 0.6 m of chosen retention trees to minimize windthrow.</td>
</tr>
</tbody>
</table>

Table 4.1. Summary of thinning protocol implemented at the Goosenest Adaptive Management Area. Information presented below was summarized from Ritchie (2005) (*dbh = diameter at breast height; 1.37 m above ground level*).
<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>Pine-preference</th>
<th>Size-preference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pre</td>
<td>Post</td>
<td>Pre</td>
</tr>
<tr>
<td>Basal area (m²/ha)</td>
<td>35.4 ± 4.3</td>
<td>44.0 ± 7.9</td>
<td>30.3 ± 3.5</td>
</tr>
<tr>
<td>QMD (cm)</td>
<td>28.4 ± 1.8</td>
<td>29.0 ± 1.5</td>
<td>42.0 ± 1.3</td>
</tr>
<tr>
<td>Percent fir by basal area</td>
<td>59 ± 4</td>
<td>50 ± 3</td>
<td>29 ± 4</td>
</tr>
<tr>
<td>Tree density (trees/ha)</td>
<td>575 ± 106</td>
<td>685 ± 147</td>
<td>215 ± 13</td>
</tr>
<tr>
<td>$P. ponderosa$ density (trees/ha)</td>
<td>286.5 ± 63.8</td>
<td>--</td>
<td>154.8 ± 30.5</td>
</tr>
<tr>
<td>Density of trees &gt;61 cm dbh (trees/ha)</td>
<td>4.2 ± 0.5</td>
<td>--</td>
<td>17.3 ± 5.8</td>
</tr>
<tr>
<td>Density of trees &lt;10 cm dbh (trees/ha)</td>
<td>102.7 ± 13.1</td>
<td>--</td>
<td>11.5 ± 3.6</td>
</tr>
</tbody>
</table>

Table 4.2. Forest structure before and after thinning at the Goosenest Adaptive Management Area. Data presented was summarized from Ritchie (2005) and represent means ± standard error of the three units per treatment that were used in this study. QMD = quadratic mean diameter (cm). Data not recorded for pre-treatment conditions is indicated by --.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Full Model</th>
<th>Treatment</th>
<th>Units/Treatments</th>
<th>Elevation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Inorganic N</td>
<td>67.80***</td>
<td>88.10***</td>
<td>0.89</td>
<td>1.21</td>
</tr>
<tr>
<td>Soil pH</td>
<td>6.63***</td>
<td>7.29***</td>
<td>4.95***</td>
<td>0.24</td>
</tr>
<tr>
<td>Available P</td>
<td>6.29***</td>
<td>0.56</td>
<td>6.62***</td>
<td>0.63</td>
</tr>
<tr>
<td>Soil Organic C</td>
<td>4.08***</td>
<td>1.02</td>
<td>0.97</td>
<td>0.09</td>
</tr>
<tr>
<td>Soil Total N</td>
<td>3.17**</td>
<td>0.32</td>
<td>2.15*</td>
<td>0.01</td>
</tr>
<tr>
<td>Soil C:N Ratio</td>
<td>3.40**</td>
<td>8.38***</td>
<td>3.07**</td>
<td>0.01</td>
</tr>
<tr>
<td>Forest Floor C</td>
<td>2.80*</td>
<td>0.35</td>
<td>3.03**</td>
<td>1.34</td>
</tr>
<tr>
<td>Forest Floor N</td>
<td>60.85***</td>
<td>17.34***</td>
<td>41.17***</td>
<td>0.09</td>
</tr>
<tr>
<td>Forest Floor C:N Ratio</td>
<td>20.86***</td>
<td>4.69*</td>
<td>10.07***</td>
<td>0.01</td>
</tr>
<tr>
<td>Acid Phosphatase</td>
<td>6.07***</td>
<td>6.15**</td>
<td>3.68**</td>
<td>0.04</td>
</tr>
<tr>
<td>Chitinase</td>
<td>3.92***</td>
<td>8.57***</td>
<td>1.65</td>
<td>0.04</td>
</tr>
<tr>
<td>Phenol Oxidase</td>
<td>7.06***</td>
<td>0.83</td>
<td>6.40***</td>
<td>5.52*</td>
</tr>
</tbody>
</table>

Table 4.3. Analysis of covariance of selected soil properties. Main effects in the model were treatment and units within treatments, with elevation as a covariate. F statistics for all model components are given with significance indicated as: *=p<0.05, **=p<0.01, ***=p<0.001.
Figure 4. 1. Map of the Goosenest Adaptive Management Area in northern California showing the placement of treatment units for the Little Horse Peak study. Units used in this study were Size-preference units 1, 11, and 14, Pine-preference units 5, 9, and 12, and Control units 4, 10, and 18. Darker lines represent logging roads and lighter lines 50 m elevation contours.
Figure 4.2. Photographs showing range of conditions in treatments at the Goosenest Adaptive Management Area, Klamath National Forest, CA. Top row: Control; middle row: Pine-preference; bottom row: Size-preference. Photographs taken in 2004 by J.R. Miesel.
Figure 4.3. Total inorganic N (TIN, mg N/kg soil), soil pH, and plant available P (μg P/kg soil) in soils of two thinning protocols and unthinned controls. Means of $n=3$ and standard errors of the means are shown. Histogram bars with the same lower case letter were not significantly different at $p<0.05$ in three way comparisons.
Figure 4. Soil organic C content (g C/kg soil), total soil N (g N/kg soil), and soil C:N ratio in soils of two thinning protocols. Means of $n=3$ and standard errors of the means are shown. Histogram bars with the same lower case letter were not significantly different at $p<0.05$ in three way comparisons, whereas * indicates a significant difference between the two thinning treatments only at $p<0.05$. 

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Figure 4.5. Phenol oxidase, acid phosphatase, and chitinase activity (mmol/kg soil/hr) in soils of two thinning protocols. Means of $n=3$ and standard errors of the means are shown. Histogram bars with the same lower case letter were not significantly different at $p<0.05$ in three way comparisons, whereas * indicates a significant difference between the two thinning treatments only at $p<0.05$. 

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Figure 4.6. Forest floor organic C and total N content (g/kg soil) and C:N ratio in forest floor of two thinning protocols. Means of \(n=3\) and standard errors of the means are shown. Histogram bars with the same lower case letter were not significantly different at \(p<0.05\) in three way comparisons.
Figure 4.7. NMS ordination of twelve soil properties among six treatment units representing two thinning treatments and eight unit-year combinations representing unthinned controls. The proportion of total variance in the site-soil parameter matrix explained by each axis is indicated in parentheses. Linear correlations between axis scores and soil variables significant at $p<0.05$ are shown.
CHAPTER 5
FOLIAR RESPONSES OF PONDEROSA PINE AND WHITE FIR TO THINNING AND PRESCRIBED FIRE

Introduction

Mixed-conifer forests in northern California today support a much greater stem density than did their historic counterparts. Early land survey records and photos, as well as recent dendrochronological analyses depict open stands dominated by large pines (Agee 1993, Skinner and Chang 1996, Taylor 2000). Low-intensity surface fires that occurred once every 2-15 years (Agee 1993, Weaver 1951) maintained dominance by thick-barked, fire-resistant pines, and limited the growth of shrubs and understory trees.

Heavy grazing, logging, and fire suppression have drastically altered the historic fire regime (Weaver 1951, Agee 1993), and forests that were once open and park-like (Laudenslayer and Darr 1990, Covington and Moore 1994) now support a dense understory of shade-tolerant species such as *Abies concolor*. Because the availability of vegetation and other fuels for fire are much greater in these modern forests, fires that do occur are of much greater intensity and severity than were historical fires (Covington 2000, Agee and Skinner 2005), and these conditions are predicted to become further exacerbated in the absence of management intervention (Fulé et al. 2004).
Management strategies such as mechanical thinning or prescribed fire may reduce stem density to a level that approximates the historic condition, and this has been shown to effectively reduce fire severity (Agee and Skinner 2005). Thinning and burning have each been shown to alter soil nutrition by reducing plant competition or converting nutrients in organic material to forms directly available for plant uptake (Raison 1979, Prescott et al. 1992, Parsons et al. 1994), and these changes in turn may influence the nutrient status in live vegetation that remains. For example, foliar nutrition of conifers has been positively correlated with soil nutrients (Wang and Klinka 1997), and foliar N concentration in conifers has been shown to exhibit significant increases following thinning or prescribed fire (Miller et al. 1976, Feeney et al. 1998, Amponsah et al. 2005), while foliar P may increase or decrease (Feeney et al. 1998, Thibodeau et al. 2000, Skov et al. 2004); these responses can precede (Amponsah et al. 2005) or positively correlate with (Wang and Klinka 1997) increases in stem height and diameter growth.

In addition to effects on foliar nutrient concentration, forest management activities may impact needle length and retention. McDonald et al. (1992) report correlations between 1-yr old needle length and stem height and diameter for *P. ponderosa* seedlings following manual and chemical treatments that reduced competition from surrounding vegetation. An increase in available nutrients may decrease conifer needle longevity in long-term fertilization treatments (Balster and Marshall 2000), and some studies suggest that this results from a fertilization-induced nutrient imbalance (see Amponsah et al. 2005); however, site characteristics also influence needle retention (Amponsah et al. 2005). Because the amount (Miller et al. 1976) and frequency
(Amponsah et al. 2005) of fertilization also influences the response of foliar nutrient concentration, comparisons of treatments designed to maximize forest productivity with those designed to increase long-term ecosystem stability and functioning in natural areas provide limited information for forest managers.

Together, these studies suggest that foliar responses may indicate responses to thinning and prescribe fire that precede responses in stem diameter growth; however, neither the actual response of foliage to treatments, nor the applicability of these responses to predictions of future tree growth and carbon sequestration has been determined in western mixed conifer forests. For example, many studies report changes in *P. ponderosa* foliar nutrient concentration following management activities, yet most address changes in juvenile, rather than mature, conifers, and none have addressed the time course of change in foliar nutrient concentration in the years following treatment. Furthermore, the impact of forest restoration activities on foliar nutrition of *A. concolor* has been largely ignored, in spite of this species’ presence in both modern and historical forests.

The primary objective of this study was to test the hypothesis that large-scale thinning and prescribed fire for forest restoration impact the nutritional status of mature trees. Specifically, this study addressed the following questions: At what point in time following restoration treatments are significant changes in N and P concentrations evident in conifer needles? and, How does a response in foliar nutrition vary (1) between two species that differ in historical and modern dominance, and (2) across a suite of experimental restoration treatments? I hypothesized that: (1) an initial increase in foliar
N concentration will be evident (relative to a control) in a particular age class of needles, indicating the time in growing seasons after treatment at which available nutrients were allocated to foliage, (2) a change in P concentration will be evident in the same needle age class as that which exhibited an increase in N concentration, and (3) because the two species differ in shade tolerance, ability to acquire nutrients, and life histories, foliar nutrient response of *Abies concolor* will differ from the response of *Pinus ponderosa*.

To evaluate these hypotheses, I sampled foliage from dominant *P. ponderosa* and *A. concolor* from experimental treatments that were conducted between 1998-2002 for two large-scale forest restoration studies in the Klamath National Forest of northern California. Because nutrient concentrations in evergreen conifers decrease with needle age due to nutrient resorption from older needles (Tyrrell and Boerner 1987, Amponsah et al. 2005); I evaluated foliar N and P concentration for each existing age class of needles for mature *P. ponderosa* and *A. concolor*, relative to needles from trees in an untreated control.

**Methods**

**Study Site**

This study took place in the Goosenest Adaptive Management Area (GAMA) of the Klamath National Forest in Siskiyou County, California (lat 41°35’N, long 121°53’W). The forests of GAMA were logged between 1900 and 1920, and all merchantable trees were removed over large areas. The gentle, dissected landscape of GAMA is the result of recent volcanic activity. Slopes are generally <10% but can locally
be >50%, with elevation ranging from 1500 to 2000 m. *Pinus ponderosa* P. & C. Lawson (ponderosa pine) and *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir) are dominant in the forest canopy, together typically comprising >90% of the basal area. *P. lambertiana* Dougl. (sugar pine), *Calocedrus decurrens* (Torr.) Florin (incense cedar), *Abies magnifica* A. Murr. var. *shastensis* Lemmon (Shasta red fir), and *P. contorta* Dougl. ex Loud. var. *murrayana* (Grev. & Balf) Englem. (Sierra lodgepole pine) are also present at low density. The shrub layer is sparse, ranging in cover from 0.0 to 5.4% of the ground area. Shrubs present include *Ceanothus* spp. (ceanothus), *Arctostaphylos* spp. (manzanita), *Purshia tridentata* (Pursh) DC. (antelope bitterbrush), *Cercocarpus ledifolius* Nutt. (curl-leaf mountain mahogany), *Chrysothamnus* spp. (rabbitbrush), and *Artemisia* spp. (sagebrush) (USDA Forest Service 1996). Forb and grass cover ranged from 3.2 to 18.3%, and averaged 8.5% among our treatment units.

The historical fire regimes of the southern Cascade range were characterized by frequent, low-intensity fires in the low to middle elevations and mixed-intensity fires in the upper montane (Taylor 2000; Skinner and Taylor 2006). Fire has largely been excluded from the forests since the early logging, and this has likely intensified the alteration of stand structure through eliminating the thinning effect of fire on developing stands.

The soils of the experimental area are dominated by the Belzar–Wintoner complex of inceptisols and alfisols (USDA Forest Service 1982). The Belzar series of loamy-skeletal, mixed, frigid Andic Xerochrepts covers the great majority of the study area. Interspersed within the matrix of Belzar series soils are areas of somewhat thinner.
pumice deposits in which the Wintoner series (pumice overburden phase) of fine-loamy, mixed, frigid Ultic Haploxeralfs are mapped. Both of these soil types have high silt and sand content, drain rapidly, have relatively low water-holding capacity, and are relatively low in nutrient availability. The climate is Mediterranean-type, and the study site receives most of the 25–100 cm annual precipitation as winter snowfall (USDA Forest Service 1996).

**Experimental Design**

The Pine-preference Thin (hereafter Pine-preference), Size-preference Thin (hereafter Size-preference), and Pine+Fire treatments, as well as the untreated Control are part of the Little Horse Peak Interdisciplinary Study, a long-term ecological study initiated in 1998; each of these treatments was randomly assigned to five 40-ha replicate units (Figure 5.1). Three 10-ha Fire-only (hereafter Fire) treatment units were interspersed among the LHPIS units in 2002, when the national Fire and Fire Surrogate network study was overlain on the LHPIS study. All units (LHPIS and FFS) were located on a predominantly northwestern aspect. Elevation ranges among units within each treatment were: Control, 1508–1692 m, Size-preference 1485–1578 m, Pine-preference 1560–1666 m, Pine+Fire 1580–1715 m, and Fire 1499-1683 m (Figure 5.1).

Whole-tree harvesting methods were applied to Pine-preference, Size-preference, and Pine+Fire treatments and processing followed standard harvesting procedure for forests in this region. Thinning prescriptions reduced understory density, and selectively removed shade tolerant species such as white fir (Table 5.1). Whole trees were
transported to central processing landings where all boles, limbs, and tops of trees 10.2-
45.7 cm dbh were removed and logs cut to appropriate length for hauling to processing
plants. Limbs and tops of trees were sorted and either chipped at landings and shipped
for pulp, or shipped for electricity generation; thus, all the slash generated by the thinning
was removed from the units. All damaged trees were removed. Sub-merchantable
understory trees were hand-cleared from both treatments within one year after larger trees
were thinned from below; this material was scattered on site. A more thorough
discussion of thinning treatment prescription and pre- and post-treatment stand conditions
is provided by Ritchie (2005).

The Pine-preference and Size-preference treatment units used in this study were
thinned in 1998 and 1999 (one unit of each treatment was thinned in each year).
Pine+Fire units were thinned in 1999 following the protocol for Pine-preference units,
and were followed by a prescribed fire in late autumn 2001. The Fire treatment consisted
of a prescribed burn in late autumn 2002. Stand structure was not modified mechanically
prior to burning in Fire treatment units. Firing techniques used in the prescribed burning
were strip-head firing and tree-centered spot ignition (Weatherspoon et al. 1989).
Weather and fuel moisture conditions (air temperature Fire 6 ± 5 ºC (mean ± standard
deviation), Pine+Fire 12 ± 5 ºC; relative humidity Fire 24 ± 13%, Pine+Fire 32 ± 16 %;
wind speed Fire 1.7 ± 1.3 km/hr, Pine+Fire 2.6 ± 1.6 km/hr) combined with the ignition
pattern to produce a low-intensity, surface fire (flame length Fire 24 ± 11 cm, Pine+Fire
40 ± 18 cm).
Field Methods

I sampled branches from the upper 1/2 to 1/3 of the tree crown of mature, dominant *Pinus ponderosa* (hereafter PIPO) in 2005 and *Abies concolor* (hereafter ABCO) in 2006. Branches were removed from PIPO trees at 6 randomly-selected locations within each of 2 units for each treatment, for a total of 12 trees for each of the 5 experimental treatments. *Pinus ponderosa* branches were removed with a 0.22 rifle operated by a Forest Service sharpshooter. *Pinus ponderosa* needle cohorts were identified by terminal bud scars, removed from branches at the end of the day in which the branch was sampled, and returned to the lab to dry at ambient temperature to constant mass. Branches were removed from ABCO trees at 4 randomly-selected locations within each of the same 2 units used for PIPO samples, for a total of 8 trees for each of the 5 experimental units. *A. concolor* branches were obtained by professional arborists using single-rope, soft climbing technique to minimize damage to trees. *Abies concolor* needle cohorts of ages 0-10 yr were identified by branch coloration and terminal bud scars, and each section of annual shoot growth containing a cohort of needles was separated from the branch. Clipped sections of annual shoot growth and the attached needles were returned to the lab and allowed to dry at ambient temperature, at which time dry needles were separated from sections of shoot growth.

Although ABCO and PIPO litter was collected from the base of every sampled ABCO or PIPO tree, respectively, it was not possible to exclude older litter from current-year litter for either species. Litter samples were processed and analyzed with the same
procedures used for needle samples; however, many samples showed extreme N or P concentrations, and, because of the uncertain age of needles in the samples, litter analyses were eliminated from this study.

**Laboratory Methods**

For both species, each cohort sample of needles was measured for average length (cm) of 3 randomly-selected needles, and the mass of 100 needles, before grinding to pass a 2 mm screen. I digested 100 mg of each ground sample in concentrated H$_2$SO$_4$ at 390°C for 1 hr in an aluminum block digester, then diluted each sample to 50 ml with deionized water. I analyzed digested samples for concentration of N (mg/g) using the microtiter methods of Sims et al. (1995) and concentration of P (mg/g) by the stannous chloride/molybdate colorimetric method (APHA 1976) adapted for microplate.

I calculated nutrient resorption as the difference in nutrient concentration (mg nutrient/g leaf tissue) and as nutrient content per unit leaf length (mg/cm) between the youngest and oldest living needle cohorts, and calculated resorption efficiency as the proportion of nutrient resorption over the nutrient concentration (or content) in the youngest cohort of needles.

**Measurements of Cone Production and Needle Length**

Because preliminary exploration of my data showed that ABCO needle length varied dramatically in alternate years, in August 2008 I measured needle length by year of production and position on the main stem, and recorded presence of male and female
cones (or evidence of past presence of cones) on two mature, recently blown-down trees, and on four discarded tops of mature trees obtained from a logging site near the GAMA, for a total of $N=64$ observations of annual shoot growth bearing evidence of female cones, $N=27$ observations of annual shoot growth with evidence of male cones, and $N=119$ observations of annual shoot growth with no signs of cones.

**Data Analysis**

The unit of replication for this experiment was the treatment unit ($N=2$) for each treatment. Although both species of trees were sampled from the same treatment units, they were sampled in different years, and species were therefore analyzed independently. For PIPO, I sampled 6 trees within each treatment unit within each treatment ($N=60$). For ABCO, I sampled 4 trees within each treatment unit within each treatment ($N=40$). I sampled needle cohorts from current year’s growth to 7 years for PIPO and to 10 years for ABCO.

I used vector analysis to evaluate tree N and P status in response to treatments, using nutrient concentration ($g/g$), sample dry mass ($g$) and nutrient content [nutrient concentration ($g/g$) x dry mass ($g$)] relativized to Control values, following Haase and Rose (1995). Vector diagrams are 3-dimensional graphical representations of treatment effects that allows plant growth, nutrient concentration and nutrient content to be evaluated simultaneously (Haase and Rose 1995), revealing responses (e.g., nutrient dilution) that may not be evident via analysis of nutrient concentration alone (Timmer and Armstrong 1987). Responses in tree nutrient status, relative to the untreated Control,
are represented as vectors that originate from the reference point of the Control; the
nutrient response (dilution, sufficiency, deficiency, or excess) is indicated by the
direction and magnitude of the vector (Timmer and Armstrong 1987).

Because the Size-preference and Pine-preference treatments each had one unit
thinned in 1998 and one in 1999, I also analyzed differences among treatments using the
units from each of these treatments that were thinned in 1998 only, followed by a
separate analysis using units that were thinned in 1999 only. These analyses showed that
differences in foliar N and P concentration between needles from the Control and units
thinned in separate years did not occur at a consistent time since treatment, and
statistically significant differences in foliar N concentration did not persist for
consecutive years; thus, it is unlikely that the different years of thinning within the Size-
preference and Pine-preference treatments affected determinations of statistical
significance among treatments when units thinned in separate years were combined.
Further, the pattern of difference between units within the two thinning treatments was
consistent across cohorts, suggesting that foliar characteristics are also affected by site-
specific factors, and both units within each treatment were therefore combined in all
analyses.

When using the complete dataset, data for ABCO 2003 and 2004 needle P
concentration, and ABCO 1997 needle mass were log-normally distributed; PIPO 1999
needle length was converted to normality using a sin transformation. Data for ABCO
2000 needle P concentration did not conform to normality under any standard
transformations and were therefore ranked before analysis; all other variables were
normally distributed.

For each cohort of needles for each species, I performed a one-way analysis of
variance (ANOVA) with variance partitioned among treatments and units within
treatments (PROC GLM, SAS 2004). I used the Ryan-Einot-Gabriel-Welsch Multiple
Range test for means separation among all treatments, as this approach minimizes the risk
of Type I errors (SAS 2004); however, I used Student’s t-test with Dunnett’s adjustment
for multiple comparisons when comparing individual treatments to the control (SAS
2004). Statistical significance is reported at \( P=0.05 \) unless indicated otherwise.

To examine the relationship between needle length and timing of cone production,
I used a Student’s t-test to determine differences in length of needles produced in cone
years and those produced in non-cone years, separately for needles in the female, male,
and non-reproductive zones of the tree. Needle length data in the female zone of the tree
data were square-root transformed to achieve normality; needle length data in male and
non-reproductive zones were normally distributed.

**Results**

**Foliar N and P Concentrations and Nutrient Resorption**

Foliar N and P concentration (hereafter, foliar [N] and [P]) decreased with needle
age in PIPO and ABCO in all treatments (Figure 5. 2). There were no among-treatment
differences in PIPO or ABCO N or P nutrient resorption or N or P resorption efficiency
when calculated on either a nutrient concentration (mg/g) or nutrient content per unit leaf length (mg/cm) basis. Averaged across all treatments, nutrient resorption between the youngest and oldest needle cohorts was 4.89±0.31 mg/g and 3.06±0.33 mg/g for PIPO and ABCO [N], respectively, and 0.99±0.04 mg/g and 0.74±0.05 mg/g for PIPO and ABCO [P], respectively. Both species had a much greater efficiency of P resorption between first-year and the oldest needle cohorts (48±1% and 45±2% for PIPO and ABCO, respectively) than of N resorption (33±2% and 25±2% for PIPO and ABCO, respectively), when data were averaged across all treatments (data not shown).

Nutrient Concentrations by Needle Age

When all sampled units were included, 2005 was the only cohort of needles in which ANOVA indicated that differences in PIPO foliar [N] among treatments existed, although the conservative means separation I used failed to indicate significant differences among treatment means for this cohort (Figure 5.3, Table 5.2). In contrast, PIPO foliar [P] differed among treatments in the 2004, 2003 and 2002 cohorts (Figure 5.4, Table 5.2). In the 2004 cohort of PIPO needles, foliar [P] was greatest in the Size-preference treatment and lowest in the Pine-preference treatment; however, the concentration in the Size-preference treatment was 4% greater than that in the Pine-preference treatment, and neither of these treatments differed significantly from the Control, Fire, or Pine+Fire treatments (Figure 5.4, Table 5.2). In contrast, PIPO foliar [P] in needles formed in 2003 was greatest in the Control and was 15% and 3% lower in the Pine-preference and Pine+Fire treatments, respectively; these treatments did not differ
significantly from the Fire or Size-preference treatments (Figure 5.4, Table 5.2). Analysis of variance for PIPO foliar [P] of needles formed in 2002 indicated that significant variation existed among treatments as well as among units, although the conservative means separation I used failed to indicate significant differences among treatment means for this cohort (Figure 5.4, Table 5.2). There were no differences in ABCO foliar [N] or [P] in any year (Table 5.2).

When using both units of each of the Size- and Pine-preference thinning treatments in analysis of the full suite of treatments, I expected to see a difference in foliar nutrient concentration relative to the Control in needles formed in 2000, which is the year that coincided with the 1st post-treatment growing season for units thinned in 1999 and the 2nd post-treatment growing season for the units thinned in 1998; however, there were no differences in N or P concentration between either the Pine-preference or Size-preference treatment and the Control in needles formed in 2000, for PIPO or ABCO (Table 5.2).

Needle Length and Mass

Average length and mass of PIPO needles varied among treatments for each cohort of needles formed from 2001-2004. In general, thinning treatments increased PIPO needle length and mass relative to the Control, whereas the use of fire alone did not (Figure 5.5, Table 5.2). In the cohort of needles produced in 2001, length and mass in all treatments that involved thinning was 22% and 45% greater than the Control, whereas
the mass of needles from the Fire treatment did not differ significantly from that of needles produced in any of the thinned treatments or the Control (Figure 5.5, Table 5.2).

This pattern persisted in needles produced in 2002, with the exception that neither length nor mass of needles from the Fire treatment differed significantly from needles produced in any of the other treatments, including the Control (Figure 5.5, Table 5.2). In the 2002 cohort, the average difference in length and mass between the thinned treatments and the Control was 17% and 35%, respectively (Figure 5.5, Table 5.2).

For the cohort of needles produced in 2003, only needles from the Size-preference treatment differed significantly from the Control for needle length and mass (by 17% and 31%, respectively) (Figure 5.5, Table 5.2). The length of needles produced in 2004 was 14% and 13% greater in the Size-preference and Pine+Fire treatments, respectively, than Control needles, and the length of Fire and Pine-preference treatment needles did not differ significantly from Control needles (Figure 5.5, Table 5.2). Mass data for the 2004 cohort followed the pattern of differences shown for needle length, with the exception that the mass of needles from the Fire treatment was also greater (by 30%) than Control needle mass (Figure 5.5, Table 5.2). PIPO needle length increased over time for the years represented by needle cohorts used in this study; however, regression analysis indicated that the relationship was weak \( y = 0.33x - 640.49, r^2=0.06; p<0.0001 \) (Figure 5.6).

ABCO needle length varied among treatments for the cohort of needles produced in 2000 only, with the longest needles produced in the Size-preference treatment and shortest needles in the Pine+Fire treatment (Figure 5.7, Table 5.2). Needle length in the
Control, Fire, and Pine-preference treatments did not differ from each other or from the Size-preference or Pine+fire (Figure 5.7). There were no differences in needle mass among treatments within any cohort of ABCO needles (Table 5.2).

The length of ABCO needles alternated distinctly between long and short lengths in successive years, and this pattern was consistent among all treatments (Figure 5.6). In contrast to PIPO, ABCO needle length showed a significant decrease over the course of time represented by the needle cohorts collected for this study (p<0.02); however, the year in which each cohort of needles were produced explained almost none of the variation in needle length (r²=0.01). Needles borne on annual shoot growth that also produced female or male cones were significantly longer than needles on shoot growth from years in which no cones were produced (p<0.0005 and p<0.0027 for female and male, respectively), whereas needles produced in the lower, non-reproductive zone of the crown did not differ in length between years in which the tree produced female cones and years in which no cones were produced (p<0.3228) (Figure 5.8). Needles from the non-reproductive zone vary in length among cohorts of needles produced between 2000-2008 (p<0.0001; data not shown); however, the pattern of variation across years appeared random, and did not exhibit the regularly alternating pattern between long and short needle lengths that is evident in the mid- and upper-crown of the tree.
In general, cones (or stalks of shattered female cones) were present in alternate years, and short-needled segments of branch growth immediately followed longer-needled segments of growth, suggesting that needles produced in cone years receive a portion of the resources directed towards cone development; however, one of the trees I sampled produced female cones for five successive years.

**Nutrient Content**

Analysis of variance indicated that differences in nutrient content existed in the PIPO needle cohorts produced in 2001 and 2004; however, the conservative means separation test we used indicated that the differences in P content among treatments were not statistically significant in 2004 (Table 5.2). The N content in PIPO needles produced in 2001 was 56% greater in the Pine-preference treatment than the Control, and the Fire, Size-preference, and Pine+Fire treatments did not differ from each other or from the Pine-preference and Control treatments (data not shown). There were no significant differences in ABCO N or P content for any cohort of needles (Table 5.2).

**Vector Analysis**

Vector diagrams indicate that the pattern of response in nutrient status differed strikingly between PIPO and ABCO current-year needles formed in 2005 and 2006, respectively (Figure 5.9). The trend in PIPO nutrient status in trees from treated units was a decrease or no change in relative nutrient concentration, an increase in dry mass, and an increase in nutrient content, suggesting a trend towards dilution of N and P.
concentration as needles increased in mass, relative to the Control. The magnitude of response was similar among treatments, with the exception of the Pine+Fire treatment P vector, which indicated a greater increase in needle mass and P content relative to all other treatments (Figure 5. 9a,b).

In contrast, the vector diagram for ABCO shows that needles from trees in treated units tended to increase or remain the same in nutrient concentration and decrease in dry mass and nutrient content, relative to the Control (Figure 5. 9c,d). The only exceptions to this pattern were the Fire and Size-preference treatments, which showed an increase in P concentration, no change in needle dry weight, and an increase in P content, relative to the Control (Figure 5. 9c,d). It is important to keep in mind, however, that these diagrams are limited to suggesting trends only for treatment responses to thinning and burning in current-year needles. As noted earlier, none of the differences in N or P concentration or needle dry mass suggested by the vector diagrams were statistically significant for either species (Table 5. 2).

Discussion

The primary objective of this study was to test the hypothesis that large-scale thinning and prescribed fire for forest restoration impact the nutrient status of mature Pinus ponderosa and Abies concolor in a northern California mixed-conifer ecosystem. Thinning was conducted between 1998-1999, and prescribed burns were conducted in 2001 and 2002 (for the Pine+Fire and Fire treatments, respectively). I found that among-treatment differences in needle nutrient concentration occurred in PIPO only, and
were evident in needle cohorts produced in 2002 – 2005. Where differences among treatments occurred, PIPO foliar [P] was reduced or unaffected by treatments, relative to the Control. There were no statistically significant differences in PIPO foliar [N]; however, there was a trend toward lower foliar [N] in PIPO current-year (2005 cohort) needles from the Fire and Pine+Fire treatments, which may be due to nutrient dilution, if leaf biomass responds to treatment more rapidly than nutrient uptake. For example, PIPO N content in the 2001 cohort of needles in the Pine-preference treatment relative to the Control, and this effect coincided with increased needle length and mass, and preceded any changes in nutrient concentration.

In general, fire increases N availability in soils in the short term (e.g., Vlamis and Gowans 1961, Antos et al. 2003), and analyses of changes in soil N availability between pre- and post-fire conditions in these treatments show increased N availability post-fire in the Fire and Pine+Fire treatments (Chapter 3). Many studies, however, have shown that fire-induced increases in soil N availability are transient, and analyses of sequential soil samples at the GAMA show that the increase in soil N availability in burned areas does not persist beyond the first growing season post-fire (Chapter 2). Because soil N availability has been shown to be directly related to foliar N concentration or content (e.g., Wang and Klinka 1997, Proe et al. 2000, Carswell et al. 2003), it would thus be likely that the Pine+Fire and Fire treatments would exhibit greater foliar [N] than other treatments in the cohorts formed in the year following prescribed fire in each treatment. I did not, however, observe increased foliar [N] in either species, for any cohort of needles. Because each of these treatments involved the application of low-intensity fire in late
Autumn 2001 and 2002, respectively, the pulse of soil N produced by the prescribed fires in these treatments may have been lost prior to uptake in the spring due to leaching as winter snowpack melted in the spring of the following year, metabolized by soil microbes, or taken up by grasses and other herbaceous plants. Alternatively, because the prescribed fires were of low intensity, the pulse of soil N they produced may have been too small in magnitude to create a detectable difference for tree growth. Further, the design of this study prevented me from identifying whether differences in foliar [N] did in fact occur in the Fire and Pine+Fire treatments, but were subsequently reduced by the effects of nutrient translocation. For example, Gough et al. (2004) showed that fertilization-induced increases in loblolly pine seedling foliar N concentration decreased to pre-fertilization levels just 100 days after treatment, and attributed this result to nutrient translocation. These authors did, however, note that fertilization-induced increases in seedling height and diameter growth persisted (Gough et al. 2004).

With the exception of ABCO P resorption efficiency, nutrient resorption efficiency for both species was within the range of mean values for evergreen trees and shrubs (46.7% ± 16.4% for N; 51.4% ± 21.7% for P) reported by Aerts (1996), and both PIPO and ABCO exhibited greater resorption efficiency for P than for N. There were no differences in PIPO or ABCO N or P resorption efficiency among treatments in this study, and Aerts (1996) reports that, in most cases of increased nutrient supply, nutrient resorption efficiency of evergreen species either remains unchanged or decreases.

Although TIN increased in the short term following prescribed fire (Chapter 3), fires also consume litter, duff and woody debris on the forest floor; thus, it is also
possible that burned treatments may experience a decrease in soil N over the intermediate
term due to the elimination of organic material otherwise available for decomposition.
Further, herbaceous and/or shrubby species that establish or increase in opened stands
may decrease the N available for tree uptake; at the GAMA site, however, this would be
more likely in the thinned and burned Pine+Fire treatment than in the unthinned Fire
treatment units, which remained heavily shaded in 2005 by standing, dead stems of
young ABCO trees killed by the prescribed fire in 2002, as well as by live stems that
survived the fire. PIPO foliage in Fire and Pine+Fire treatments may therefore show a
trend towards decreased [N] due to lower soil N relative to other treatments that results
from either reduced mineralization of organic matter, increased competition by
herbaceous and shrubby species, or both; however, the foliar [N] of current-year, upper
crown needles of both species used in this study were above the level that has been
suggested to indicate deficiency in conifers (Leaf 1973, Oliver and Ryker 1990).

Powers (1980) reported that growth of Pinus and Abies species in northern
California increased on nutrient poor (<16 mg/kg mineralizable N), frigid, volcanic or
metasedimentary soils in response to fertilization with 224-448 kg N/ha, whereas there
was no growth response on soils of greater (≥19 mg/kg mineralizable N) nutrient
availability. Because the GAMA soils fit these criteria, it is likely that an increase in
available soil N would contribute to a growth response in PIPO and ABCO if the
magnitude of increase due to treatment was sufficient. For example, burning increased
total inorganic N (TIN) in soil from Fire and Pine+Fire treatments in the first year
following prescribed fire by 327±133 kg N/ha and 207±31 kg N/ha; however, by 2-3
years post-burn, the change relative to pre-burn levels was 9±20 kg N/ha in the Fire
treatment and -25±13 kg N/ha in the Pine+Fire treatment (Boerner et al., 2009). In
contrast, the magnitude of change in TIN as a result of thinning alone in the Pine-
preference treatment ranged from an increase of 22±1 kg N/ha to a decrease of 13±16 kg
N/ha between 2002 and 2004 (Boerner et al. 2009).

In general, PIPO needle length at the GAMA was increased by all treatments that
involved thinning in every cohort formed between 2000-2004, indicating that a growth
response to release from competition occurs within 1-2 years post-treatment, and
continues at least 5 years post-treatment. Likewise, McDonald et al. (1992) showed that
current-year needle length is positively correlated with Pinus ponderosa seedling height
and diameter growth 2-4 years following treatments that reduced competition for
resources. The variation among units within treatments (specifically, in the Control and
Fire treatments) in the current-year (2005) cohort of needles may explain why differences
in PIPO needle lengths among treatment were not statistically significant.

The small, but statistically insignificant, increase in PIPO needle length and mass
in the Fire treatment in each cohort was likely due to reduced competition for resources
that result from the reduction of live stems by the fire, without the subsequent
establishment of abundant shrubs, forbs and grasses that occurred in thinned stands. The
reduction in live stem density due to thinning, averaged across each of Size-preference
and Pine-preference units used in this study, was 295±119 stems/ha (Ritchie 2005),
whereas the reduction in live stems in the Fire treatment 2 years post-burn was 209±50
stems/ha (C. Skinner, unpublished data).
Personal observation of increment cores obtained from three dominant PIPO in the Size-preference treatment in 2005 showed no obvious increases in diameter growth increments produced following the thinning treatments; however, McDonald et al. (1992) showed that changes in needle length may occur prior to any increase in diameter growth, at least for Pinus ponderosa seedlings. It is important to remember that this study addressed the response of mature, rather than juvenile trees or seedlings. Because the trees used in this study were mature, dominant trees in the forest canopy, their response to release by thinning or prescribed fire may be less pronounced than the response of a subcanopy tree or seedling that experiences a dramatic increase in light availability following stand treatment; however, the sparse occurrence of subcanopy trees and near absence of seedlings currently prevent any comparison of tree response across life stages. It is possible that dominant trees in the GAMA may respond to treatments by initially increasing total leaf biomass, which in turn will contribute to increases in stem diameter growth and increased cone and seed production. For example, Sullivan et al. (2006) has shown that thinning increases crown volume in Pinus contorta stands, and Proe (2000) showed that total biomass of current-year Pinus sylvestris seedlings increased with nutrient availability; however, estimations of changes in leaf biomass at the GAMA would be limited to comparisons of average total foliar biomass between Control and treated areas, and is beyond the scope of this study.

The regularly alternating pattern of ABCO needle lengths, with long needles coinciding with production of female and male cones, suggests that resources directed towards cone initiation are also used by needles produced on the same segment of annual
growth on branches. Although ABCO tends to produce cones in alternate years, one of
the trees sampled for needle length and occurrence of cones had produced female cones
for 5 consecutive years; this tree was located in a Pine+Fire treatment unit, which was an
open stand that likely provided more resources to individual trees than would the more
closed conditions of unthinned areas, where the majority of trees used for this analysis
were located. Because records of ABCO cone production do not exist in this region, I
was unable to correlate needle length with size of cone crops over time; thus, my data is
limited to suggesting a relationship between reproductive and vegetative growth via
needle length and presence or absence of cones on annual shoot growth of lateral
branches. Morris (1951), however, reported a 73% decrease in new foliage for *Abies
balsamifera* in years of abundant cone production, compared to non-cone years.

Similarly, the pattern of PIPO needle length at the GAM shows approximately 6 years
between the production of the shortest and longest needles, and this pattern corresponds
to published records of a 3-8 year cycle between abundant cone production in this and
other *Pinus* species (Oliver and Ryker 1990, Barnes et al. 1998).

Overall, I observed significant effects of treatments on foliar characteristics in
most cohorts of PIPO needles examined, and no effects on ABCO foliar characteristics.
Treatment differences in PIPO foliar characteristics that did occur are likely to result in
positive growth responses for this species; however, in a study of containerized scots pine
(*Pinus sylvestris*) seedlings, Proe et al. (2000) found that the rate of net photosynthesis
per unit needle mass or per unit needle N was not affected by high or low nutrient
conditions. Because ABCO foliar characteristics were, in general, unaffected by treatments, it is not likely that thinning or prescribed fire will increase fir vigor over that of pine.

In contrast to my expectations, the most consistent response to treatments was expressed via increases in needle length and mass, rather than nutrient concentration. Because photosynthetic capacity increases with specific leaf area (see Lambers et al. 1998), as well as N concentration (Reich and Schoettle 1988, Lambers et al. 1998), it is likely that increases in leaf size will lead to increased growth in trees at the GAMA, even in the absence of increased foliar [N]. However, Duursma et al. (2005) found no significant correlation between light-saturated assimilation rate and N concentration for *Pinus ponderosa* or *Abies grandis* in Idaho, although there was a weak correlation when several evergreen species were combined. These authors note that most studies of the photosynthesis-nitrogen relationship have focused on a mixture of plant species, rather than explicitly on coniferous species, which may not be accurately described by generalizations of plant physiological functioning (Duursma et al. 2005).

Because significant variation in foliar characteristics existed between units within treatments, it is likely that localized site factors also influence foliar characteristics; however, the absence of significant differences among treatments in the 1999 cohort of needles supports the view that differences observed in needle cohorts produced post-treatment are due primarily to treatment effects, rather than to specific site factors. It is also possible that nutrient translocation may confound treatment differences; however, I
found no differences in nutrient resorption and resorption efficiency for either species in this study, and a more detailed investigation of nutrient translocation using stable isotopes is beyond the scope of this study.

Because treatments at the GAMA increased needle length and mass relative to the Control, it is possible that trees in treated stands will store more carbohydrates due to increased photosynthesis, relative to their counterparts in unthinned stands. Further, the interaction among site nutrient availability, carbohydrate storage, and precipitation of the previous and current growing seasons may determine the actual growth response. For example, Cook and Jacoby (1977) showed that tree diameter growth is correlated with temperature and precipitation that occurred in the previous year. Annual precipitation recorded at the Goosenest Ranger Station (1300 m elev.), averaged across the 11-year period 1995-2006, was 13.2±0.5 cm (USDA Forest Service 2008). The annual precipitation of the years during which each of the PIPO needle cohorts were formed (1999-2005) was 1.0-5.9 cm below the 11-year average. In contrast, precipitation during 1998 was 4.9 cm above the 11-year average, and no among-treatment differences in PIPO foliar characteristics were observed in 1999; thus, above-average precipitation in the year prior to needle production does not appear to be a causal factor in among-treatment differences in needle characteristics. Similarly, precipitation of the years 1995-1998 was between 2.2-5.7 cm above the 11-year average, and no differences in ABCO foliar characteristics were observed in foliar cohorts produced following these years.

These restoration treatments are designed to either re-create the historical forest structure by thinning, to re-introduce low-intensity fire as a natural disturbance, or to
simultaneously restore historic forest structure and ecosystem processes. Because prescribed fire and thinning each increase the amount of sunlight reaching the forest floor, each of the restoration strategies used in this study has the potential to increase dominance by PIPO in the long term, as shade-intolerant PIPO seedlings establish naturally. Although prescribed fire alone was successful at killing the understory of young white fir, the forest floor in the Fire treatment to date remains more shaded than in treatments that were thinned, due to the standing dead stems as well as live stems that survived the fire. It is likely that the Pine+Fire treatment will result in the greatest (or earliest) recruitment of PIPO seedlings, due to the open nature of the stand combined with the bare mineral soil exposed by the prescribed fire in 2001. To date, however, natural germination of PIPO seedlings is virtually absent.

Because the trees sampled in this study were dominant or co-dominant in the forest canopy, it is not likely that they were greatly light-limited prior to treatment. Vector analysis indicated that PIPO needles experienced nutrient dilution in treated stands, as nutrient concentration decreased or remained constant, while needle mass and nutrient content increased (Timmer and Stone 1978). These responses suggest a positive response by PIPO to restoration treatments, and a potential negative response in ABCO. Because both species were sampled from the same locations within treatment units, these data support Oliver and Ryker’s (1990) statement that PIPO is more efficient at nutrient uptake and has a “superior” ability to satisfy its nutritional needs, relative to other species in nutrient-poor soils. Vector analysis clearly indicates that the two species respond to
treatments in distinctly different directions, although the magnitude of response in nutrient concentration, nutrient content, and dry mass of needles collected in 2005 and 2006 (for PIPO and ABCO, respectively) was not statistically significant.

In conclusion, my results show that the response of foliar characteristics of mature conifers differs between the historically dominant *Pinus ponderosa* and the currently dominant, shade-tolerant *Abies concolor*. I observed the greatest response to treatment in PIPO foliar characteristics, and in general no response in ABCO foliar characteristics. Treatments that involved thinning produced the greatest change in foliar characteristics, relative to Control foliage. Among-treatment differences in needle length and mass became evident within the first two growing seasons following treatment, and persisted, whereas differences in foliar [N] and [P] appear to occur randomly across cohorts. Changes in foliar [N] and [P] did not occur in the same cohort of needles. Thus, it is likely that each of these restoration strategies will increase PIPO growth, thereby facilitating re-establishment of a pine-dominated ecosystem that more closely approximates historical conditions than does current forest structure in much of California’s mixed-conifer ecosystem. Because ABCO foliar characteristics do not appear to be positively or negatively impacted by these treatments, it is unlikely that any of these restoration strategies will preferentially favor ABCO vigor over PIPO.

The vast majority of studies that address conifer growth and nutrient concentration responses to nutrient availability are limited to seedlings, and the applicability of these studies to large-scale forest restoration treatments is relatively limited. Thus, it is of great practical importance to investigate the response of mature
trees to large-scale thinning and prescribed fire that are applied to restore forests to a
desired condition, as changes in the nutrient status and productivity of these trees
determine current and future stand characteristics and ecosystem function. Continued
investigations of the ecological effects of large-scale forest management strategies is
essential to adaptive ecosystem management (Covington 2000), and this study serves to
inform best practices for ecosystem restoration in mixed conifer forests of northern
California.
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Table 5.1. Forest structure in Control and thinned treatments at the Goosenest Adaptive Management Area. Shown are post-treatment means ± standard errors of the two units per treatment that were used in this study (adapted from Ritchie 2005).
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Table 5.2. ANOVA of foliar N and P concentration, needle length and mass, and nutrient content per needle. Main effects of the model were treatment and units within treatments. F statistics for all parameters are given, with significance indicated as * p<0.05, ** p<0.01, *** p<0.001. PIPO = Pinus ponderosa; ABCO = Abies concolor.
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† indicates marginal significance (p<0.06)
Figure 5.1. Map of the Goosenest Adaptive Management Area in the Klamath National Forest, CA, showing placement of treatment units for the Little Horse Peak and Fire and Fire Surrogate studies. Units used in this study were Control units 10 and 18; Fire units F1 and F3, Size-preference units 1 and 14; Pine-preference units 9 and 12; and Pine+Fire units 13 and 15. Darker lines represent logging roads and lighter lines represent 50-m elevation contours.
Figure 5.2. Nitrogen (N) and phosphorus (P) concentration in needles produced in current year and older needles for (A, B) *Pinus ponderosa* (PIPO) and (C, D) *Abies concolor* (ABCO) trees in the Goosenest Adaptive Management Area, Klamath National Forest, CA. All needle cohorts were from branches collected in 2005 (PIPO) and 2006 (ABCO), and 2006 and 2005 represent current-year needles for PIPO and ABCO, respectively. Shown are means ± s.e. for needles from Control unit trees (N=12 for PIPO; N=8 for ABCO); statistical differences between Control and treatment cohort nutrient concentrations are indicated in the text. Note differences in x- and y-axis scaling.
Figure 5.2.

(C) ABCO Control

(D) ABCO Control
Figure 5.3. Means and standard errors of foliar N concentration in *Pinus ponderosa* needles formed in 2005 (current-year needles at time of harvest).
Figure 5.4. Means and standard errors of foliar P concentration in *Pinus ponderosa* needles formed in 2002, 2003 and 2004 (1, 2 and 3 years old at time of harvest, respectively). Letters denote significant differences among treatments within each cohort of needles.
Figure 5. Means and standard errors of *Pinus ponderosa* needle (A) length and (B) dry mass of 100 needles, for needles produced 1997-2006 in each treatment in the Goosenest Adaptive Management Area, Klamath National Forest, CA.
Figure 5.6. Means and standard errors of Pinus ponderosa and Abies concolor needle length for needles produced in each year between 1997-2006 in four treatments and an untreated control in the Goosenest Adaptive Management Area, Klamath National Forest, CA.
Figure 5.7. Length of Abies concolor needles produced in 2000, which represents the first and second growing season post-thinning in the Size- and Pine-preference treatments, and the first growing season post-thinning in the Pine+Fire treatment; thinning in Pine+Fire was completed late in 1999. Letters denote statistical differences among means.
Figure 5.8. Means and standard errors of *Abies concolor* needle length on annual shoot growth occurring with and without cones in the female and male reproductive zones of trees, and length of needles in the lower crown of the tree that are produced in years in which the same tree produced or did not produce female or male cones, in the Klamath National Forest, CA.
Figure 5.9. Vector diagrams of current-year Pinus ponderosa (PIPO) and Abies concolor (ABCO) relative needle N and P concentration, content, and dry mass in experimental treatments at the Goosenest Adaptive Management Area. All values are expressed relative to needles from an untreated Control.
CHAPTER 6

CONCLUSIONS

This study was part of the national Fire and Fire Surrogates (FFS) network study, which was designed to evaluate the ecological effects of forest management strategies that reduce the threat of catastrophic fire. The specific objectives of my study were to evaluate the effects of thinning and prescribed fire in a northern California mixed-conifer ecosystem on soil physical, chemical, and microbial properties, and to investigate the response of mature conifers to these treatments via nutrient concentrations in needle cohorts formed over the course of the experimental period.

My objective for the study presented in Chapter 2 was to evaluate the response of soil and forest floor characteristics to a suite of alternative forest management strategies. I found that FFS treatments decreased soil compaction and increased soil surface disturbance. Soil organic matter quantity and quality was reduced by fire alone, but not in combination with thinning, and the effect on organic matter quality did not persist. Fire, alone and in combination with thinning, increased total inorganic N (TIN) and pH, although only the effect on pH persisted in 2004. Although N mineralization and nitrification all differed from the Control in the first sampling period, the pattern of treatment effects in the second sampling period differed from that in the first. In general, FFS treatments reduced soil microbial activity, although the pattern of differences among
treatments varied among response parameters and between sampling years. Finally, I found that FFS treatments increased forest floor C content in the first sampling period, and increased forest floor N content in the second. Although FFS treatments affected many of these soil and forest floor characteristics, the magnitude of response was generally small, and many of the effects were transient.

The objective of the study detailed in Chapter 3 was to investigate the influence of thinning on the proximate effects of prescribed fire. I demonstrated that the effects of fire on soil nutrient status and microbial activity differed between areas that were thinned prior to fire and those that were unthinned. Prescribed fire reduced soil organic matter quantity and quality in unthinned stands, whereas there was no significant effect on these variables in areas that had been thinned prior to prescribed fire. Although both treatments increased soil TIN, N mineralization and net nitrification were reduced by fire in thinned stands only. Acid phosphatase activity was reduced by fire in thinned and unthinned stands, whereas chitinase activity was reduced by fire in thinned stands only, and there was no effect of fire on phenol oxidase activity. The results of this portion of my study have been published as Miesel et al. (2007).

The objective of the study presented in Chapter 4 was to compare the effects of two different thinning prescriptions on the soil and forest floor. My results show that when thinning is used as a surrogate for fire, the species composition of trees that remain in the forest influences soil and forest floor characteristics. For example, post-thinning TIN, soil C and phenol oxidase activity were greater in stands that were thinned to create a forest dominated by large trees, regardless of species, whereas potential nutrient
availability (i.e., forest floor nutrient content) was greater in stands that were thinned to restore dominance to *Pinus ponderosa*. These results have been published as Miesel et al. (2008).

In the study presented in Chapter 5, I sought to investigate the effects of thinning and prescribed fire treatments on foliar characteristics of mature *P. ponderosa* and *Abies concolor*. In general, my results show that thinning treatments, with or without fire, impacted leaf size and nutrient concentration, whereas fire alone did not. I found that among-treatment differences in needle nutrient concentration occurred in *P. ponderosa* only, and that foliar P concentration was reduced, whereas there was no significant effect on foliar N concentration. Vector analysis indicated that *P. ponderosa* and *A. concolor* respond in distinctly different directions to the restoration treatments, although treatment effects on individual foliar characteristics of each species were generally not statistically significant. Because there was no clear correspondence between the year in which a treatment was implemented and the year in which changes in foliar characteristics occurred, it is likely that differences in foliar physical and chemical attributes may have been due more to the physical change in forest structure than to a direct response of mature trees to fire- or thinning-induced changes in soil nutrient availability. By showing that thinning increases the potential growth capacity of individual trees, whereas a single application of low-intensity prescribed fire has no measurable impact on leaf size or N and P concentrations, these results may help alleviate public concern over restoration-based selective thinning and the re-introduction of fire in western forests.
The modern occurrence of high-severity, catastrophic fires in forests that historically experienced fires of only low- to moderate severity clearly demonstrates a need for restoration (Covington 2000, Agee and Skinner 2005). Although Covington (2000) argues that sufficient ecological information exists to begin appropriate restoration treatments immediately, he emphasizes that “all restoration should be conducted in an explicitly formal, adaptive management context; and that multiple approaches should be tested and carefully monitored.” Thus, it is important that a broad view of ecological processes be considered before and during the implementation of such treatments; however, even though several studies have documented the effectiveness of fuel reduction treatments on reducing real or predicted fire behavior (e.g., Agee and Skinner 2005, Schmidt et al. 2008), the effects of these treatments on ecosystem processes are less clear (SNEP 1996). The national FFS study, of which this dissertation is a part, is among the first to approach these questions via an experimental, rather than a correlative or retrospective design (Weatherspoon 2000).

One of the key advantages of the experimental approach used for the FFS study was to identify treatments that may serve as an effective replacement for fire, and to identify variables or processes for which fire is unique (Weatherspoon 2000). Although other authors have directly addressed the influence of FFS treatments on potential fire behavior (Schmidt et al. 2008, Youngblood et al. 2008), the consequences of effects on ecosystem components such as soils and foliar characteristics is much less clear.

The results presented here suggest that in general, the use of fire had the greatest impact on soil characteristics, and these effects were either mediated or enhanced by thinning, depending on the variable of interest. In contrast, thinning resulted in the
greatest response in mature conifers, suggesting that reductions in stand density, rather than treatment-induced changes in soil nutrient availability, are most readily detectable by mature, dominant trees. Taken together, these results indicate that measureable differences in treatment effects exist among the suite of thinning and prescribed fire treatments used for this study; however, in most instances, the differences in soil characteristics among treatments were small and transient. Further, even though the magnitude of increase in soil TIN in the prescribed fire treatments (with and without thinning) was much greater than that of other soil variables, there was no clear response in mature conifers to the increased TIN, based on the foliar characteristics I measured.

Thus, at this relatively early stage, it appears unlikely that the small differences in soil nutrients will have biologically significant impacts on the forest ecosystem. Of greater long-term interest are the effects on the potential availability of nutrients stored in soil organic matter and the forest floor, and whether among-treatment differences in rates of decomposition and nutrient cycling will in turn create differences in site productivity and, therefore, fuel production and future fire behavior.

Understanding the ecological effects of experimental thinning and prescribed fire is essential to the ability to use fire effectively in current forest management as well as to design management strategies on a landscape level that provide for long-term ecosystem health and stability. Specifically, effects on key characteristics of soil and vegetation may serve as an early indication of ecosystem response. Although repeated treatment in non-control units was planned in order to fulfill the long-term objectives of the FFS study, the GAMA FFS site had received a single application of prescribed fire at the time this research was conducted, and additional thinning is not yet necessary. Thus, the study...
presented here serves as an early- to intermediate-term evaluation of treatment impacts on important ecosystem characteristics, and will serve as a valuable benchmark in a long-term, interdisciplinary study of the effects of thinning and prescribed fire in a northern California mixed-conifer ecosystem.


