Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL

Mechanical Restoration of California Mixed-Conifer Forests: Does it Matter Which Trees Are Cut?

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Abstract

The montane ecosystems of northern California have been subjected to repeated manipulation and active fire suppression for over a century, resulting in changes in community structure that contribute to increased wildfire hazard. Ecosystem restoration via reduction of stand density for wildfire hazard mitigation has received substantial attention in recent years; however, many ecological questions remain unanswered. This study compares belowground effects of two alternative forest thinning treatments designed to restore the large, old tree component of late-seral structure, one of which focuses on restoring *Pinus ponderosa* dominance (Pine-preference) and the other of which promotes development of large trees regardless of species (Size-preference). We evaluated forest floor and soil chemical and microbial parameters in six experimental thinning treatment units of 40 ha each in the Klamath National Forest of northern California 5–6 years after thinning. Inorganic N availability, soil organic C content, phenol oxidase activity, and forest floor C:N ratio were greater in the Size-preference treatment, whereas forest floor N and soil pH were greater in the Pine-preference treatment. Our results indicate that these two thinning strategies produce differences in the soil environment that has the potential to affect growth rates of trees that remain, as well as the growth and survivorship of newly established seedlings. Thus, which species/individuals are removed during structural restoration of these mixed-conifer forests matters both to the belowground components of the ecosystem today and the vegetation and productivity of the ecosystem in future decades.

Key words: **forest floor, microbial activity, mixed-conifer forests, soil nutrients, soil organic matter, thinning.**

Introduction

Descriptions of the pre-settlement mixed-conifer forests of northern California and southern Oregon describe open, park-like stands of trees, with Ponderosa pine (*Pinus ponderosa* P. & C. Lawson) 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 White fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) 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 & 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 & 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 & 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

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doi: 10.1111/j.1526-100X.2008.00414.x

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 (Sierra Nevada Ecosystem Project 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 1992; 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 U.S. Department of Agriculture (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 less than 10% but can locally be greater than 50%, with elevation ranging from 1,500 to 2,000 m. Ponderosa pine (*Pinus ponderosa* P. & C. Lawson) and White fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) are dominant in the forest canopy, together typically comprising greater than 90% of the basal area. Sugar pine (*P. lambertiana* Dougl.), Incense cedar (*Calocedrus decurrens* (Torr.) Florin), Shasta red fir (*Abies magnifica* A. Murr. var. *shastensis* Lemmon), and Sierra lodgepole pine (*P. contorta* Dougl. ex Loud. var. *murrayana* (Grev. & Balf) Englem.) 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 (*Ceanothus* spp.), Manzanita (*Arctostaphylos* spp.), Antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), Curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt.), Rabbitbrush (*Chrysothamnus* spp.), and Sagebrush (*Artemisia* spp.) (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 & 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 cover 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 three replicate 40-ha units, each of which contains a 100-m permanent grid (Fig. 1). All units were located on a predominantly northwestern aspect. Elevation ranges among units within each treatment were: Control, 1,560–1,692 m, Size-preference 1,485–1,578 m, and Pine-preference 1,560–1,666 m (Fig. 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 1). Whole trees were transported to central processing landings where all boles, limbs, and tops of trees 10.2–45.7 cm diameter at breast height (dbh) were removed and logs cut to appropriate length for hauling to processing plants. Submerchantable trees less than 10.2 cm dbh and tops and limbs of trees greater than 45.7 cm dbh were chipped at the landings and removed; thus, all the slash generated by the thinning was removed from the units. All damaged trees were removed. Submerchantable understory trees were hand cleared from both treatments within 1 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. 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 were greater in Pine-preference than Size-preference, whereas 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 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 2). The QMD, proportion of basal area represented by fir, and density of larger trees were similar for both thinning treatments (Table 2). A more thorough discussion of treatment prescription and pre- and posttreatment 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 less than 1.0 cm of precipitation fell during the month prior to sampling or during the period during

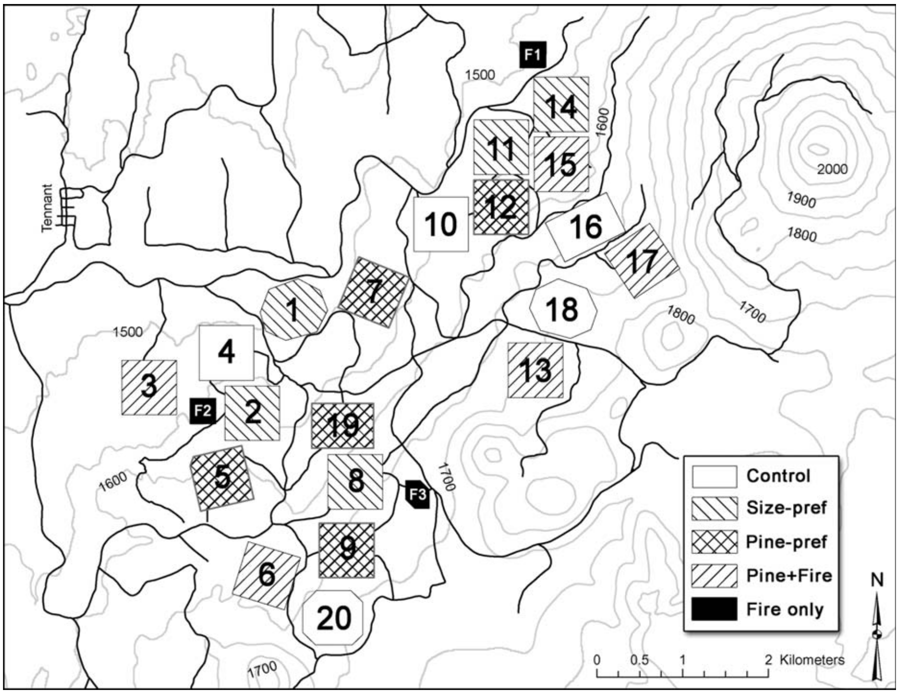

Figure 1. Map of the GAMA in northern California showing the placement of treatment units for the Little Horse Peak study. Units used in this study were Size-preference units 1, 11, and 14; Pine-preference units 5, 9, and 12; and Control units 4, 10, and 18. Darker lines represent logging roads and lighter lines represent 50-m elevation contours.

Table 1. Summary of thinning protocol implemented at the GAMA.

	Pine-Preference	*Size-Preference*
Treatment objectives	To reestablish dominance by Ponderosa pine (*Pinus ponderosa*) by thinning from below to achieve an 80% composition of Ponderosa pine by basal area	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
Mandatory retention trees	Retained trees included all White fir (*Abies concolor*) >76 cm dbh, all dominant and codominant Ponderosa pine >31 cm dbh, all Sugar pine (*Pi. lambertiana*), all Incense-cedar (*Calocedrus decurrens*) >25 cm dbh, all Douglas-fir (*Pseudotsuga menziesii*), trees similar in size to, and within 0.61 m of, mandatory retention trees (to minimize windthrow), all snags >38 cm dbh	Retained all trees >76 cm dbh
Spacing criteria	Determined based on the diameter of the larger tree, according to the function $S = 5 + \text{dbh}$, where S = spacing in feet, and dbh is determined in inches; however, mandatory tree retention criteria was given priority over tree spacing guidelines	Applied only to trees <76 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
Treatment completion date	November 1998, July 1999, and September 1999	August 1998, June 1999, and May 2000

Information presented was summarized from Ritchie (2005). dbh = 1.37 m above ground level.

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 pretreatment 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_2SO_4 for NO_3^-, NH_4^+, and P (Olsen & Sommers 1982); NO_3^- and NH_4^+ were analyzed using the microtiter methods of Hamilton and 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 (CE Elantech, Inc., Lakewood, NJ, U.S.A.) 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 ($n = 60$ for Control and Pine-preference, $n = 90$ for Size-preference).

Table 2. Forest structure before and after thinning at the GAMA.

		Pine-Preference		*Size-Preference*	
	Control	*Pre-treatment*	*Posttreatment*	*Pre-treatment*	*Posttreatment*
Basal area (m^2/ha)	35.4 ± 4.3	44.0 ± 7.9	30.3 ± 3.5	29.5 ± 1.2	22.3 ± 0.3
QMD (cm)	28.4 ± 1.8	29.0 ± 1.5	42.0 ± 1.3	36.1 ± 2.2	43.9 ± 0.5
Percent fir by basal area	59 ± 4	50 ± 3	29 ± 4	39 ± 12	34 ± 8
Tree density (trees/ha)	575 ± 106	685 ± 147	215 ± 13	295 ± 31	147 ± 4
Pinus ponderosa density (trees/ha)	286.5 ± 63.8	—	154.8 ± 30.5	—	87.3 ± 12.9
Density of trees >61 cm dbh (trees/ha)	4.2 ± 0.5	—	17.3 ± 5.8	—	12.3 ± 1.1
Density of trees <10 cm dbh (trees/ha)	102.7 ± 13.1	—	11.5 ± 3.6	—	2.5 ± 1.0

Data presented were summarized from Ritchie (2005) and represent means ± SE of the three units per treatment that were used in this study. Data not recorded for pre-treatment conditions are indicated by —.

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 l-3,4-dihydroxyphenylalanine (L-DOPA), 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 lognormally distributed and were log transformed prior to further analysis. Lognormal 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 (ANCOVA) (PROC GLM, SAS Institute 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 treatment units nested within each treatment. In the Pine-preference treatment and Control, we had 180 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 Institute 2004). Statistical significance is reported at $p = 0.05$ unless otherwise indicated.

Although the primary ANCOVA 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 pairwise 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 nonmetric multidimensional scaling (NMS) ordination (McCune & 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 3; Fig. 2). 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 3; Fig. 2). 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 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 3; Fig. 3), though pairwise comparison of the two thinning treatments indicated significantly greater soil organic C in Size-preference than Pine-preference ($p < 0.01$) (Fig. 3). Variation in soil organic C among units within treatments was greater than the variation among treatments (Table 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 3; Fig. 3).

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 3; Fig. 4). Phenol oxidase activity did not vary significantly among the three treatments (Table 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 (Fig. 4). Phenol oxidase activity was the only variable for which elevation was a significant covariate (Table 3).

Table 3. ANCOVA of selected soil properties.

Parameter	*Full Model*	*Treatment*	*Units/Treatments*	*Elevation*
TIN	67.80***	88.10***	0.89	1.21
Soil pH	6.63***	7.29***	4.95***	0.24
Available P	6.29***	0.56	6.62***	0.63
Soil organic C	4.08***	1.02	0.97	0.09
Soil total N	3.17**	0.32	2.15*	0.01
Soil C:N ratio	3.40**	8.38***	3.07**	0.01
Forest floor C	2.80*	0.35	3.03**	1.34
Forest floor N	60.85***	17.34***	41.17***	0.09
Forest floor C:N ratio	20.86***	4.69*	10.07***	0.01
Acid phosphatase	6.07***	6.15**	3.68**	0.04
Chitinase	3.92***	8.57***	1.65	0.04
Phenol oxidase	7.06***	0.83	6.40***	5.52*

Main effects in the model were treatment and units nested within treatments, with elevation as a covariate. *F* statistics for all model components are given with significance indicated as $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

Forest Floor C and N Concentrations

Forest floor organic C concentration did not differ among treatments (Table 3; Fig. 5). In contrast, total N concentration and C:N ratio did differ significantly among treatments (Table 3, Fig. 5). 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% (Fig. 5). 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 of 91% between the two thinning treatments (Table 3; Fig. 5). 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.

Ordination

NMS ordination arrayed the six manipulated treatment units and the nine control unit–year combinations along two axes which together explained 96.7% of the variance in the data matrix (Fig. 6). 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 (Fig. 6). The three Size-preference units were arrayed in the upper left corner of the ordination, indicating relatively high soil organic C, total soil N, 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 (Fig. 6).

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 and 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 postdisturbance 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 vs. stem only) have different effects on soil pH and N status (Nykvist & Rosén 1985; Staaf & Olsson 1991; 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 NH_4^+ versus NO_3^-, 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

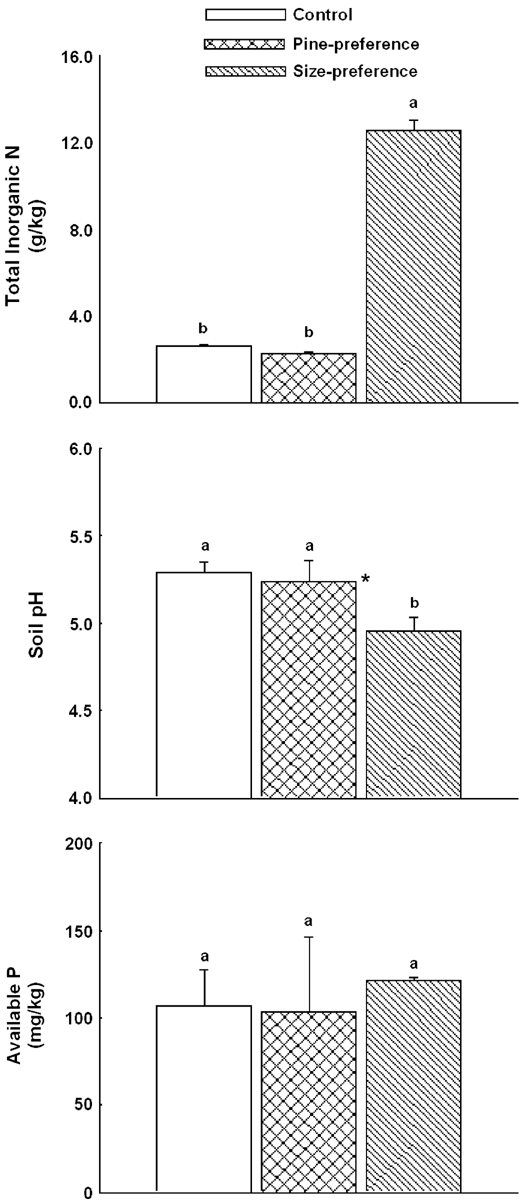

Figure 2. TIN (mg N/kg soil), soil pH, and plant-available P (mg P/kg soil) in soils of two thinning protocols and unthinned controls. Means of $n = 3$ and SEs of the means are shown. Histogram bars with the same lowercase letter were not significantly different at $p < 0.05$ in three-way comparisons, whereas * indicates a significant difference between the two thinning treatments only at $p < 0.05$.

remaining tree stratum is more likely to have been a cause of the differences we observed in soil pH and N availability.

TIN 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 posttreatment differences in N uptake, N mineralization, N fixation, or the posttreatment 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 & 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 are currently analyzing N concentrations in age-specific needle classes of both White fir and Ponderosa pine in an effort to test this.

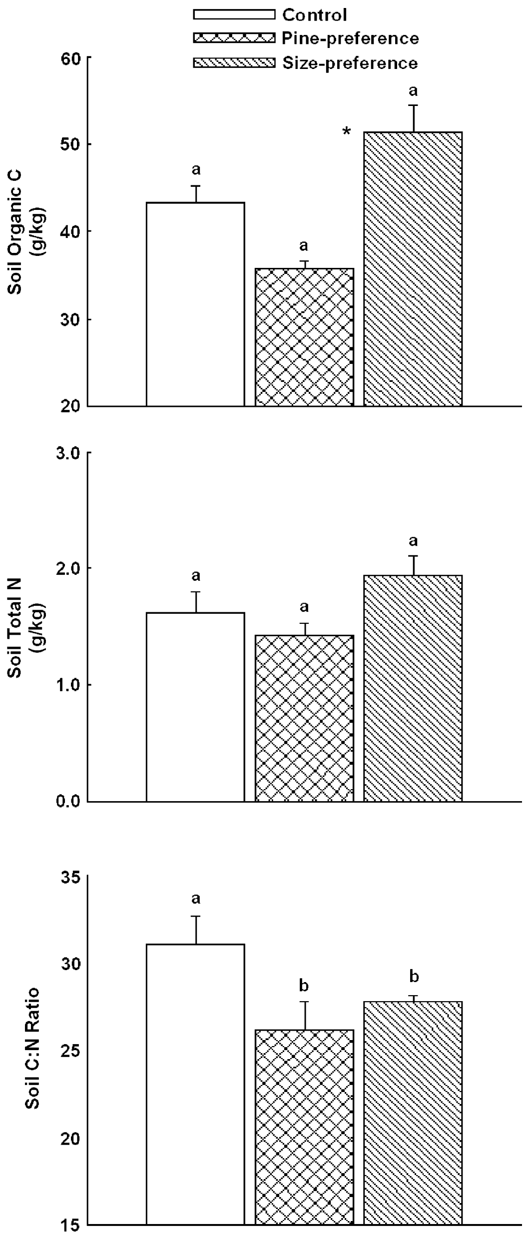

Figure 3. Soil organic C content (g C/kg soil), total soil N (g N/kg soil), and soil C:N ratio in soils of two thinning protocols. Means of $n = 3$ and SEs of the means are shown. Histogram bars with the same lowercase letter were not significantly different at $p < 0.05$ in three-way comparisons, whereas * indicates a significant difference between the two thinning treatments only at $p < 0.05$.

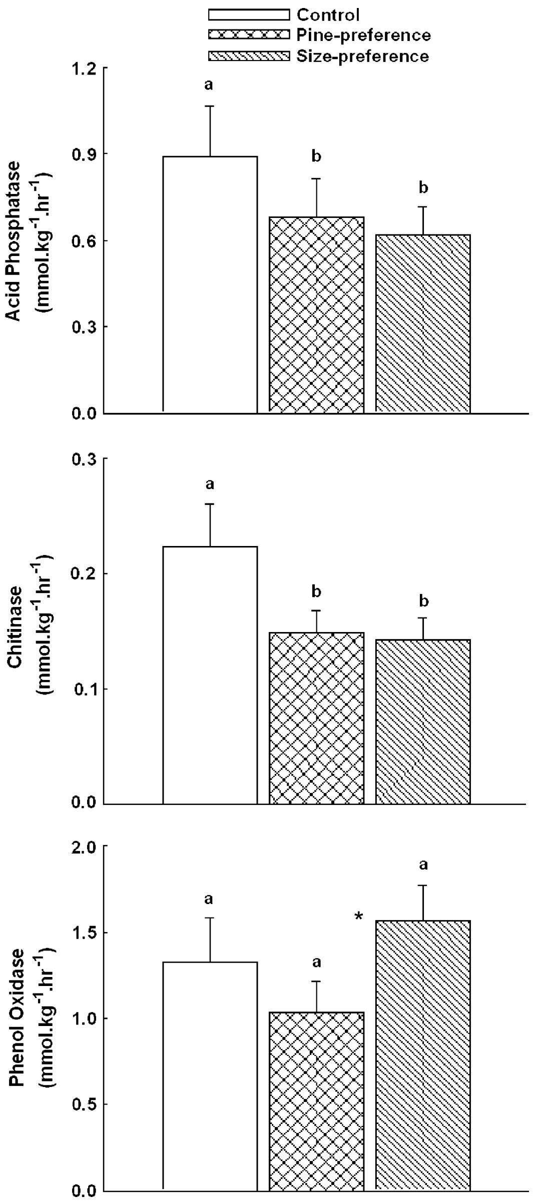

Figure 4. Phenol oxidase, acid phosphatase, and chitinase activity (mmol/kg soil/hr) in soils of two thinning protocols. Means of $n = 3$ and SEs of the means are shown. Histogram bars with the same lowercase letter were not significantly different at $p < 0.05$ in three-way comparisons, whereas * indicates a significant difference between the two thinning treatments only at $p < 0.05$.

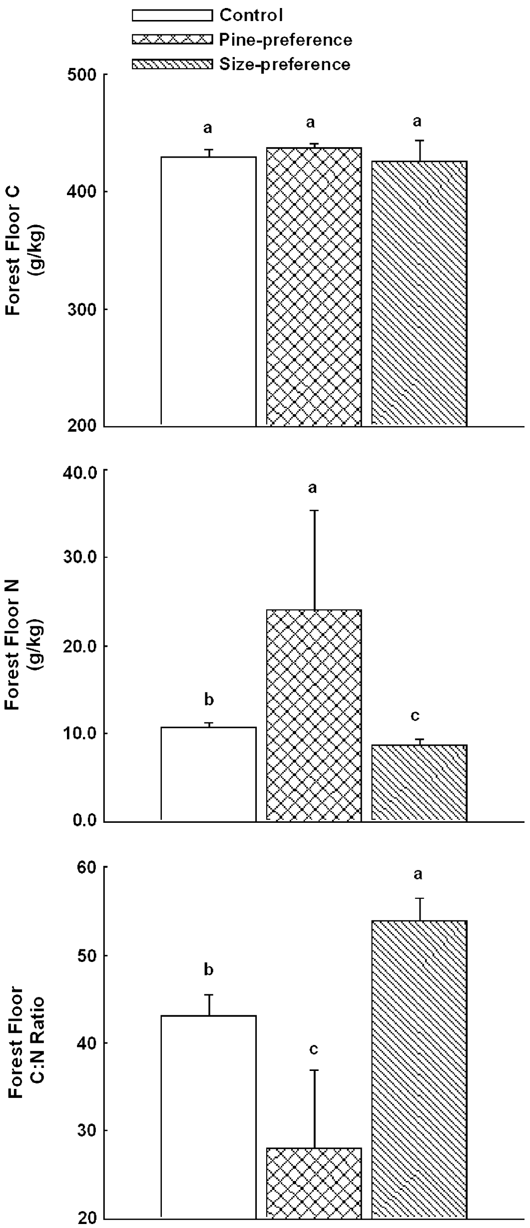

Figure 5. Forest floor organic C and total N content (g/kg soil) and C:N ratio in forest floor of two thinning protocols. Means of $n = 3$ and SEs of the means are shown. Histogram bars with the same lowercase letter were not significantly different at $p < 0.05$ in three-way comparisons.

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, 2 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 vs. Pine-preference 0.025 ± 0.06; 2004: Control 0.001 ± 0.005 vs. Pine-preference 0.004 ± 0.006; Miesel, unpublished data).

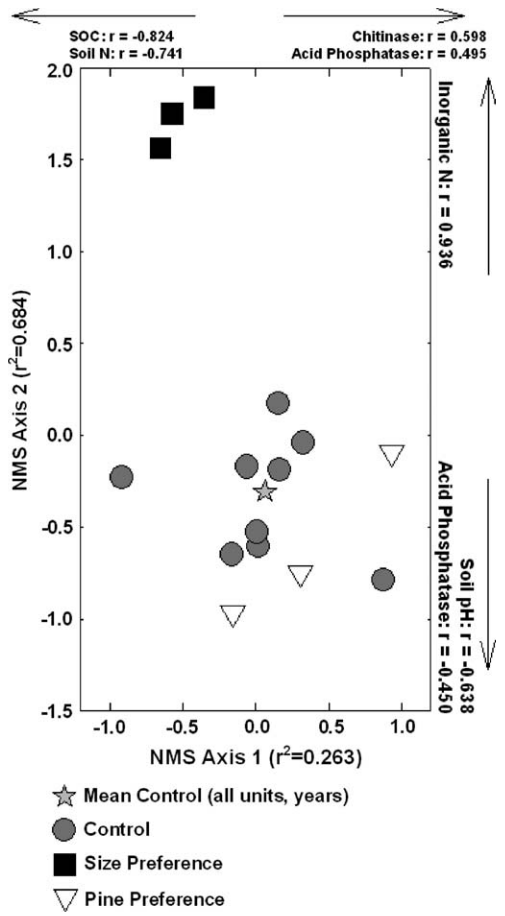

Figure 6. NMS ordination of 12 soil properties among six treatment units representing two thinning treatments and nine unit–year combinations representing unthinned controls. The proportion of total variance in the site soil parameter matrix explained by each axis is indicated in parentheses. Linear correlations between axis scores and soil variables significant at $p < 0.05$ are shown.

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-year-old Lodgepole pine (*Pinus contorta*) stand in Wyoming were greater in gaps created by removing at least 15 trees than in uncut areas and was greatest in 30 tree gaps (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 1989), 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 & 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 2-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 in 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 ANCOVAs 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 *Ceanothus* spp. (the only common N-fixing plant in this ecosystem) showed that unit 12 had significantly greater cover of *Ceanothus* 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 unit 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 less than 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 because 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.

Implications for Practice

- Selection criteria for the species/individuals removed during structural restoration of a California mixed-conifer forest produce measurable differences in available soil nutrients and in those stored in soil and forest floor organic material.
- Although the process of restoring stand structure through mechanical means is resource consumptive (e.g., personnel, equipment, and energy) over a short time, the impacts on belowground parts of ecosystems (and therefore ecosystem sustainability) may remain over many years.
- Forest management strategies that alter stand structure should also consider the effects of species composition on soil and forest floor material in the posttreatment forest, as these effects have the potential to influence long-term forest health and sustainability.

Acknowledgments

This paper is contribution number 14 of the GAMA Ecological Research Project and publication number 135 of the Fire and Fire Surrogate Network Study. Funding for this project was provided by the Joint Fire Sciences

Program. We thank C. Abbott and USDA Forest Service field crews for field assistance and J. Brinkman, C. Giai, J. Huang, P. Ruse, and A. Shenoy for laboratory assistance.

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