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Initial response of conifer and California black oak seedlings following fuel reduction activities in a Sierra Nevada mixed conifer forest

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Abstract

Forest structure, fuel characteristics, and fire regimes of mixed conifer forests in the Western United States (US) have been dramatically altered since the early 20th century. Fuel treatments have been suggested as a means to limit the size and intensity of wildfires but few experiments are available to analyze the ecological effects of different treatments. The objective of this study is to determine how mechanical, prescribed fire, and mechanical and fire combination fuel treatments affected seedling density by species in a Sierra Nevada mixed conifer forest. The relative influences of stand-level light availability and substrate quality on conifer and black oak seedling densities are assessed. For all species combined, seedling densities increased when the fire only treatment was applied and no change was detected for the other treatments. The fire only treatment as well as the combined fire plus mechanical treatment had the effect of significantly increasing Douglas-fir seedling density. Ponderosa pine seedling densities significantly increased when the fire plus mechanical treatment was applied. California black oak seedling density decreased when the fire only treatment was applied but no change was detected for the other treatments. Previous studies have found a decline in sugar pine and ponderosa pine in dense stands of Sierran mixed conifer forests. The findings reported here corroborate these studies in that current conditions are not conducive to recruitment of ponderosa pine and sugar pine species. Our initial results indicate, that in this case, treatments used to reduce fire hazard may not result in retention or recruitment of California black oak and sugar pine seedlings.

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Keywords: Fuel treatments; Prescribed fire; Fire surrogates; Fire hazards; Regeneration; Wildfire

1. Introduction

Forest structure, fuel characteristics, and fire regimes of mixed conifer forests in the Western United States (US) have been dramatically altered since the early 20th century (Kilgore and Taylor, 1979; Biswell, 1989; Skinner and Chang, 1996; Swetnam, 1993; Graham et al., 2004; Stephens and Collins, 2004; Taylor and Beaty, 2005; Moody et al., 2006; Stephens et al., 2007). Sierra Nevada mixed conifer forests have experienced changes in fire regimes during the last 90–100 years; past harvesting practices, introduced pathogens such as white pine blister rust (*Cronartium ribicola* J.C. Fishch. Ex Raben) (van Mantgem et al., 2004), and changing climates are other factors that affect forest structure and potential fire behavior (Millar and Woolfenden, 1999; Millar et al., 2007).

These factors have contributed to increased stand densities of shade tolerant species such as white fir (*Abies concolor* Gord. & Glend), incense-cedar (*Calocedrus decurrens* [Torr.] Floren.) and decreased recruitment of ponderosa pine (*Pinus ponderosa* Laws) and sugar pine (*Pinus lambertiana* Dougl.) throughout mixed conifer forests in the Sierra Nevada (Parsons and DeBendeetti, 1979; Beesley, 1996; Ansley and Battles, 1998; North et al., 2002; Taylor and Skinner, 2003; Franklin and Agee, 2003; Romme et al., 2003; Gray et al., 2005; van Mantgem et al., 2004; Schmidt et al., 2006).

Currently over 10 million ha of coniferous forests in the Western US are in moderate or high fire hazard condition classes (NWGC, 2001). Several recent fire policies and initiatives such as the National Fire Plan (USDA–USDI, 2000), 10-year comprehensive strategy (WGA, 2001), and Healthy Forest Restoration Act (USDA, 2004a) have been enacted to address the national US wildfire management problem (Stephens and Ruth, 2005; Husari et al., 2006). All of the statutes emphasize forest thinning, and to a lesser extent,

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prescribed fire, as integral tools for reducing high fire hazards in Western US forests. The National Fire and Fire Surrogate Study (FFS) has implemented a series of controlled empirical experiments to study the effects of alternative fuel treatments on vegetation structure, fuel loads, and a suite of other ecological variables at 13 locations across the continental US (Weatherspoon and McIver, 2000). In this paper, we report results from the Blodgett forest FFS study site in the north-central Sierra Nevada, California.

Understanding the effects of mechanical and prescribed fire-based fuel treatments on conifer and hardwood recruitment is essential for long-term ecosystem management. Seedling establishment, the first stage of recruitment following a disturbance such as a fuel treatment, is fundamental in influencing stand dynamics and shaping future species composition and structure. As stands develop following treatments, so will associated effects on wildlife habitat, resilience, resistance to disturbance, and future seed sources. Multiple environmental factors interact to influence the timing and patterns of understory vegetation in Sierra Nevada forests (North et al., 2005; van Mantgem et al., 2006; Collins et al., 2007). At least two key abiotic factors influencing regeneration and hence future forest composition and structure in Sierra Nevada forests are the availability of germination substrate and sunlight (Oliver and Dolph, 1992; Gray et al., 2005). At Blodgett forest in the central Sierra, substrate and light availability are altered to varying degrees depending on the choice of silvicultural practice and the details of implementation. While each of the overstory species present can typically regenerate to some degree under a wide variety of silvicultural methods, species are thought to have different regeneration responses to some methods versus others (Laacke and Fiske, 1983). Numerous stand-level studies have indeed revealed general patterns of regeneration responses that allow managers to coarsely predict how species will respond to a given choice of traditional regeneration method (Burns and Honkala, 1990a).

Effects of traditional even and un-even aged silvicultural treatments and reserve (no active management) treatments have been previously studied at Blodgett Forest Research Station (Olson and Helms, 1996). None of these treatments were designed specifically for reduction of fire hazard nor included the use of prescribed fire for reduction of surface fuels (Stephens and Moghaddas, 2005c). Stand-level studies of fuel treatments are still needed to predict patterns of seedling regeneration following modern fuel reduction treatments proposed for broad implementation across Western US forests. Although not traditionally considered to be a regeneration treatment, these fuel treatments will nevertheless have a profound effect on regeneration and hence future stand composition and structure.

The objective of this study is to determine how four different experimental fuel treatments affected seedling density by species and to describe the relative influences of stand-level light availability and substrate quality on seedling densities. The four treatments include: (1) mechanical thinning and mastication, (2) prescribed fire, and (3) a combination of

mechanical thinning, mastication, and prescribed fire, and (4) controls (no treatment). We tested for treatment effects at 4 years post-treatment.

2. Methods

2.1. Study area

This study was performed at the University of California Blodgett Forest Research Station (Blodgett forest), approximately 20 km east of Georgetown, California. Blodgett forest is located in the mixed conifer zone of the north-central Sierra Nevada at latitude 38°54′45″ N, longitude 120°39′27″ W, between 1100 and 1410 m above sea level, and encompasses an area of 1780 ha. Mixed conifer forests cover 3.2 million ha (7.8%) of California's land base (CDF, 2003). Tree species in this area include sugar pine, ponderosa pine, white fir, incensecedar, Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), and California black oak (Quercus kelloggii Newb.). Species present in minor abundance include tan oak (Lithocarpus densiflorus (Hook. & Arn.) Rehder), bush chinkapin (Chrysolepis sempervirens (Kell.) Hjelmg.), and Pacific madrone (Arbutus menziezii Pursh). Experimental units were very similar in terms of stand structure and species composition. Prior to treatment, there were no significant differences in species composition, quadratic mean diameter, tree density, surface fuel loads, and canopy cover between treatment types (Stephens and Moghaddas, 2005a).

Soils at Blodgett forest are well-developed, well-drained Haploxeralfs (Alfisols), derived from either andesitic mudflow or granitic/granodiorite parent materials (Hart et al., 1992; Moghaddas and Stephens, 2007). Cohasset, Bighill, Holland, and Musick are common soil series. Soils are deep, weathered, sandy-loams overlain by an organic forest floor horizon. Common soil depths range from 85 cm to 115 cm. Slopes across Blodgett forest average less than 30%.

Climate at Blodgett forest is Mediterranean with a summer drought period that extends into the fall. Winter and spring receive the majority of precipitation which averages 160 cm (Stephens and Collins, 2004). Average temperatures in January range between 0 °C and 8 °C. Summer months are mild with average August temperatures between 10 °C and 29 °C, with infrequent summer precipitation from thunderstorms (averaging 4 cm over the summer months from 1960 to 2000) (Stephens and Collins, 2004). Precipitation during the study (2003–2006) varied between 62% and 150% of the average 42-year rainfall record at UC Blodgett forest.

Fire was a common ecosystem process in the mixed conifer forests of Blodgett forest before the policy of fire suppression began early in the 20th century. Between 1750 and 1900, median composite fire intervals at the 3–5 ha spatial scale were 6–14 years with a fire interval range of 2–29 years (Stephens and Collins, 2004). Forested areas at Blodgett forest have been repeatedly harvested and subjected to fire suppression for the last 90 years reflecting a management history common to many forests in California (Laudenslayer and Darr, 1990; Stephens, 2000) and elsewhere in the Western US (Graham et al., 2004).

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2.2. Treatments

The primary objective of the treatments was to modify stand structure such that at least 80% of the dominant and codominant trees in the post-treatment stand would survive a wildfire modeled under 80th percentile weather conditions (Weatherspoon and Skinner, 2002). The secondary objective was to create a stand structure that maintained or restored several forest attributes and processes including, but not limited to, snag and coarse woody debris recruitment (Stephens and Moghaddas, 2005b), floral and faunal species diversity (Apigian et al., 2006a,b), and seedling establishment. To meet these objectives, three different treatments: mechanical only, mechanical plus fire, and prescribed fire only, as well as untreated control were each randomly applied (complete randomized design) to 3 of 12 experimental units that varied in size from 14 ha to 29 ha. Total area for the 12 experimental units was 225 ha. To reduce edge effects from adjoining areas, data collection was restricted to a 10 ha core area in the center of each experimental unit.

Control units received no treatment during the study period (2000-2005). Mechanical only treatment units had a two-stage prescription; in 2001 stands were moderately to heavily thinned from below (Graham et al., 1999) to maximize crown spacing while retaining 28-34 m² ha⁻¹ of basal area. The thin from below mechanical treatment included the removal of intermediate and some co-dominant conifers at least 25 cm DBH, with relatively larger dominant and co-dominant trees in the stand given overall preference for retention. The harvest treatment favored the removal of trees showing disease or physical damage first, followed by relatively smaller trees then larger diameter trees to achieve vertical and horizontal crown separation. Marking prescriptions favored retention of conifer species such that a relatively even proportion of each species would be represented by the five conifers types present on the study site after treatment (Stephens and Moghaddas, 2005a).

Individual trees were felled, limbed, and cut into specified saw log lengths using a chainsaw, and removed with either a rubber tired or track laying skidder for eventual processing at a saw mill. All limbwood and tops were left in the experimental unit after removal from harvested trees. During harvests, some hardwoods, primarily California black oak, were coppiced to facilitate their regeneration (McDonald and Tappeiner, 1996). All residual trees were well spaced with little overlap of live crowns in dominant and co-dominant trees. Following the harvest, approximately 90% of understory conifers and hardwoods between 2 cm and 25 cm diameter at breast height (DBH) were masticated in place using an excavator mounted with a rotary masticator. Mastication shreds and chips standing small diameter (2–25 cm DBH in this case) live and dead trees in place. Mastication has become a common fuel treatment in plantations and some mixed forest stands in California. Masticated material was not removed from the experimental units. The remaining unmasticated understory trees were left in scattered clumps of 0.04-0.20 ha in size.

Mechanical plus fire experimental units underwent the same treatment as mechanical only units, but in addition, they were prescribed burned using a backing fire (Martin and Dell, 1978). Fire only units were burned with no pre-treatment using strip head-fires (Martin and Dell, 1978). All prescribed burning was conducted during a short period (23 October 2002 to 6 November 2002) with the majority of burning being done at night because relative humidity, temperature, wind speed, and fuel moistures were within pre-determined levels to produce the desired fire effects (Knapp et al., 2004). Prescribed fire prescription parameters for temperature, relative humidity, and wind speed were 0–10 °C, >35%, and 0.0–5 km h⁻¹, respectively. Desired 10 h fuel stick moisture content was 7–10%. All prescription parameters were met with the exception of fuel moisture which was drier at 5–9% (Stephens and Moghaddas, 2005a; Collins et al., 2007; Kobziar et al., 2007).

2.3. Seedling surveys

Detailed summaries of forest stand structure measurements and results have been previously published (Stephens and Moghaddas, 2005a,b; Collins et al., 2007). Each of the 12 experimental areas has twenty 0.04 ha circular inventory plots (240 total plots). These permanent plots are established on a systematic 60-m grid with a random starting point and provide the pre- and post-treatment monitoring points for all measurements. Plot centers were permanently marked with a pipe and were spatially referenced to witness trees to facilitate plot relocation after treatments.

Measurement of conifer and hardwood seedlings were conducted on 10 randomly chosen plots in each of the 12 experimental units (120 plots total). Within these plots, four 1 m² circular sub-plots (480 sub-plots total) were located 5 m from the plot center at azimuths of 20°, 110°, 200°, and 290°. On each 1 m² sub-plot, all conifer and hardwood tree species seedlings (<50 cm tall) were tallied by species. All sub-plots, including controls, were measured between June and August in 2001 (pre-treatment) and in July in 2006 (4 years post-treatment).

2.4. Substrate light availability and change in total tree biomass

Substrate quality and light availability, two dominant influences on mixed conifer seedling regeneration (York et al., 2003; Gray et al., 2005; van Mantgem et al., 2006), were measured as possible explanations for the effects of treatments on seedling densities. Substrate quality was expressed as the percent of ground surface that had bare mineral soil (%BMS). Each plot was ocularly estimated for %BMS 2 years following treatments to a precision of 5% (Moghaddas and Stephens, 2007). Prior to treatments, %BMS was generally low. The 95% confidence interval of mean %BMS for all plots was 2.7–7.2%, with all 95% confidence intervals overlapping between each treatment type. The amount of light reaching the forest floor was measured with hemispherical photography on a 120 m grid across all study areas 4 years following treatments. Photos were taken at 1 m height using a Canon film-camera and fish-eye lens (Nikkor 8 mm f/2.8) that provides a 180° view of the canopy. Photos were taken early or late in the day when the sun was low in the sky. Color slides were converted to digital images (900 dpi) using a Nikon CoolScan slide scanner. By restricting photo acquisition to near-isotropic sky conditions, we minimized the need for digital image enhancement. Digital images were analyzed using the Gap Light Analyzer (vers. 2.0.4) image processing software (Frazer et al., 2000) to calculate the percent of total transmitted radiation (%TTR) reaching the photo point. This method provides an integrated measure of light level based on canopy geometry and light penetration (Canham, 1988; Battles, 1999). Local incident photosynthetically active radiation, used to calculate %TTR, was derived from standard equations of solar geometry and a site-specific atmospheric transmission coefficient (K_T), computed from daily solar flux data collected from a stand within the study area. Precision from a 5% subset of randomly chosen photos was calculated as <10% relative root mean square error.

Using over 9000 individual pre- and post-treatment tree measurements, total live standing tree volume (m³ ha⁻¹) was calculated using published equations for Sierra Nevada conifer (Wensel and Olson, 1995) and hardwood (McDonald, 1983) species. The relative severity of the treatments was derived by taking the total post-treatment live tree biomass and dividing by the pre-treatment total live tree biomass.

2.5. Data analysis

Seedling frequency 4 years after the treatments is characterized by calculating the % of plots in a given treatment that had a given species present. To match the study design, the experimental unit for all statistical analyses is the individual stand (n = 12). This level of inference avoids pseudoreplication problems typically associated with studies of fire treatments (van Mantgem et al., 2001). Plots within stands are therefore averaged to give stand-level measurements. The first step in the analysis was to test for influences of the three treatments on change in seedling density. Each species was assessed individually, and also by all species combined. Pre-treatment densities were measured 1 year before treatments and then remeasured 4 years after treatments. We used a multivariate approach (MANOVAR) to analyze the repeated measures of seedling densities and to avoid assumptions of symmetry in the variance-covariance matrix that typically limits a univariate approach (Von Ende, 2001). In the MANOVAR model, time was the within-subject treatment. The three between subject treatments were presence/absence of fire, mastication, and fire + mastication. The treatments were coded into ordinal data by assigning a 0 value if the treatment was not present and a 1 value if the treatment was present. Each repeated measure therefore has three assignments. For example, a repeated measure of seedling density in a fire only treatment is modeled with three predictor variables: a value of 1 for fire presence, 0 for mastication presence, and 0 for fire + mastication presence. Controls were given 0 values for all treatments. The primary relationships of interest were the tests for significance in the interaction between time and treatment. The time by treatment interaction tests whether the trend in seedling density is different when a given treatment is applied (value of 1) versus when it is not applied (value of 0). Statistical conclusions were based on Pillai's trace statistics with the determination of significance at p < 0.10. Given high variability typical of seedling densities and the lack of power typically associated with MANOVAR (Stephens, 1986), 0.10 was judged to be appropriate prior to analysis.

The second step in the analysis was to explore relationships between post-treatment seedling densities and the measurements of substrate quality and light availability. We used a multiple regression with seedling density as the response variable. Seedling density was natural log transformed to achieve normality in model residuals (0 values were avoided by adding 1). The predictor variables were stand means of %TTR and %BMS. The goal of this analysis was to assess light versus substrate in the degree to which either factor was correlated with seedling density. Partial F-tests were used to judge the relative contributions of light versus substrate (significance determined at p < 0.05). Overall model performance is not of primary interest in this case, but correlation coefficients are reported to show the differences in model performance between species.

A one-way ANOVA with a Tukey–Kramer HSD was used to determine differences in severity between treatments (Sall et al., 2001). The Jump statistical package was used for all analyses (Sall et al., 2001).

3. Results

3.1. Seedling frequency and treatment effects on change in seedling density

All species except sugar pine (none found in controls) had at least one seedling present per treatment type 4 years after treatments were installed (Table 1). Douglas-fir had the highest frequency at the plot level, while sugar pine was least frequent.

For all species combined, seedling densities increased when the fire only treatment was applied (p = 0.008) and no change was detected for the other treatments (Fig. 1). For incensecedar, sugar pine, and white fir, there were no differences in

Table 1
Plot level frequency of seedling presence by species and treatment in the fire and fire surrogate study at UC Blodgett forest

Species	% of plots with species present						
	Control	Fire only	Mechanical only	Mechanical plus fire	All plots		
ВО	40	23	57	3	31		
SP	0	20	13	17	13		
WF	33	77	43	80	58		
DF	33	97	67	83	70		
PP	10	40	13	93	39		
IC	50	80	40	80	43		

BO, California black oak; SP, sugar pine; WF, white fir; DF, Douglas-fire; PP, ponderosa pine; IC, incense-cedar.

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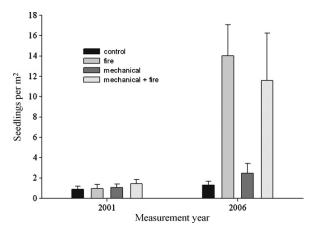


Fig. 1. Combined conifer and California black oak seedling density in the fire and fire surrogate study at UC Blodgett forest with standard error bars. Note scale change from other graphs.

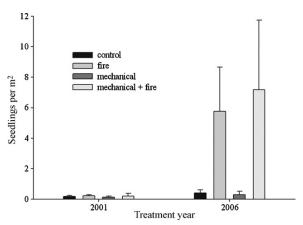


Fig. 2. Incense-cedar seedling density in the fire and fire surrogate study at UC Blodgett forest with standard error bars. Note scale change from other graphs.

seedling density trends for any of the treatments (Figs. 2–4). California black oak decreased when the fire only treatment was applied (p = 0.06), but no change was detected for the other treatments (Fig. 5). The fire only treatment (p = 0.01) as

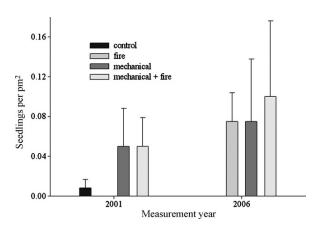


Fig. 3. Sugar pine seedling density in the fire and fire surrogate study at UC Blodgett forest with standard error bars. Note scale change from other graphs.

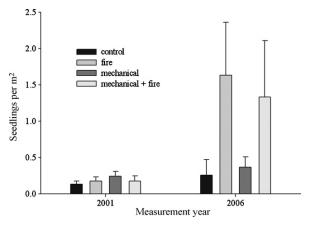


Fig. 4. White fir seedling density in the fire and fire surrogate study at UC Blodgett forest with standard error bars. Note scale change from other graphs.

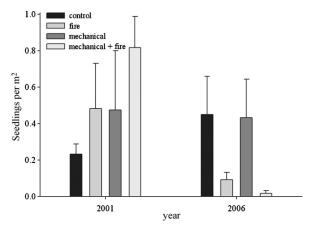


Fig. 5. California black oak seedling density in the fire and fire surrogate study at UC Blodgett forest with standard error bars. Note scale change from other graphs.

well as the fire + mechanical treatment (p = 0.08) had the effect of increasing Douglas-fir seedling density (Fig. 6). Ponderosa pine seedling densities increased when the fire + mechanical treatment was applied (p = 0.03; Fig. 7).

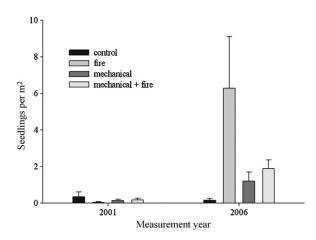


Fig. 6. Douglas-fir seedling density in the fire and fire surrogate study at UC Blodgett forest with standard error bars. Note scale change from other graphs.

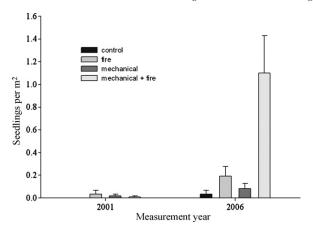


Fig. 7. Ponderosa pine seedling density in the fire and fire surrogate study at UC Blodgett forest with standard error bars. Note scale change from other graphs.

3.2. Total transmitted radiation, percent bare mineral soil, and change in total tree biomass

Percent total transmitted radiation was significantly higher in the fire + mechanical treatment; all other treatments were statistically similar. Percent total transmitted radiation varied from a minimum of 7.6% in one of the control treatments to a maximum of 40.7% in a fire + mechanical treatment. Betweenstand variability was highest for the control treatment (Table 2). As expected, percent bare mineral soil was markedly higher in the fire only and fire + mechanical treatment areas. %BMS varied from a minimum of 1.3% in a control treatment to a maximum of 78% in a fire + mechanical treatment. Forest floor depth after both treatments that included fire averaged 1 cm, control and mechanical only forest floor depths were approximately 5 cm (Moghaddas and Stephens, 2007). Coarse woody debris cover was relatively low in the treatments, varying from 0.4% to 2.8% for the fire and control treatments, respectively (Stephens and Moghaddas, 2005b).

In general, the amount of bare mineral soil present had much more leverage than light availability when explaining post-treatment seedling density when all species were combined (Table 3). The relative importance of %TTR and %BMS were different for individual species. Sugar pine, white fir, and Douglas-fir seedling densities were not well correlated with either %TTR or %BMS, but whole-model correlation coefficients were all greater than 0.27. Black oak and ponderosa pine seedling densities were mainly attributable to differences in %TTR. Incense-cedar densities were highly variable, but could be explained sufficiently with differences in %BMS.

Table 3
Results from a multiple regression with 4-year post-treatment seedling density as the response variable (In transformed) and percent total transmitted radiation and percent bare mineral soil as predictor variables

Species	r^2	Partial F-test for %TTR	Partial <i>F</i> -test for % soil	RMSE
All	0.69	p = 0.85	p = 0.02	0.32
BO	0.68	0.04	0.55	0.84
SP	0.27	0.74	0.18	1.43
WF	0.32	0.63	0.36	1.08
DF	0.41	0.66	0.22	0.65
PP	0.81	< 0.01	0.8	0.78
IC	0.42	0.43	0.05	1.14

BO, California black oak; SP, sugar pine; WF, white fir; DF, Douglas-fire; PP, ponderosa pine; IC, incense-cedar.

After treatment, remaining total tree biomass was statistically decreased (p < 0.05) in the mechanical and mechanical plus fire treatments when compared to the control and fire only treatments (Table 2). The total remaining live tree biomass was statistically similar between control and fire only treatments.

4. Discussion

The vast area of forestland in the Sierra Nevada where fire and other disturbances have been excluded has not been conducive for recruitment of species with low shade tolerance or those requiring a bare soil substrate for establishment (Biswell, 1989; Ansley and Battles, 1998; van Mantgem et al., 2004; Husari et al., 2006). Indeed, ponderosa pine and sugar pine were virtually absent prior to the experimental treatments in this study. If fire or its surrogates are used to restore the structures and processes that were present prior to fire exclusion, then the different influence these treatments have on seedling regeneration is a key factor in how effective the treatments are at restoring forest species composition.

Spatial and temporal variability in seedling density is typically very high because of the multiple factors influencing regeneration in mixed conifer forests including seed production (McDonald, 1992), climate (van Mantgem et al., 2006), substrate (Gray et al., 2005), and resource availability (York et al., 2003). Because of high variability and the stand level of inference for this experiment, even large differences in seedling density were not necessarily detectable with statistical tests (e.g. Figs. 2 and 4). Current seedling composition does not necessarily reflect what the future composition of the mature canopy will be since mortality and recruitment rates can be expected to vary between species. Hence this study should be

Table 2
Percentage of live tree biomass remaining after treatment, percent of total transmitted radiation reaching forest floor, and bare mineral soil by treatment type in the fire and fire surrogate study at UC Blodgett forest

	Control	Fire only	Mechanical only	Mechanical plus fire
Percentage of live tree biomass remaining after treatment (SE)	103.1 a (.06)	99.7 a (1.3)	79.4 b (3.3)	88.1 b (2.9)
Percent total transmitted radiation (SE)	15.7 a (5.1)	24.2 a (1.0)	21.3 a (3.5)	34.4 b (3.2)
Percent bare mineral soil (SE)	4.6 a (2.7)	46.9 b (8.9)	6.4 a (0.9)	58.8 b (10.3)

Mean values in a row followed by the same letter are not significantly different (p < 0.05).

limited to inferences of seedling establishment over a relatively short-time period and not long-term recruitment.

The mechanical only treatment was relatively ineffective at influencing regeneration of any of the species. Because the treatment removed mostly smaller trees in the under- and midstory, the amount of light made available to seedlings was not altered to a large degree (Table 2). Additionally, and perhaps more importantly, the treatment did not alter substrate quality to sufficiently increase the amount of bare mineral soil available. Presence of exposed mineral soil is more important for establishment of some species than others, but all of these species generally establish more readily on a mineral soil substrate (Minore, 1979). After treatment, mechanical only units had high cover of natural and activity generated surface fuels (Stephens and Moghaddas, 2005a) and %BMS similar to the controls.

Light availability is traditionally thought of as being the dominant factor in the establishment of shade tolerant versus intolerant species (e.g. Kimmins, 1987). However, substrate quality and physical microsite environments are also commonly found to have a fundamental influence on the regeneration process (e.g. Harmon and Franklin, 1989; Simard et al., 1989). We used exposure of bare mineral soil as a general indicator of substrate quality differences between treatments at the stand level. More fine-scale substrate changes may have included soil pH, nutrient content, structure, and soil strength (Moghaddas and Stephens, 2007). The two coarse-scale measurements of light availability and bare mineral soil at the stand level were surprisingly good as explanatory variables in the model (Table 3), but many other factors should be expected to influence seedling density as well.

The presence of fire resulted in levels of light availability that were similar to the mechanical treatments, yet seedling densities in general and specifically Douglas-fir densities increased when fire was present. As with the mechanical treatment, the fires mainly removed the under- and mid-story trees (Stephens and Moghaddas, 2005a). A major influence the fire treatment had on seedling density was to improve the substrate for seed establishment. Much of the variability in Douglas-fir seedling density, however was unexplained by either light or substrate (Table 1). Patchiness in the amount and quality of ash substrate may explain some variability, as Douglas-fir has been observed to germinate more readily on ash substrates (Fisher, 1935). Other important factors of Douglasfir regeneration, such as availability of mycorrizae (Trappe, 1977) or soil water (York et al., 2003), may also be interacting with fire to explain the positive effect of fire on seedling density. van Mantgem et al. (2006) found Abies species were recruited heavily into both burned and un-burned sites. We did not see a similar result in this study, indicating that over the short term, recruitment of Abies species may not consistently recruit into areas which have been burned.

For the 4 years following the treatments, seed production was not quantified in the treatment areas. However, observations of seed production are made annually at the research site for purposes of collecting seed for artificial regeneration at Blodgett. In addition, seed production was closely monitored in

an adjacent stand in 2006. All of the conifer species present had at least 1 year that was judged to be "moderate" in terms of cone production and all treatment units had statistically similar species composition of conifers and California black oak preand post-treatment (Stephens and Moghaddas, 2005a). Although seed production is highly variable and was not directly accounted for, we can rule out the possibility that a lack of seedlings in any treatment was caused by a differential abundance of species between units or a noticeable lack of seed production. Seed production is highly variable from year to year, and species are not synchronized in the amount of seed produced. For example, in 2006, species composition of seeds in traps from a nearby stand were occupied by 75% white fir and 0% sugar pine (York, unpublished data). Incense-cedar and Douglas-fir, the two most common species found in the seedling surveys of the treatment areas, occupied less than 15% of the seed traps. Ponderosa pine had only 10% composition, but this equated to over 50,000 seeds ha⁻¹. Thus even when seed production by ponderosa was small compared to total production by all species, the total number of seeds produced resulted in a substantial pool of available seeds for germination. No masting years, where seed composition could be expected to be occupied by more than 90% of one species, were observed during the 4 years following FFS treatments.

The number of years between abundant cone crops for Sierra Nevada conifers vary from 2 to 7 years (Gordon, 1978; Oliver and Ryker, 1990; McDonald, 1992). The two species that have been observed to occasionally have no seed production at all (incense-cedar and Douglas-fir), were the most abundant in the study area. Seed production over the 4 years following treatment therefore resulted in seed sources that were likely adequate for detecting large differences in seedling densities due to treatment effects. Because of high variability in seed production and the fact that seed dispersal was not measured in the study area, however, the relevant results in this case are the differences between treatments within species and not between species. The degree to which differences were detectable for any given species are related to the total amount of seed production in the study area, which varies from year to year.

Fire related mortality, top kill, and resulting sprouting response of mature California black oak trees has been documented in the scientific literatures (McDonald, 1990; Stephens and Finnery, 2002). Less documented are the effects of fuel treatments on existing California black oak seedlings and subsequent regeneration responses. The decline of existing California black oak seedlings when fire was present may be expected as small seedlings would have been susceptible to fire related mortality. The lack of California black oak regeneration response from either resprouting or acorns 4 years after treatment, however, is concerning as retention and recruitment of California black oak is often a desired management goal on public lands in the Sierra Nevada (USDA, 2004b). Mast years for California black oak can be highly variable (Burns and Honkala, 1990b) and, unlike with the other species at the study site, no observations on levels of acorn production were made during the time period. While it is therefore inconclusive whether or not enough acorns were produced to initiate a new cohort following treatments, it is clear that sprouting following the fire treatments was not abundant. It will be necessary to continue monitoring California black oak regeneration to confirm whether the decrease in seedling density persists.

The interaction between climate and the fire regime can influence the long-term species composition of mixed conifer forests (North et al., 2005; Gray et al., 2005). Due in part to these factors, it can be difficult to predict future species composition based on the current distribution of species (North et al., 2005). If seedlings are not recruited as a result of treatments, one can conclude that these species will not be present in high numbers over the short term, for example, the first 5–10 years after treatment.

4.1. Management implications

When relying on natural regeneration to provide adequate seedling recruitment, the disturbance employed must be intensive enough to create light and substrate conditions which will facilitate germination of seedlings when seeds and moisture are available. The high seedling densities in the burned areas suggests that, in general, the initial phase of the regeneration process that will lead to a new cohort is well underway. Because densities can change dramatically between the germination, establishment, and recruitment phases, however, the relevant results in this study so far are the comparisons between the treatments rather than absolute seedling densities. For example, in a seed sewing experiment done near the study area in the fourth year after the treatments, 67% of germinants died by the end of the growing season (York, unpublished data). Most of this mortality (99%) occurred early in the growing season, by June 22. The surveys in this study were done after most of the first year germinants would have died out because of poor microsites or substrates. Most of these seedlings could therefore be considered "established," and future density reductions will likely be related to competition for resources instead of substrate quality. Our expectation is that the burned areas will continue to have higher seedling densities in the future, but cohort recruitment rates will have to be assessed with continued monitoring.

In management settings where regeneration is achieved via the periodic harvesting of trees either individually or in groups, the occurrence of natural regeneration as a result of these treatments could conflict with management objectives. If regeneration is focused spatially in areas where larger trees have been removed, as with the group selection method of regeneration (Stephens et al., 1999; York et al., 2004), then the forested areas between the patches of regeneration can be treated with fire or other treatments designed to reduce potential wildfire severity. Initiation of a dense cohort of seedlings, however, could modify fire behavior to reduce the effectiveness of the original fuel treatment (Stephens and Moghaddas, 2005a,c). In this case, implementing a treatment that does not create a soil substrate (such as the mastication treatment applied in this study) might better achieve objectives. Managers should consider the tradeoffs between enhancing the potential for conifer and hardwood regeneration versus the potential decrease in fuel treatment effectiveness that regeneration may cause in the future in the form of ladder fuels. Where recruitment of specific conifer species and black oak are desired in the short term, managers may need to consider using planted material grown from local seed sources.

5. Conclusion

The species composition and density of seedling recruitment resulting from a treatment can greatly influence future stand structure and corresponding habitat quality and fire resistance. Previous studies have found a decline in sugar pine and ponderosa pine in dense stands of Sierran mixed conifer forests (Ansley and Battles, 1998; van Mantgem et al., 2004). The findings reported here corroborate these studies in that current conditions are not conducive to recruitment of ponderosa pine and sugar pine species. Our initial results indicate, that in this case, treatments used to reduce fire hazard may not result in retention or recruitment of California black oak and sugar pine seedlings. Managers should monitor seedling density and species composition where recruitment is considered a primary treatment goal. Where initiation of new cohorts of specific hardwood and conifer species is a key restoration goal, managers may need to consider planting individuals grown from local seed sources to augment natural regeneration.

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