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Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA

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ABSTRACT

Fire is a driver of ecosystem patterns and processes in forests globally, but natural fire regimes have often been altered by decades of active fire management. Following almost a century of fire suppression, many western U.S. forests have greater fuel levels, higher tree densities, and are now dominated by fire-sensitive, shade-tolerant species. These fuel-loaded conditions can often result in high-intensity crown fires replacing historic low- to moderate-intensity fire regimes. In the mixed-conifer forests of the California Sierra Nevada, thinning and prescribed fire are widely used to reduce fuels and shift future stand composition from shade-tolerant species to more fire-resistant pines (*Pinus lambertiana* and *Pinus jeffreyi*) that were historically more abundant. The impacts of these treatments, however, on forest regeneration composition and abundance are unclear. We examined the effects of prescribed fire and common thinning treatments (understory and overstory thinning) on microsite conditions, seed rain, and tree regeneration in an old-growth, mixed-conifer forest in the Sierra Nevada, California, USA. Treatments significantly altered environmental conditions, but there was substantial variation and overlap in conditions among treatments. Seed rain of shade-tolerant *Abies concolor* and *Calocedrus decurrens* was 5–26 times greater than *P. jeffreyi* and *P. lambertiana*, creating inertia in efforts to shift stands towards increased pine abundance. Survival of *Pinus* germinants was greatest in burned microsites. The burn-overstory thin treatment had both the highest mortality of advanced *A. concolor* and *C. decurrens* regeneration and the greatest increase in pine regeneration. Species occupied microsites gradating from low light/high moisture to high light/low moisture in the order: *C. decurrens*, *A. concolor*, *P. lambertiana*, and *P. jeffreyi*. Results suggest prescriptions may need to thin mature *A. concolor* and *C. decurrens* to significantly reduce their seed rain, create an abundance of burned open microsites, or plant *Pinus* seedlings to shift regeneration composition in treated stands.

1. Introduction

Fire is an important disturbance agent in many forests worldwide, shaping ecosystem patterns and processes (Naveh, 1974; Philips, 1974; Wein and MacLean, 1983; Gill et al., 1990; Coutinho, 1990; Agee, 1993). Natural fire regimes have been altered in many forest ecosystems from decades of active fire management (Cooper, 1960; Linder and Östlund, 1998; Fulé and Covington, 1998; Ward et al., 2001; Vigilante and Bowman, 2004; North et al., 2007). Fire exclusion is believed to be especially important in forests that were previously characterized by frequent, low- to moderate-intensity surface fires such as southwestern ponderosa pine, Sierra Nevada mixed-conifer, and central hardwood forests of North America (McKelvey et al., 1996; Covington, 2000; Shang et al., 2007). Fire exclusion in these forest types can result in greater canopy cover and density of shade-tolerant trees, higher fuel loads, and increased fuel continuity, increasing the potential for high-intensity stand replacement fires (Kilgore, 1973; Parsons and DeBenedetti, 1979; McKelvey et al., 1996; Weatherspoon and Skinner, 1996; North et al., 2005; Shang et al., 2007).

In response, federal and state forest agencies have increasingly focused on reducing forest fuels (SNEP, 1996; HFRA, 2003;

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California Board of Forestry, 2004; SNFPA, 2004). Thinning and/or prescribed fire have become common management tools in fire-suppressed forests to reduce the probability of high-intensity, stand-replacing wildfires (Graham et al., 2004; SNFPA, 2004; Agee and Skinner, 2005). In Sierran mixed-conifer forests a common secondary objective is to promote a composition change from fire-sensitive, shade-tolerant firs and incense-cedar (*Abies* sp. and *Calocedrus decurrens*), toward more fire-resistant, shade-intolerant species (*Pinus* sp.) which were more abundant prior to fire suppression (Stephens, 2000; SNFPA, 2004; North et al., 2007). There has been little research, however, on the effects of these restoration treatments on mixed-conifer regeneration dynamics which will affect future forest composition and fire resilience.

It is difficult to predict how fuel reduction treatments will affect regeneration in Sierran mixed-conifer forests. These forests have a spatially variable patch structure that interacts with thinning and fire to significantly change microsite conditions and competing vegetation (Wayman and North, 2007). Understory tree abundance and resource conditions differ between undisturbed mixed-conifer's three main vegetation patch types: open-canopy, closed-canopy, and shrub patches (North et al., 2002; Gray et al., 2005). Reductions in canopy cover can reduce regeneration of some species through exposure to high levels of direct solar radiation, resulting in desiccation (Fowells and Stark, 1965; McDonald, 1976). However reducing stem density with mechanical thinning can increase soil moisture availability, ameliorating exposure effects if seedlings are able to establish sufficient root depth before surface layers dry out (Haig et al., 1941). Disturbance of intact litter layers can promote seedling establishment under high insolation, since intact litter can dry out rapidly and reach high surface temperatures, causing high mortality of tree germinants (Isaac, 1943; Gray and Spies, 1997). Thinning and/or prescribed fire also impact shrub composition and abundance. Shrubs can provide protective cover facilitating regeneration, or compete with and suppress regeneration, depending on the ecosystem, shrub species, and tree species of interest (Tappeiner and Helms, 1971; Lanini and Radosevich, 1986; Gomez-Aparicio et al., 2004). To examine how fire and thinning treatments will affect mixed-conifer regeneration, inter- and intra-treatment changes in microsite conditions, seed abundance, seedling establishment, and seedling survival need to be followed to infer abiotic and biotic influences.

The objectives of this study were to investigate understory tree mortality and regeneration in response to burning and thinning treatments for the dominant tree species in a Sierra Nevada mixed-conifer forest: white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), sugar pine (*Pinus lambertiana* Dougl.) and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf). All overstory species reproduce exclusively by seed. We examined tree regeneration through its early life-cycle phases including seed quantity, germination, and establishment. We measured fixed plots before and after thinning and prescribed fire treatments, and quantified regeneration composition and abundance in relation to (1) seed production, (2) sown seedling germination and early survival in controlled microsites, (3) the distribution and frequency of understory tree mortality and natural regeneration, and (4) relationships between microsite conditions, burning and thinning treatments, and post-treatment regeneration. Our previous studies of regeneration in untreated stands (Gray et al., 2005) found all overstory species (except for *P. jeffreyi*) had greater regeneration under shadier conditions, suggesting increased understory light via canopy cover reductions may not promote seedling regeneration of both pine species (*P. lambertiana* and *P. jeffreyi*). We hypothesize that (1) burning would kill most established seedlings and saplings but would promote all species regeneration by reducing litter and shrub cover; (2) in all burning and thinning treatment combinations, seed rain for shade-tolerant *A. concolor* and *C. decurrens* will be much greater than pine seed rain, but total seed rain by species will be proportionally reduced by basal area removal; (3) germination and survivorship of sown seed will be highest for shade-tolerant species (*Abies* sp. and *Calocedrus* sp.) in closed-canopy conditions and understory thin treatments, while pine germination and survivorship will be highest in open conditions and overstory thins; (4) thinning would primarily affect resource levels, with shade-tolerant (*A. concolor* and *C. decurrens*) natural regeneration favored by higher soil moisture and shade conditions in light thinning (understory) treatments, and inhibited by high light levels in heavy thinning (overstory) treatments.

2. Materials and methods

2.1. Description of study site

The study was conducted in an unmanaged, old-growth forest at the Teakettle Experimental Forest (hereafter Teakettle) approximately 80 km east of Fresno, CA (36°58′N, 119°02′W) in the Sierra National Forest. Elevation within the study area ranges from 1900 to 2600 m. Common soils are well-drained Dystric and Lithic Xeropsamments of loamy sand to sandy loam textures derived from granitic rock (USDA Forest Service and Soil Conservation Service, 1993), and exposed granitic rock is common throughout the study area. The climate is Mediterranean, with annual precipitation of 125 cm falling almost entirely as snow between November and April (North et al., 2002). The mixed-conifer forest is dominated by *A. concolor* and *C. decurrens*, although the largest individual trees are *P. lambertiana* and *P. jeffreyi*. Red fir (*Abies magnifica* A. Murr.), California black oak (*Quercus kelloggi* Newberry), and bitter cherry (*Prunus emarginata* (Dougl. ex Hook.) D. Dietr.) are also present in small quantities. Prior to 1865 the fire return interval at Teakettle was 12–17 years, with only two small fires having occurred since 1865 (North et al., 2005). Stand structure changed dramatically during the 20th century, with an increase in smaller diameters classes, especially shade-tolerant white fir and incense-cedar (North et al., 2007).

2.2. Treatments and experimental design

Experimental treatment plots were established as a full factorial in a restricted randomized design, contrasting two levels of burning and three levels of thinning. The six treatments combinations (and abbreviations used in this paper) were as follows: no burn, no thin control (NB-NT); no burn, understory thin (NB-UT); no burn, overstory thin (NB-OT); burn, no thin (B-NT); burn, understory thin (B-UT); and burn, overstory thin (B-OT). The understory thinning prescription followed guidelines in the California spotted owl (CASPO) report (Verner et al., 1992). Only trees between 25 and 76 cm diameter at breast height (1.37 m, DBH) were removed, while retaining at least 40% canopy cover. Initially designed to minimize impact to spotted owl habitat, the CASPO guidelines are now widely used for fuel management treatments (SNFPA, 2004). The overstory prescription removed trees > 25 cm DBH, retaining approximately 22 regularly spaced large diameter trees (generally > 100 cm DBH) per hectare. Overstory thinning was widely practiced in Sierran forests before CASPO. In the Sierra Nevada, small trees (< 25 cm DBH) are sometimes removed with a separate service contract but are often left on site, as they were at Teakettle, with the intention that many would be killed by the logging and/or prescribed burning operations (Mark Smith, Sierra National Forest Silviculturist, pers.

commun.). Thinning treatments occurred during the fall of 2000 in the burn and thin plots (allowing slash to dry in place for 1 year). Thinning occurred on the thin only plots during the summer of 2001. Trees were limbed where they fell and slash was left in place.

Following typical management prescriptions, burning was applied after the first substantial fall rain in late October 2001 to avoid overstory ignition yet still consume surface fuels and small trees. Fire weather conditions at the time of burning were mild, with clear skies, dry bulb temperatures of 5–13 °C, relative humidity of 39–46%, and variable winds ranging from 0 to 8 km/h. This resulted in a slow creeping ground fire with mean flame heights under 2 m. Overstory thin plots were planted with 2-year-old container stock in 2002; planted stock accounted for less than 3% of total regeneration, and was excluded from analyses of regeneration.

Treatments were applied to eighteen 4 ha plots. The size and spatial placement of plots were determined following variogram and cluster analysis of mapped sample quadrats (North et al., 2002). Each treatment combination was applied to three 4 ha plots. A permanent sampling grid was established in each plot, with 49 grid points established on a 25 m × 25 m spacing in one of the three replicate plots per treatment combination (to facilitate spatial modeling of measurements from multiple studies, $n = 6$), and 9 grid points established on a 50 m × 50 m spacing in the remaining two plots per treatment ($n = 12$).

Experimental treatment combinations were assigned with restricted randomization because prescribed fire plots were clustered in three groups for practical and containment reasons. All plots were individually lit under similar weather conditions. We believe plots, because they were individually lit, are replicates of burn conditions, rather than pseudoreplicates (sensu Hurlbert, 1984), however, determining what qualifies as an independent sample within a burn perimeter is the subject of ongoing debate (Bataineh et al., 2007).

2.3. Data collection

Stand structure, microsite environmental variables, understory vegetation, and seedling composition and abundance were measured prior to and after treatments, while cone crop, and sown seed germination/survival data were collected post-treatment. All live and dead trees ≥ 5 cm DBH in each 4 ha plot were mapped, tagged, measured, and identified to species prior to treatment (1998–2000) and after treatment (2002–2003). We used these inventories to calculate pre- and post-treatment basal areas.

Cover of shrubs and herbs by species, cover of substrates (coarse woody debris by decay class, mineral soil, litter, rock), and litter depth were estimated within a 1.78 m radius (10 m^2) microplot around each grid point during the pretreatment summers of 1998–1999 and postreatment summers 2002–2004 (Wayman and North, 2007). Pre- and post-treatment solar radiation above each grid point was estimated using digital hemispherical photographs taken during the summer of 2000 and September 2003 as described by Gray et al. (2005). Estimated solar radiation variables were full-year indirect site factor (ISF), direct site factor (DSF) and total site factor (TSF, calculated as 0.9DSF + 0.1ISF), or the estimated proportion of indirect, direct, and total radiation compared to an open site at the same latitude, respectively.

Volumetric soil water content in the top 15 cm of soil at each grid point was measured prior to treatments during October 1998 and May 1999, and multiple times after treatments during the growing seasons of 2002, 2003, 2004, and 2005. We attempted to sample soon after snowmelt (mid-May to early June), in early fall, and four to five times in between. Soil moisture was estimated at each grid point using time domain reflectometry (TDR, model 1502C, Tektronix Inc., Beaverton, OR), with permanently installed 30 cm stainless steel probes inserted at an angle to sample the upper 15 cm of mineral soil. TDR measurements were calibrated with six relatively undisturbed soil cores, with the same methods used by Gray and Spies (1995) (except that rods were spaced 5 cm apart instead of 10 cm). Three calibration cores were taken from both closed-canopy and open-canopy sites. A single cubic polynomial equation describing all six cores provided the best fit for calibrating TDR measurements to volumetric water content ($F_{3,146} = 2563.2$, $p < 0.0001$, $R^2 = 0.98$):

$$H_2O = 10.8049 - 18.7982\frac{1}{V} + 10.2857\left(\frac{1}{V}\right)^2 - 1.0168\left(\frac{1}{V}\right)^3 \qquad (1)$$

where H_2O = volumetric soil moisture (%), and V = TDR measured velocity of the electric pulse (mm/ns).

Seedling germination and survival by species, treatment, and vegetation patch type was studied in a sown seed experiment. The three dominant vegetation patch types at Teakettle, closed-canopy forest, whitethorn ceanothus (*Ceanothus cordulatus* Kellogg), and open canopy, were sampled using a randomized complete block design. Within each of the 6 treatment plots with 49 sample points, 3 grid points per each of the 3 vegetation patch types were randomly selected (54 grid point total). At each of these grid points, two 0.49 m^2 seed–predator exclosures made of galvanized hardware cloth (1.25 cm mesh grid size) were installed. Exclosure sides were buried in the substrate at least 15 cm deep and hardware cloth tops secured to the sides. Seeds of *A. concolor*, *A. magnifica*, *C. decurrens*, *P. jeffreyi*, and *P. lambertiana* were obtained for the appropriate seed zone from the USDA Forest Service Nursery in Placerville, CA, and sown within exclosures during the fall of 2002. We attempted to sow comparable numbers of viable seed for each species based on nursery tests; number of seed, viability rates (percent), and numbers of estimated viable seed sown in each exclosure were 70–72–50 for *A. concolor*, 50–91–46 for *A. magnifica*, 100–47–47 for *C. decurrens*, 50–99–50 for *P. jeffreyi*, and 55–54–30 for *P. lambertiana* (fewer seeds were available for *P. lambertiana*). Germination rates, growth, damage, and mortality were tracked biweekly from May to October of 2003, and recorded again in early June and mid-September in 2004.

Counts of all visible current year cones were made with binoculars on one large diameter tree of each *Abies* and *Pinus* species in each of the 18 plots in July and most Septembers of 2000–2003 from permanently marked locations. Counts do not represent absolute tree totals, but provide relative standing cone crop differences between species, treatments, and years. The density of tree seed reaching the ground was sampled post-treatment with bear-proof seed traps of 0.25 m^2 surface area. Twenty-five seed traps were arranged 25 m apart on a grid within the central hectare of each plot, providing a 75 m buffer between seed traps and plot edges. Wind dispersal of most *P. lambertiana* and *P. jeffreyi* seed is within 30 m of the parent tree (Kinloch and Scheuner, 1990; Vander Wall, 1992), while the majority of *A. concolor* and *A. magnifica* seed disperses up to 40–60 m into forest openings (Gordon, 1970). The high wing to weight ratio of *C. decurrens* seeds may permit abundant dispersal beyond this study's buffer size, although exact distances have not been documented (Powers and Oliver, 1990). Seed traps were installed in the NB-NT plots in August 2000, and in all other no-burn plots in August 2001. Burn treatments in October 2001 occurred after the fall period of most conifer seed dispersal and were closely followed by winter snows, so traps were installed in the burn treatments in June and July 2002. Every spring after snow melt, seed traps were visited and seed deposited during the prior fall and winter was removed, dried, and counted by species.

Seedlings and saplings were tallied on 3.5 m radius (38.5 m^2) regeneration microplots centered on each grid point prior to treatments (summer of 2000) and after treatments (summers of 2002, 2003, 2004). All trees 5 cm tall and < 5 cm DBH were counted by species and quadrant in two size classes: 5–50 cm tall (“seedlings”) and > 50 cm tall (“saplings”). The 5 cm minimum height cutoff excluded the more temporally variable pool of first-year germinants. In overstory thinned plots, bareroot seedlings were planted; these planted seedlings within microplots were identified and excluded from analyses.

2.4. Statistical analyses

Changes in overstory basal area and microsite conditions by treatment combination were compared for pre- and post-treatment data with a Tukey’s studentized range test (HSD) evaluated using the likelihood ratio Type I *F*-test value with a $p < 0.05$ (GLM procedure, SAS Institute Inc., 1999). We also analyzed selected post-treatment environmental variables simultaneously at the microplot level by burning, thinning, and burning thinning treatment interactions using a permutation multivariate analysis of variance (PerMANOVA procedure, McCune and Mefford, 1999; Anderson, 2001). Environmental variables were included in the PerMANOVA procedure if they exceeded a threshold variance (R^2 0.05) in the NMS ordination of seedling frequency in relation to all environmental variables (see below). PerMANOVA was set up as a factorial experimental design, and used a relativized Euclidean distance metric for the environmental data matrix. Initial starting configuration was random, with 4999 runs of randomized data. A Monte Carlo test using the randomized data runs indicated environmental space was significantly different from the randomized data for post-treatment environmental variables ($p = 0.0002$).

The effect of treatments and vegetation patch types on germinant survival in the seed-sowing experiment was analyzed with a mixed-model ANOVA. The experiment was a randomized complete block (treatments were blocks, patches were selected randomly within them), so the effect of vegetation type treat-treatment interactions could not be tested. Germinant survival was calculated as the number of live seedlings found in the two exclosures on a grid point at the end of the second growing season in September 2004, divided by the maximum number of germinants (total live and dead) counted in the same two exclosures for any sample date. Grid point exclosure pairs without germinants were treated as missing cells in the analysis. Germinant survival was arcsin, square-root transformed to reduce inequality of variance (Sabin and Stafford, 1990). Each species-specific model was weighted by the maximum number of germinants in 2003.

Seed rain density and cone counts in relation to treatments and treatment interactions were analyzed by species with a repeated measures randomized design ANOVA (MIXED procedure, SAS Institute Inc., 1999). Seed rain analyses only used the fully sampled fall 2003 and 2004 data. Because the desired scope of inference was the sampled years (as opposed to all years), sample year was included as a fixed effect. Density was square-root transformed to reduce inequality of variances across treatments. To assess patterns of seed production in relation to basal area, seed counts were summed for 2003 and 2004, and the ratio of each species’ seed density to its basal area per plot was analyzed with a randomized design ANOVA, with the ratio being log-transformed prior to analysis. For all ANOVAs, effects were considered significant if the likelihood ratio Type III *F*-test value associated resulted in a $p < 0.05$. Least-square means tests on significant effects were applied to assess significant differences among means using the Tukey adjustment to keep experiment-wise error rates to $p < 0.05$.

The analysis of treatment effects on seedlings used the ratio of seedling frequency (hereafter referred to as “frequency”) as the dependent variable, calculated as the number of quadrants occupied by a species over the total number of quadrants per grid point (4). Although seedling density is a commonly used metric in regeneration studies, we believe frequency may be a better measure of site suitability than density at our study site. Seedling density can be more sensitive to many additional factors than seedling frequency, including seed production and predation. In our study, dense patches of seedlings were common, yet will result in only a few surviving saplings due to density-dependent mortality. Seedling frequency was averaged at the plot level. The effects of burning, thinning, and their interaction on seedling frequency were assessed for each species with ANOVA (GLM procedure, SAS Institute Inc., 1999). Seedling frequencies were weighted by the number of grid point microplots per plot. Models tested for three types of treatment effects: frequency differences between pre-treatment (2000) and immediate post-treatment (2002) measurements (referred to as treatment “immediate change”), differences between immediate post-treatment and 2004 (referred to as treatment “response”), and differences between pre-treatment and 2004 (referred to as “overall change”). The analyses of immediate change, response, and overall change allow for examination of mortality, short-term regeneration responses after treatment, and their directional change in relation to pre-treatment abundance. Although our sampling protocol did not track the fate of individual seedlings, the annual census at the quadrant level did capture important mortality and regeneration events. Seedling frequency was insufficient across treatments to develop models for *A. magnifica*, *P. emarginata*, or *Q. kelloggi*. Immediate change, response, and overall change of sapling frequency with respect to treatment combinations was analyzed using the same ANOVA model used for seedlings described above. Only *A. concolor* and *C. decurrens* sapling frequencies were examined, due to extremely low sapling frequencies for all other species.

The post-treatment relationship between environmental variables and response seedling frequency (i.e. frequency of 2004 regeneration less regeneration frequency in 2002) was evaluated using nonmetric multidimensional scaling (NMS procedure, McCune and Mefford, 1999) (Krustal, 1964; Mather, 1976; McCune and Grace, 2002). The frequency of each species at each microplot comprised the main data matrix and post treatment environmental variables (light levels, soil moisture, shrub cover, etc.) at each microplot comprised the secondary matrix. The ordination used relativized Euclidian distance measures, starting configuration was random, with 50 runs of real data, 50 runs with randomized data, and a maximum of 200 iterations. Dimensionality and solution stability were assessed as described by Gray et al. (2005), and the final solution was two-dimensional. A Monte Carlo test indicated the ordination was significantly different from randomized data ($p = 0.032$). A joint plot of environmental variables was overlain on the two-dimensional ordination graph to better visualize which environmental variables were associated with patterns in species composition. The direction and length of each joint plot vector indicates the directionality and strength of each environmental variable in relation to the ordination structure as described by McCune and Grace (2002).

3. Results

3.1. Stand structure and environmental variables

Total live tree basal area reductions by treatment were as follows: B-NT, 7%; NB-UT, 32%; B-UT, 42%; NB-OT, 61%; B-OT, 69%, with the largest reductions attributed to *A. concolor* (Table 1). All treatments except B-NT greatly reduced densities of trees less than 75 cm DBH. Understory thins and unthinned plots had no major reductions in large tree (> 75 cm DBH) stem densities, while overstory thinning reduced large tree densities (see North et al., 2007). For saplings (trees 50 cm tall and < 5 cm DBH), there was a significant reduction in *A. concolor* frequency immediately (2000 vs. 2002) after treatments in thinned compared to unthinned plots ($F_{2,12} = 7.84$, $p = 0.007$) (Fig. 1). Reductions in *C. decurrens* sapling frequency were greater in burned than unburned treatments ($F_{1,12} = 6.02$, $p = 0.030$), and greater in thinned versus unthinned treatments ($F_{2,12} = 4.43$, $p = 0.036$), with the greatest reductions occurring in B-UT, B-OT, and NB-UT treatments. Additional mortality and growth in the subsequent 2 years post-treatment did not alter initial treatment effects.

Ground cover was burned on approximately 37, 67, and 73% of the B-NT, B-UT, and B-OT treatment areas, respectively. Calculated scorch heights on saplings were 1–2 m; there were some flare-ups in pockets of small trees, but tree mortality from fire was apparently low to moderate. Tree densities in the 5–25 cm DBH size class were approximately 20% lower in the no thin and 45% lower in the thin plots when comparing burn to no-burn treatments.

Estimated light levels (ISF, DSF, and TSF) varied slightly prior to treatment, with lowest levels in the NB-UT and NB-OT treatments and highest levels in the B-OT treatments. After treatment ISF, DSF, and TSF were greatest in overstory thins and lowest in no thin treatments (Table 2). Within a given thin type, light levels tended to be slightly higher in burn than in no-burn treatments. *C. cordulatus* and total shrub cover decreased with thin intensity (NT to UT to OT) immediately following treatments in 2002, but by 2004 increased with thinning intensity. Post-treatment forb cover was low in the unburned and B-NT treatments, but 2–10 times greater in the B-UT and B-OT treatments and greater in 2003 than in 2002. Pre-treatment early season (1999) and late season (1998) soil moisture did not differ among treatments. Post-treatment mean growing season soil moisture was greatest in the NB-OT treatments and usually lowest in the NT treatments, although B-OT became drier than the other treatments with time. Post-treatment soil disturbance was greater in OT than in UT treatments and greater in burn than in no-burn treatments. Post-treatment litter cover was lowest in the B-UT, B-OT, and NB-OT treatments, while post-treatment litter depth was lowest in the B-UT and B-OT treatments. Post-treatment cover of coarse and fine wood was lower in burn than in no-burn treatments and high in the NB-UT and NB-OT treatments. Using permutation MANOVA to compare microsite conditions simultaneously at the microplot level, treatments significantly differed by thin, burn, and thin burn interaction effects ($F_{2,396} = 23.6$, $p = 0.0002$; $F_{1,396} = 62.5$, $p = 0.0002$; $F_{2,396} = 16.0$, $p = 0.0002$, respectively).

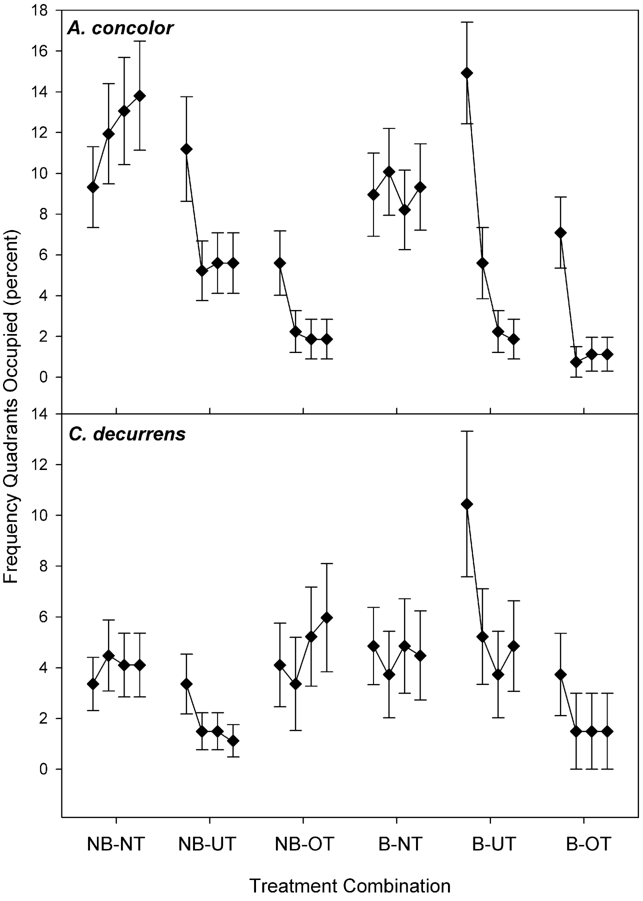

Fig. 1. Mean (S.E.) frequency of *Abies concolor* and *Calocedrus decurrens* saplings (trees 50 cm tall and < 5 cm DBH) by year, and treatment combination. Each group of bars connected by the darker tend line represents 4 years of observations (2000, 2002, 2003, and 2004 moving from left to right). Treatment combination codes refer to burn treatment (NB = no burn, B = burn) and the letters after the dash refer to thinning treatment (NT = no thin, UT = understory thin, OT = overstory thin).

3.2. Cone crops and seed rain

Pinus species produced as many or more cones per tree in most years than did *A. concolor* (Table 3). The number of cones per tree was greater in overstory thins than in other treatments for *P. lambertiana* ($F_{2,12} = 3.9$, $p = 0.048$), and was greater in burn than no-burn treatments for *P. jeffreyi* ($F_{1,12} = 11.5$, $p = 0.005$). Seed rain

Table 1

Pre-treatment total basal area, post-treatment species basal area, and post-treatment total basal area by treatment combination

Species	Basal area (m^2/ha) by treatment combination					
	NB-NT	NB-UT	NB-OT	B-NT	B-UT	B-OT
Total pre-treatment	51.4 (3.5)^{a}	62.4 (0.3)^{b}	57.5 (5.0)^{ab}	57.7 (3.3)^{ab}	64.9 (2.9)^{b}	55.6 (2.2)^{ab}
Abies concolor	26.8 (3.9)^{ab}	19.6 (2.8)^{abc}	8.8 (0.3)^{c}	31.8 (1.8)^{a}	14.4 (3.6)^{bc}	7.5 (1.5)^{c}
Abies magnifica	6.6 (3.9)^{a}	4.5 (4.5)^{a}	0.6 (0.6)^{a}	0.0 (0.0)^{a}	0.3 (0.2)^{a}	0.0 (0.0)^{a}
Calocedrus decurrens	5.4 (2.9)^{a}	5.2 (3.3)^{a}	1.6 (1.3)^{a}	8.5 (2.2)^{a}	11.7 (3.1)^{a}	2.4 (0.1)^{a}
Pinus jeffreyi	3.6 (1.4)^{a}	2.8 (1.1)^{a}	3.8 (0.9)^{a}	3.9 (1.1)^{a}	7.4 (1.9)^{a}	2.6 (0.9)^{a}
Pinus lambertiana	9.0 (3.1)^{a}	10.2 (1.8)^{a}	7.8 (1.7)^{a}	9.5 (3.0)^{a}	3.4 (0.7)^{a}	4.4 (1.2)^{a}
Other*	0.1 (0.0)^{a}	0.0 (0.0)^{a}	0.2 (0.1)^{a}	0.0 (0.0)^{a}	0.3 (0.1)^{a}	0.5 (0.4)^{a}
Total post-treatment	51.4 (3.5)^{a}	42.3 (2.4)^{b}	22.7 (1.6)^{c}	53.7 (2.2)^{a}	37.5 (0.9)^{b}	17.4 (2.2)^{c}

Values are means with standard errors in parentheses. Values within a row with different superscripts are different at the a = 0.05 level.

* includes *P. emarginata* and *Q. kelloggi*.

Table 2
Selected microsite environment variables by treatment combination

Microsite environmental variables	Treatment combination					
	NB-NT	NB-UT	NB-OT	B-NT	B-UT	B-OT
ISF (pre-treatment)	0.3 (0.01)^{ab}	0.25 (0.01)^{b}	0.28 (0)^{b}	0.3 (0.01)^{ab}	0.29 (0.01)^{ab}	0.34 (0.01)^{a}
ISF (post-treatment)	0.29 (0.01)^{d}	0.38 (0.01)^{c}	0.50 (0.01)^{b}	0.28 (0.01)^{d}	0.42 (0.01)^{c}	0.55 (0.01)^{a}
DSF (pre-treatment)	0.31 (0.05)^{ab}	0.22 (0.02)^{b}	0.28 (0)^{ab}	0.33 (0.02)^{ab}	0.27 (0.01)^{ab}	0.36 (0.02)^{a}
DSF (post-treatment	0.35 (0.02)^{c}	0.44 (0.02)^{b}	0.58 (0.02)^{a}	0.36 (0.02)^{c}	0.50 (0.02)^{b}	0.65 (0.02)^{a}
TSF (pre-treatment)	0.31 (0.04)^{ab}	0.22 (0.02)^{b}	0.28 (0)^{ab}	0.32 (0.02)^{ab}	0.27 (0.01)^{ab}	0.36 (0.02)^{a}
TSF (post-treatment)	0.35 (0.02)^{c}	0.44 (0.02)^{b}	0.57 (0.02)^{a}	0.35 (0.02)^{c}	0.49 (0.02)^{b}	0.64 (0.02)^{a}
C. cordulatus cover 1999 (%)	14.6 (7.6)^{a}	9.1 (4.7)^{a}	11.1 (4.2)^{a}	13.6 (3.2)^{a}	5.9 (1.8)^{a}	11.1 (4.0)^{a}
C. cordulatus cover 2002 (%)	8.5 (2.5)^{a}	5.4 (1.7)^{abc}	0.8 (0.5)^{c}	7.5 (2.3)^{ab}	2.4 (0.9)^{abc}	1.2 (0.6)^{bc}
C. cordulatus cover 2004 (%)	8.7 (2.4)^{bc}	6.0 (1.7)^{b}	3.8 (1.5)^{ab}	6.7 (2.0)^{bc}	3.5 (1.1)^{a}	6.7 (1.6)^{bc}
Shrub cover 1988–1999 (%)	21.8 (6.0)^{a}	11.2 (4.5)^{a}	12.0 (4.3)^{a}	21.4 (6.6)^{a}	12.9 (2.2)^{a}	18.0 (2.0)^{a}
Shrub cover 2002 (%)	12.5 (2.9)^{a}	8.7 (2.4)^{abc}	1.5 (0.7)^{c}	10.2 (2.6)^{ab}	3.6 (1.1)^{bc}	1.3 (0.6)^{c}
Fine wood cover 2002 (%)^{1}	9.6 (1.5)^{a}	14.2 (1.8)^{a}	20.5 (2.6)^{b}	6.3 (1.2)^{a}	8.5 (1.3)^{a}	10.0 (1.4)^{a}
Coarse wood cover 2002 (%)^{1}	8.6 (2.2)^{ab}	13.2 (2.6)^{b}	10.9 (2.0)^{ab}	4.9 (1.1)^{a}	3.3 (0.8)^{a}	8.5 (1.7)^{ab}
Litter depth 2002 (cm)	2.7 (0.4)^{a}	2.0 (0.3)^{a}	2.4 (0.3)^{a}	2.3 (0.3)^{a}	1.6 (0.2)^{a}	0.8 (0.1)^{b}
Litter cover 2002 (%)	61.6 (3.6)^{a}	57.8 (3.8)^{ab}	46.0 (3.6)^{b}	67.6 (3.6)^{a}	47.2 (3.7)^{b}	16.5 (2.6)^{c}
Forb cover 2003 (%)	5.1 (1.7)^{c}	3.0 (1.1)^{c}	2.8 (1.0)^{c}	7.4 (1.9)^{bc}	14.8 (2.5)^{ab}	15.6 (2.8)^{a}
Forb cover 2004 (%)	3.9 (1.5)^{c}	5.7 (1.9)^{c}	5.6 (1.7)^{c}	5.7 (1.9)^{c}	25.0 (3.7)^{b}	40.0 (3.6)^{a}
H_2O_1998 (%)^{2}	6.2 (1.6)^{a}	4.6 (0.4)^{a}	4.6 (0.4)^{a}	5.2 (1.9)^{a}	4.9 (0.6)^{a}	3.8 (0.2)^{a}
H_2O_1999 (%)^{2}	14.2 (1.6)^{a}	13.3 (1.8)^{a}	14.2 (0.6)^{a}	12.6 (2.2)^{a}	14.9 (0.1)^{a}	11.2 (0.3)^{a}
H_2O_2002 (%)^{2}	4.3 (0.2)^{a}	7.3 (0.3)^{bc}	7.9 (0.5)^{c}	4.7 (0.2)^{a}	6.8 (0.3)^{bc}	5.9 (0.2)^{ab}
H_2O_2003 (%)^{2}	8.3 (0.8)^{ab}	8.9 (0.4)^{ab}	10.9 (1.0)^{a}	7.6 (0.6)^{b}	9.6 (0.5)^{ab}	7.9 (0.4)^{b}
H_2O_2004 (%)^{2}	5.7 (0.8)^{ab}	5.5 (0.3)^{ab}	7.4 (0.9)^{a}	4.8 (0.5)^{b}	5.5 (0.3)^{ab}	4.5 (0.2)^{b}
H_2O_2005 (%)^{2}	8.6 (0.9)^{b}	11.2 (0.8)^{ab}	12.9 (1.2)^{a}	9.0 (0.7)^{b}	11.8 (1.1)^{ab}	9.1 (0.5)^{b}
Burn disturbance 2002 (%)^{3}	0	0	0	37	67	73
Soil disturbance 2002 (%)^{3}	0	7.5	10.5	0	12	18

Values are means with standard errors in parentheses. Values within a row with different superscripts are different at the $a = 0.05$ level. ISF, DSF, and TSF are proportions of indirect, direct, and total light compared to open conditions. Numbers in variable names refer to year of measurement. (1) The cutoff between coarse and fine wood was 10 cm diameter, (2) H_2O refers to volumetric soil moisture in the top 15 cm of soil, (3) burn and soil disturbance are the percent of all grid points in a treatment combination with over 40% of their surface area burned, or disturbed (by skid trails, slash piles, etc.), respectively.

differed among species, treatments, and years. Seed rain density was much higher for *A. concolor* and *C. decurrens* than for the *Pinus* species (Fig. 2). Few seeds were detected from the fall 2000 crop in the NB-NT treatments (not shown), but seed rain was abundant in fall 2001 and 2003 for most species. Seed density declined with increased thinning intensity (NT to UT to OT) for *A. concolor* ($F_{2,12} = 8.3$, $p = 0.005$). Higher *C. decurrens* seed density was suggested by the ANOVA analysis in the understory thins ($F_{2,12} = 3.1$, $p = 0.085$). For other trees species there were no significant differences by thinning treatment.

Seed density was higher in burn than in no-burn treatments for *C. decurrens* ($F_{1,12} = 5.1$, $p = 0.044$) and *P. jeffreyi* ($F_{1,12} = 6.6$, $p = 0.025$). For *P. jeffreyi* the interaction effect with thinning was significant ($F_{2,12} = 4.8$, $p = 0.029$), apparently caused by low seed density in B-NT compared to other burn treatments. *P. lambertiana* seed density did not differ significantly among treatments. Although the late October 2001 burn prescriptions occurred after the main period of seed dispersal for these species (Fowells and Schubert, 1956), consumption of forest floor was not complete (Table 2), so it is likely that some of the unmeasured fall 2001 seed crop contributed to the seedlings found in subsequent years in the burn treatments. The seed rain measurements tended to show similar inter-annual patterns as cone crop abundance (e.g., high *A. concolor* seed and cone crop densities in 2001 and 2003, and low in 2002).

The ratio of seed to basal area did not differ by thinning treatment for *A. concolor* ($F_{2,12} = 1.8$, $p = 0.203$) (Fig. 3), suggesting that most of the decline in seed density with thinning intensity was a result of the decline in basal area (Table 1). However, seed ratios for *C. decurrens* were greater in thin treatments than in no-thin treatments ($F_{2,12} = 9.0$, $p = 0.004$). The interaction effect was also significant for *C. decurrens* ($F_{2,12} = 4.2$, $p = 0.042$), apparently caused by low seed ratios in NB-OT compared to the other thin treatments. For *P. lambertiana* there was a suggestive increase in the ratio of seed per unit basal area with thinning ($F_{2,12} = 3.7$, $p = 0.056$) and with burning ($F_{1,12} = 3.6$, $p = 0.083$).

3.3. Sown seed survival

Germination rates in the seedling exclosures were often lower for *A. concolor* and *C. decurrens* than other species, but all treatment by patch combinations had germinants from which to assess survival. Germination was higher in burn treatments than in no-burn treatments for *P. jeffreyi* ($F_{5,45} = 2.60$, $p = 0.038$) and suggestive for *P. lambertiana* ($F_{5,45} = 2.25$, $p = 0.066$). Full emergence of germinating seedlings and timing of mortality occurred

Table 3
Mean number of cones (standard error) per tree by species and post-treatment date

Date	*A. concolor* (*n* = 18)	*Abies magnifica* (*n* = 5)	*P. jeffreyi* (*n* = 18)	*P. lambertiana* (*n* = 18)
July 2001	316.3 (46.0)	72.8 (21.4)	18.9 (9.2)	83.3 (22.1)
July 2002	22.7 (10.8)	37.8 (29.4)	21.0 (4.0)	141.8 (18.0)
July 2003	87.4 (19.6)	70.2 (23.6)	96.6 (23.7)	101.9 (25.9)
September 2003	118.2 (26.7)	96.8 (34.1)	149.4 (27.7)	149.5 (27.6)
July 2004	11.0 (4.9)	6.0 (1.2)	35.4 (6.2)	91.2 (23.0)
September 2004	1.7 (0.6)	3.3 (1.7)	4.6 (1.3)	82.6 (12.2)

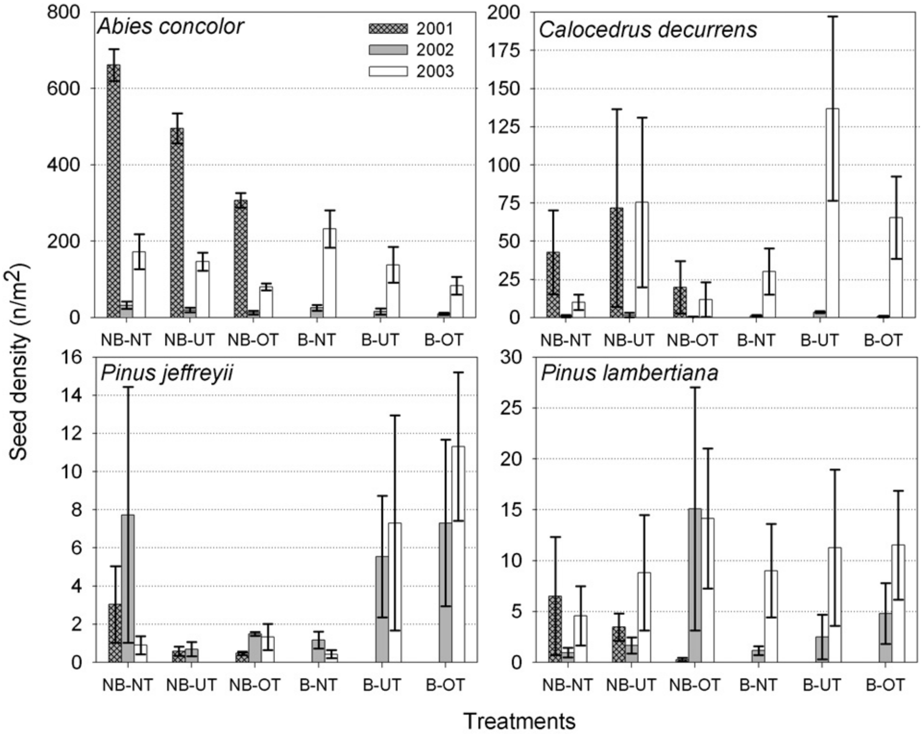

Fig. 2. Mean (S.E.) seed rain by treatment, species and year of fall dispersal ($n = 3$). The letters before the dash of each treatment code refer to burn treatment (NB = no burn, B = burn) and the letters after the dash refer to thinning treatment (NT = no thin, UT = understory thin, OT = overstory thin). Burn (B) treatments were not completed in time for sampling in 2001. Note that the *Y*-axes have different scales.

later in the growing season (about 2 weeks) in no thin treatments compared to understory and overstory thin treatments. For *A. concolor* in particular, most of the first-year mortality occurred during the first week of June (Fig. 4). Thereafter, mortality rates were steady during the months of June through August, with fairly low mortality after the first growing season. Of the 2735 dead germinants observed, the estimated cause of mortality for most was apparent desiccation (59%), but clipping (probably by cutworms, *Noctuidae*) was common (20%), and 20% died from unknown causes. Species' survival at the end of the second summer, as a percent of total seedlings germinated, was 16.7% for *P. jeffreyi*, 13% for *P. lambertiana*, 6.6% for incense-cedar, 4.6% for *A. concolor*, and 2.6% for *A. magnifica*.

Germinant survival was significantly lower in the NB-NT control than in the B-UT treatment for *A. magnifica* ($F_{5,45} = 3.64$, $p = 0.008$) and *P. jeffreyi* ($F_{5,42} = 4.08$, $p = 0.004$). Survival in the control was lower than the B-NT treatment for *P. lambertiana* ($F_{5,38} = 2.54$, $p = 0.044$) (Fig. 5a). Survival for the *Pinus* species tended to be highest in the burned treatments. Survival was lower in bare ground patch types than in the (previously) closed-canopy patch types for *A. concolor* ($F_{2,39} = 3.61$, $p = 0.036$), *A. magnifica* ($F_{2,45} = 3.26$, $p = 0.048$), *P. jeffreyi* ($F_{2,42} = 3.89$, $p = 0.028$), and *P. lambertiana* ($F_{2,38} = 6.24$, $p = 0.005$). Germinant survival in bare patches was also lower than in *C. cordulatus* patches for *A. concolor* and *P. jeffreyi* (Fig. 5b).

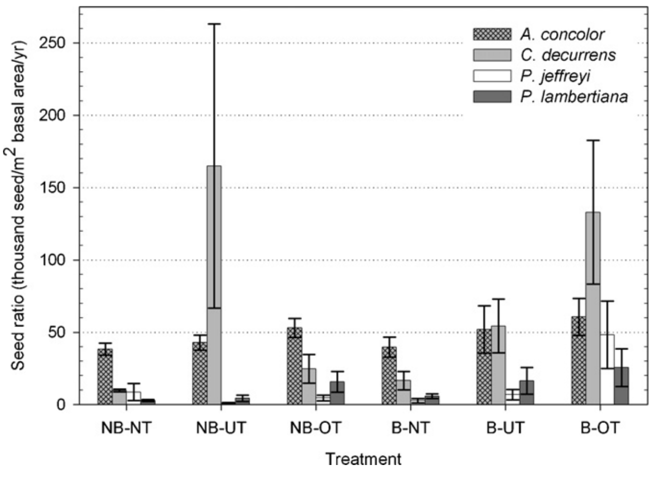

Fig. 3. Mean (S.E.) ratio of seed rain to basal area by species and treatment combination for the fall 2003 seed crop ($n = 3$).

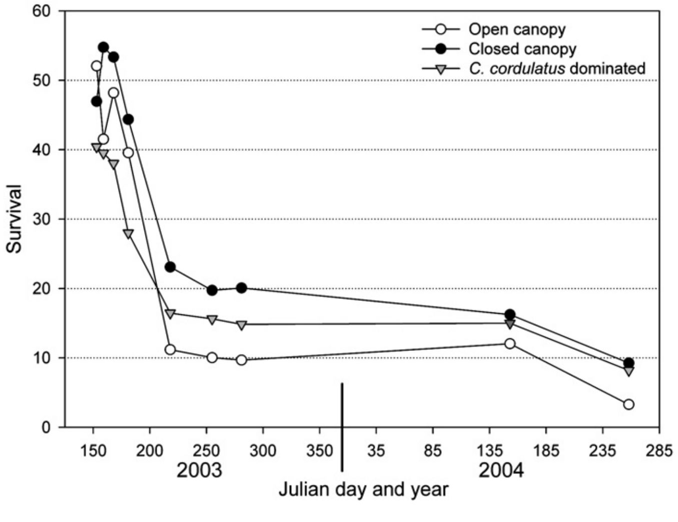

Fig. 4. Mean survival (percent) of all germinated seedlings in sown seed study grouped by vegetation patch time over time.

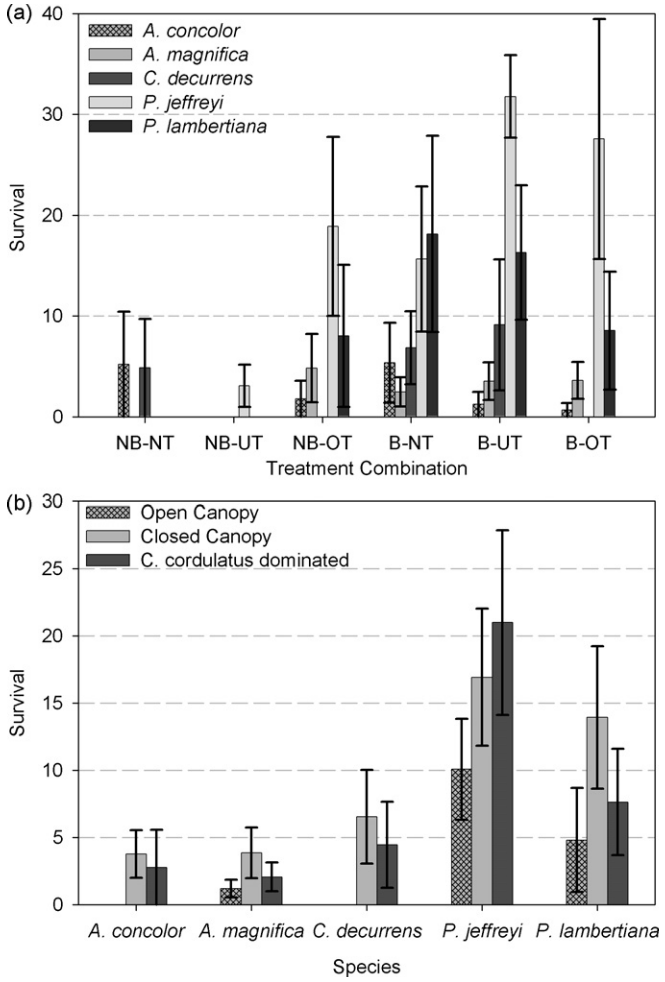

Fig. 5. Mean (S.E.) survival (percent) of germinated seedlings at the end of the second growing season in the sown seed study by species in relation to (a) treatment combination and (b) patch type ($n = 9$ and < 18, respectively; grid points without germinants were excluded).

3.4. Recruited seedling response to treatments

Treatment effects on seedling (individuals 5–50 cm tall) frequencies were evaluated over three periods: immediately after treatments (difference in 2000 and 2002 frequencies), subsequent response (difference in 2002 and 2004 frequencies) and overall changes from pre-treatment values (difference between pre-treatment and 2004 frequencies) (Fig. 6; actual frequencies by year are shown). Immediate change from thinning reduced seedling frequencies for *A. concolor* ($F_{2,12} = 7.85$, $p = 0.0066$). *C. decurrens* frequencies were reduced in burned ($F_{1,2} = 11.61$, $p = 0.0052$) and thinned ($F_{2,12} = 10.78$, $p = 0.0021$) treatments. *P. jeffreyi* frequencies were reduced in the thinned treatments ($F_{2,12} = 10.89$, $p = 0.0020$), but there were no seedlings present in half of the treatment combinations prior to treatment. Burn, thin, and burn thin interactions were not associated with immediate impacts to seedling frequencies for *P. lambertiana.*

Subsequent seedling frequency responses (2002–2004) tended to increase from immediate post-treatment levels in thinned areas, but varied with treatment type and species. Thinning increased seedling response frequency for *C. decurrens* ($F_{2,12} = 10.20$, $p = 0.0026$) and *P. jeffreyi* ($F_{2,12} = 4.37$, $p = 0.0376$). *C. decurrens* increases were greater in understory versus overstory thins, while the reverse was true for *P. jeffreyi*. *A. concolor* response frequencies increased in the burn treatments ($F_{2,12} = 7.72$, $p = 0.0167$). *P. lambertiana* frequency responses were not associated with burn, thin, or burn thin interaction. *P. lambertiana* frequency responses increased most in the B-NT treatment, but increases during the post-treatment period occurred in all treatments except the NB-NT control.

Overall (2000–2004) changes in regeneration frequency varied by species and treatment combination. Overall change for *A. concolor* was associated with both burning ($F_{1,12} = 8.64$, $p = 0.0124$) and thinning ($F_{2,12} = 9.03$, $p = 0.0040$). *A. concolor* frequency declined the most in the NB-OT treatment (15.1 change), while the greatest increases were in the B-NT and B-UT treatments (15.8 and 14.8 change). Thinning increased *C. decurrens* seedling frequencies ($F_{2,12} = 7.82$, $p = 0.0067$), with large increases in understory thins (21.7 change), and the lowest increases in

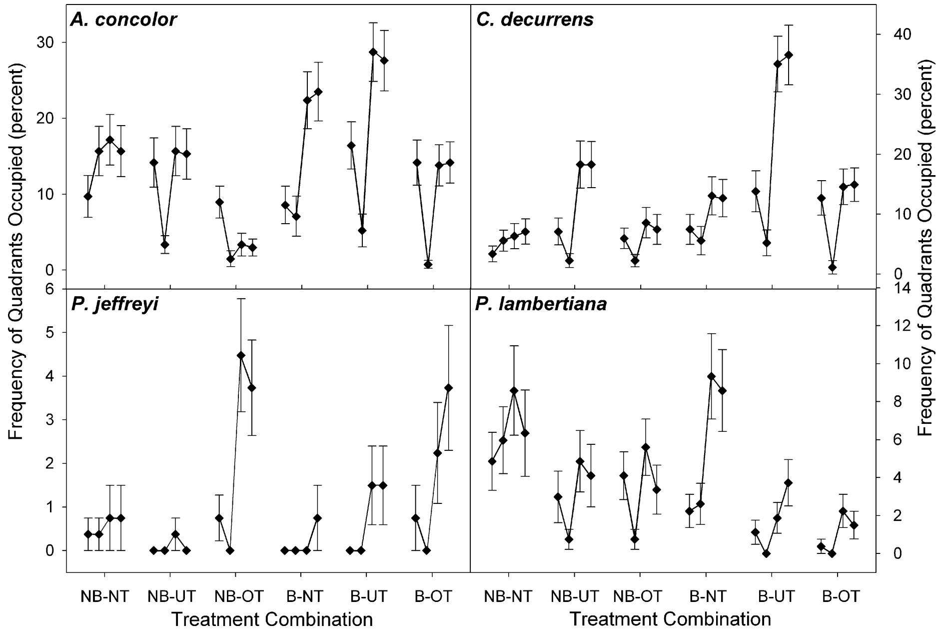

Fig. 6. Mean (S.E.) frequency of seedlings (trees 5–50 cm tall) by species, year, and treatment combination. Each group of bars connected by the darker tend line represents 4 years of observations (2000, 2002, 2003, and 2004 moving from left to right). Treatment combinations as described in text.

Table 4
Mean seedling frequency ± S.E. by patch type prior to treatments (2001), and for 3 years after treatments (2002, 2003, and 2004)

Species	Patch type	2001	2002	2003	2004
A. concolor	Bare ground	8.6 (2.1)	3.3 (1.5)	11.5 (2.6)	9 (2.3)
A. concolor	Closed canopy	14.3 (1.6)	5.9 (1.2)	20 (1.9)	20.4 (1.9)
A. concolor	Ceanothus	7.8 (2.4)	5.9 (2.1)	10.3 (2.6)	10.8 (3)
C. decurrens	Bare ground	8.6 (2.5)	3.7 (1.7)	12.3 (3.1)	12.7 (3.2)
C. decurrens	Closed canopy	9.6 (1.4)	3.9 (0.9)	19.2 (1.9)	19.5 (2)
C. decurrens	Ceanothus	4.9 (1.9)	2.9 (1.5)	10.8 (3.2)	10.8 (3.2)
P. jeffreyi	Bare ground	1.2 (0.9)	0	0.4 (0.4)	0.4 (0.4)
P. jeffreyi	Closed canopy	0.1 (0.1)	0	1.8 (0.5)	2 (0.5)
P. jeffreyi	Ceanothus	0.5 (0.5)	0.5 (0.5)	2.5 (1.3)	2.5 (1.3)
P. lambertiana	Bare ground	2 (0.9)	1.2 (0.7)	2.5 (1)	2.5 (1)
P. lambertiana	Closed canopy	3.2 (0.6)	1.8 (0.5)	6.6 (1)	5.6 (0.9)
P. lambertiana	Ceanothus	1.5 (0.8)	0.5 (0.5)	3.9 (1.5)	2.5 (1.3)

Number of grid points per patch type: $n = 61$ for bare ground, $n = 259$ for closed canopy, and $n = 51$ for ceanothus shrub.

overstory thins (1.1 change). *P. lambertiana* ($F_{1,12} = 3.58$, $p = 0.0828$) frequency change was suggestive of thinning treatments, while *P. jeffreyi* did not appear associated with burn, thin, or burn × thin interactions. *P. jeffreyi* frequency increases were highest in the overstory thin treatments (6.8 change), and unchanged for the understory thin (0.7 change) and unthinned (0.3 change) treatments. In contrast, the greatest frequency change of *P. lambertiana* occurred in the B-UT and B-NT treatments (5.4 change, 9.1 change in the B-NT treatment), with reduced frequency in the overstory thins (−1.5 change).

3.5. Seedling relations to vegetation patches and microsite conditions

Prior to treatment, seedling frequency did not differ significantly among the three vegetation patch types for the dominant tree species. Three years after treatment (2004) the legacy of those patch types was apparent for some species. Frequency of *A. concolor* differed significantly among patches ($F_{2,370} = 6.764$, $p = 0.001$), with greater amounts in former closed-canopy patches compared to open or *Ceanothus* patches (Table 4). The burn × patch interaction was significant for *P. jeffreyi* ($F_{2,370} = 3.49$, $p = 0.032$), with higher frequencies found on former closed-canopy and *Ceanothus* sites than on bare sites.

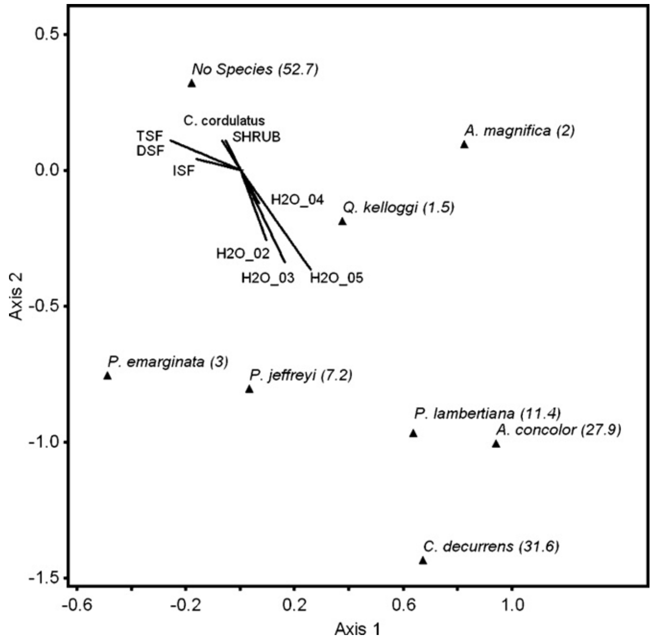

Fig. 7. NMS ordination graph of seedling species regeneration frequency in 2004 in relation to dominant microsite variables. Numbers in parentheses are the proportion of the 402 grid points occupied by each species. Species and variable codes are described in Fig. 1.

The NMS ordination of grid point seedling frequency in environmental space represented 97.5% of the variation in the dataset, with axis 1 accounting for 67.4% and axis 2 accounting for 30.1%. The directions and lengths of the joint plot vectors indicated the two axes were related to (in order of declining variance described) soil moisture in multiple years (H_2O prefix); light levels (ISF, DSF, and TSF, respectively); percent cover of *C. cordulatus*; and total shrub cover (SHRUB) (Fig. 7). Most of the tree species were arranged along a gradient from high soil moisture and low light levels to low moisture and high light. *C. decurrens, A. concolor*, and *P. lambertiana* seedlings tended to be found on sites at the moist end of the gradient, with *P. jeffreyi*, *P. emarginata*, and *Q. kelloggi* found on progressively drier, more open sites. *A. magnifica* seedlings did not fit well along the primary moisture/light gradient, and only occupied 2% of the grid points sampled. Sites with no seedlings (“no species”) were much drier, had more open canopy, and higher shrub cover than sites containing seedlings.

4. Discussion

Increasing the forest’s pine composition after almost a century of fire suppression may be difficult because shade-tolerant *A. concolor* and *C. decurrens* are now large co-dominants that survive moderate fuels treatments and are prolific seed producers. Although *P. jeffreyi* and *P. lambertiana* had high germinant survival, *A. concolor* and *C. decurrens* seed rain and seedling frequency were up to an order of magnitude higher than the pines. Treatments significantly altered understory light, soil moisture and surface substrates; resource conditions that strongly influence western conifer regeneration dynamics (Haig et al., 1941; Gordon, 1970; Gray and Spies, 1997). While the thin and burn treatments produced resource conditions generally favoring pine recruitment, persistence of microsites favorable to shade-tolerant species and heavy seeding created a strong shade-tolerant inertia against shifting future forest composition. By following cones, seeds, germination, seedlings and saplings, we found that after 3 years, regeneration composition and frequency had generally returned to pre-treatment conditions.

Following our prediction (hypothesis 1), burning did kill many shade-tolerant seedlings and saplings (Fig. 1), and after treatment there was increased seedling frequency for three (*A. concolor*, *C. decurrens*, and *P. jeffreyi*) of the four species in the burns (Fig. 6). This is consistent with other studies which have found high fire mortality in smaller tree size classes, but litter substrate reduction and mineral soil exposure favor higher seedling germination (Kilgore, 1973; McDonald, 1976; Helms and Tappeiner, 1996). Thinning increased the amount of litter and slash on the forest floor, while burn treatments reduced litter and woody debris to levels below those found in controls. Establishment was particularly poor in the no-burn/overstory thin treatment, where amounts of both surface litter and direct radiation were high. In the more controlled conditions of the sown seed experiment, *Pinus* species had higher germination and survival in the burn compared to no-burn treatments. Other studies (McDonald, 1976; Bailey and Covington, 2002) have found similar results, suggesting prescribed fire (rather than thinning) may be the fuels treatment most effective at increasing pine composition in stand regeneration.

We also found seed rain of shade-tolerant species was substantially higher than either pine species (hypothesis 2) in all treatments including the control (Fig. 2). Seed rain density was substantially lower for the *Pinus* species than for the other species by about a factor of 10. These differences among species, however, were not evident in the cone counts. The *Abies* and *Pinus* species have several important animal seed–predators, but *Pinus* seeds are favored by rodents, which can clip anywhere from 5 to 99% of *Pinus* cones prior to ripening, and cache and consume the majority of seeds that are wind-dispersed (Fowells and Schubert, 1956; Yeaton, 1984). Although rodents may consume most of a seed crop, with only 2–12% of seed surviving to germination (depending on species and year), they are also the primary seed-dispersal agent for *Pinus* (Vander Wall, 2002). Virtually all natural *Pinus* regeneration found in our study germinated in clumps, apparently from rodent seed caches. Studies have found that seed collected by squirrels in the genus *Tamiasciurus* have a much lower probability of germinating than those collected by chipmunks (genus *Tamias*) (Benkman et al., 1984; Gworek et al., 2007). Both of these taxa were abundant at our study site. Our initial results suggest that the seed to seedling stage may not be limiting for *A. concolor* and *C. decurrens*, particularly in moderately disturbed stands, but may be a serious limitation on *P. jeffreyi* and *P. lambertiana* in mixed-conifer forests.

Shade-tolerant germinant survivorship was higher in closed-canopy patch conditions (hypothesis 3) but was also higher in burn/no thin than in understory thinning treatments contrary to our prediction. This may result from the burn/no thin treatment having little impact on canopy cover and understory light (Table 2). Before and after treatment, patch type continued to have a strong influence on regeneration composition and survival. Several important resource attributes, including light, air temperature, soil moisture, respiration, and nitrogen cycling, differ among mixed-conifer's patch types (Oakley et al., 2003; Ma et al., 2004, 2005; Erickson et al., 2005). The bare open patch types, which were the least impacted by the treatments, were poor locations for seedling establishment before and after treatment. While many open patches have shallow soils (Meyer et al., 2007) and are often near rock outcrops, others had no obvious physical constraints and consisted of deep sandy soil with no vegetation. For most of the species in this study, the former closed-canopy patches were the locations with the highest survival of germinating seedlings, and the greatest abundance of established seedlings. In disturbed *C. cordulatus* patches, germinant survival was intermediate between the open- and closed-canopy patches, but seedling abundance dramatically increased following treatment. Seedlings may have established more readily with decreased competition from shrubs (Gray et al., 2005), or with the greater availability of organic nitrogen found in *C. cordulatus* patches before and after burning (Oakley et al., 2003; Erickson et al., 2005). Although shrub cover was reduced by treatments, particularly in burn treatments, shrub expansion in the subsequent 2 years was dramatic in the overstory thins (Table 1). For tree regeneration, fuels treatments which include burning may be most effective at reducing shrub competition, but that reduction may be short-lived if treatments significantly reduce overstory canopy cover.

Treatments significantly altered resource levels (hypothesis 4). Shade-tolerant species were associated with higher soil moisture (Fig. 7) and lower understory light (closed-canopy values in Fig. 5b). Light levels predictably increased with thinning intensity and there was a slight increase with burning due to crown scorch and understory leave (DBH < 25 cm) tree mortality. Soil moisture tended to increase with thinning intensity, agreeing with other studies (Ziemer, 1964; Gray et al., 2002; Iverson et al., 2004) which have suggested the response may be due to less water uptake as stem density is reduced. The ordination analysis (Fig. 7) shows seedling species arrayed along soil moisture and direct light gradients. Each species' post-treatment microsite preferences were very similar to those found for pre-treatment conditions by Gray et al. (2005). This suggests regeneration composition and abundance may be more closely related to microsite variation than inter- and intra-specific competition between seedlings.

In spite of treatment changes in resource levels, shade-tolerants still dominate seedling frequencies in the thin and burn treatments (Fig. 6). An ordination analysis of grid points in environmental space (not shown) found that microsite conditions were highly variable within treatments and overlapped greatly among treatments. With this variability, post-treatment conditions in burned and heavily thinned treatments still include many microsites favorable to *A. concolor* and *C. decurrens*.

4.1. Management implications

Although this study occurred on 72 ha of Sierran mixed-conifer forest, its findings may have wider applicability. Stand structural conditions which contributed to inertia towards increased pine regeneration, such as increased abundance of shade-tolerants and few large pines, are widespread within Sierran mixed-conifer forests (McKelvey and Johnston, 1992). The U.S. Forest Service has set a goal of using these fuels treatments on more than 1.5 million ha of western conifer forest each year (GAO, 2003). Many of these forests have similar conditions, where the reduction in fire frequency has increased the density of fire-sensitive, shade-tolerant species (Lunan and Habeck, 1973; McNeil and Zobel, 1980; Agee, 1993; Arno et al., 1995). Bond and Keeley (2005), noting fire's strong influence on biomass and succession around the world, refer to fire and its suppression as the loss of a 'global herbivore'. We believe the trends in our data may apply to other mixed-species, fire-suppressed forests where shade-tolerant species have increased after fire suppression. However, we also stress that each forest community has a unique combination of species regeneration strategies, successional dynamics, and disturbance regimes.

The alternative treatments examined in this study have been proposed to meet different management goals, including: (1) reducing surface and ladder fuels, (2) restoring historic forest composition, and (3) maintaining and promoting late-successional forest habitat. Our study's initial results suggest that meeting all of these objectives at the same time with current treatments may not be possible. Under the cool, late fall conditions of our prescribed burn, the burn–no thin treatment failed to significantly reduce fuels or change stand composition. Historically, most fires in southern Sierra Nevada forests occurred during summer or early fall (Caprio and Swetnam, 1995), however most prescribed fires in the Sierra are lit during cool spring or fall conditions because of containment concerns and air quality restrictions. Only when fuels were supplemented with thinning slash did the prescribed fire significantly affect stand conditions and tree regeneration. Understory thinning, however, left many large *A. concolor* and *C. decurrens* which produced abundant seed, creating inertia in efforts to restore historic composition in the regeneration. Overstory thinning removed large, seed-producing *A. concolor* and *C. decurrens* and provided more open conditions favored by *P. jeffreyi*. In many second-growth forests, however, fir and incense-cedar are the only large structures left for managers attempting to accelerate old-growth development. To meet all three treatment goals, managers many need to create more favorable microsites for *Pinus* species with hotter or more frequent prescribed fire, or bypass pine's seeding limitation by planting pine seedlings.

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