Research Article

Giant Sequoia Regeneration in Groves Exposed to Wildfire and Retention Harvest

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ABSTRACT

Both wildland fire and mechanical harvest have been proposed to achieve ecological restoration goals in giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz) groves of the southern Sierra Nevada, but their effectiveness on giant sequoia regeneration has received little attention. In the summer of 2010, we examined giant sequoia regeneration in four groves subjected to: 1) moderate- to high-severity wildfire in 1987 (Case Mountain, Redwood Mountain groves), 2) low-severity wildfire in 2008 (Black Mountain grove), 3) retention harvest (removal of all trees except large-diameter giant sequoia) followed by prescribed burning in the mid-1980s (Black Mountain, Bearskin groves), and 4) nearby unburned and unharvested (control) stands in all groves. Density of giant sequoia regeneration was greater in the moderate- and high-severity wildfire stands than control stands, but there was no difference in giant sequoia regeneration between low-severity burned and control stands. Stands thinned by retention harvest and prescribed burning had greater giant sequoia regeneration than control stands. Across all control and low- to moderate-severity wildfire stands, giant sequoia regeneration was positively associated with canopy gaps. In wildfire and retention harvest stands, giant sequoia regeneration was positively associated with distance to gap edge, direct and indirect solar radiation, and soil moisture. Our results corroborate previous studies in finding that giant sequoia regeneration benefits from fire. Both wildfire and prescribed fire (preceded by harvest or not) can serve to promote giant sequoia regeneration, providing that fire intensity is sufficient to create canopy gaps, increase understory light, and remove surface litter.

Keywords: canopy gap, giant sequoia, regeneration, retention harvest, wildfire

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INTRODUCTION

Giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz) depends on fire for natural regeneration (Hartesveldt *et al*. 1975, Harvey *et al*. 1980). Fire in these ecosystems creates forest canopy gaps, increases understory light penetration, exposes mineral soil, and removes shade-tolerant competitors from the forest understory (Harvey *et al*. 1980, Stephenson 1994), creating conditions suitable for giant sequoia regeneration (Hartesveldt *et al.* 1975, Shellhammer and Shellhammer 2006). However, the majority (82%) of giant sequoia groves in the Sierra Nevada have not been exposed to fire for almost a century (Stephenson 1994, 1999). The elimination of fire from these forest ecosystems has created conditions unsuitable for giant sequoia regeneration, specifically closed forest canopies, thick litter layers, and a high density of shade-tolerant competitors (Harvey *et al*. 1980). Additionally, the absence of fire has greatly amplified ladder fuels and wildfire risk (Kilgore and Sando 1975) and substantially altered forest structure and composition (Bonnickson and Stone 1982).

Giant sequoia seedling establishment is one of the most critical stages in the life cycle of this species (Harvey *et al*. 1980). However, reproduction in most giant sequoia groves has been declining for more than a century, with regeneration almost completely lacking in a number of groves (Rundel 1971). Much of this lack of reproduction can be attributed to the exclusion of fire from these ecosystems (Kilgore and Biswell 1971, Harvey *et al*. 1980). Reintroduction of wildland fire (e.g., wildfire, prescribed fire) can be an effective restoration tool for enhancing giant sequoia regeneration within fire-suppressed groves (Stephenson 1999). Fires with a component of high-severity effects are especially effective at initiating seed release and creating open canopy gaps (0.07 ha to 1.17 ha in size) that favor giant sequoia seedling growth and survivorship (Harvey *et al*. 1980, Stephenson 1994, Demetry 1995). Such areas may result in high seedling densities and recruitment provided that there is sufficient soil moisture, light availability, and presence of friable mineral soils for increased root penetration (Stark 1968, Harvey *et al*. 1980).

Retention harvest, group selection, and other mechanical methods are alternative management treatments for improving regeneration in giant sequoia groves and have several advantages and disadvantages compared to the use of wildland fire. Mechanical harvest is often a more precise method for creating canopy gaps to increase light penetration, remove competitors, and produce conditions suitable for growth of giant sequoia seedlings and saplings (Benson 1986, Piirto and Rogers 2002). It is not limited by fire safety or smoke generation concerns and may provide revenue to offset the cost of forest restoration treatments (Stephenson 1996). Coupled with planting of giant sequoia seedlings (Stephens *et al*. 1999), mechanical harvest can be effective at enhancing giant sequoia regeneration by providing increased light availability in closed canopy forests (York *et al*. 2004). However, mechanical methods do not reproduce many of the ecological effects of fire, most notably increased structural heterogeneity, nutrient cycling, bare mineral soil substrates, and augmented seed germination from serotinous cones (Harvey *et al*. 1980, Stohlgren 1993).

The objectives of this project are to: 1) examine the response of giant sequoia regeneration to wildfire (across a gradient of fire severities) and retention harvest (with prescribed burning), and 2) evaluate microsite variables (e.g., canopy gaps, solar radiation, soil moisture) associated with giant sequoia regeneration. For our first objective, we predicted that giant sequoia regeneration (seedlings, saplings, and small-diameter trees) increases following wildfire but only at moderate- and high-severity, or in response to retention harvest followed by burning (prescribed or pile burning). For our second objective, we predicted that giant sequoia regeneration is positively associated with canopy gaps, thinner litter layers, soil moisture, and direct and indirect solar radiation.

METHODS

Study Sites

Our study was located in four giant sequoia groves of the southern Sierra Nevada of California, USA (proceeding from north to south): Bearskin (1887 m elevation), Redwood Mountain (1967 m), Case Mountain (1797 m), and Black Mountain (1937 m) (Figure 1). Bearskin, Redwood Mountain, and Black Mountain groves are located within Giant Sequoia National Monument, administered by the Forest Service's Sequoia National Forest. Case Mountain grove is administered by the Bureau of Land Management and located near the southwestern edge of Sequoia National Park. Between 1959 and 2009, there have been only three recorded wildfires burning into giant sequoia groves in the Sierra Nevada: the Pierce Fire (1987) in Redwood Mountain grove, Case Fire at Case Mountain grove (1987), and Solo II Fire (2008) of the Black Mountain grove. Small portions of all three groves were also selectively harvested (removing all trees except large-diameter giant sequoia) in the mid-1980s.

Giant sequoia groves within the study area have warm, dry summers, and cool and wet winters, and precipitation falls almost exclusively in the form of snow during the winter. Mean annual precipitation was 125 cm at the Giant Forest grove (1950 m elevation; located 16 km north of Case Mountain grove and 50 km north of Black Mountain grove) and 108 cm at Grant Grove (2012 m elevation; located 4.5 km west of Bearskin grove and 7 km north of Redwood Mountain grove) located in Sequoia and Kings Canyon national parks (Western Regional Climate Center 2010). Dominant overstory tree species are typical of other giant sequoia groves, with high stem densities of

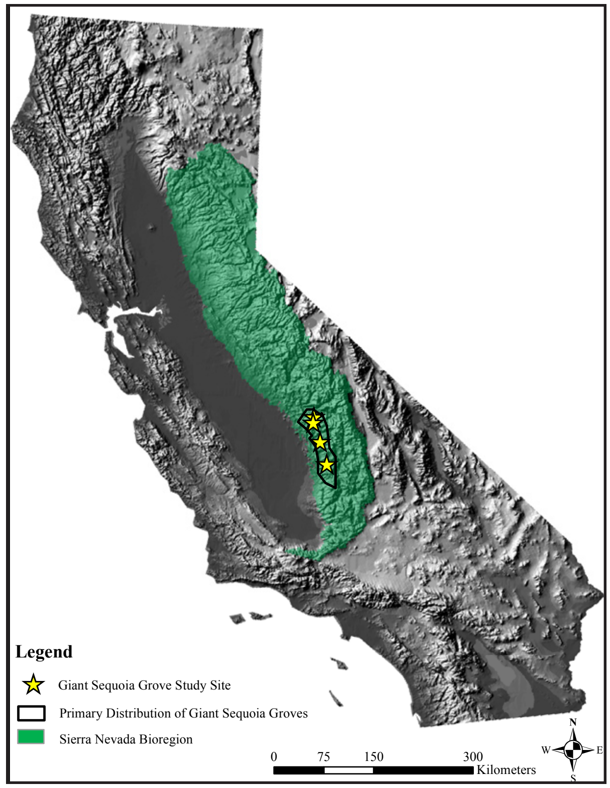

Figure 1. Locations of four giant sequoia grove study sites, located within the Giant Sequoia National Monument (Bearskin, Redwood Mountain, Black Mountain) and Bureau of Land Management Bakersfield Field Office District (Case Mountain), California, USA. The primary distribution of giant sequoia groves (approximately 60 total) does not include seven isolated groves to the north.

white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) and relatively high canopy cover and basal area of giant sequoia (Rundel 1971). Other common associates included sugar pine (*Pinus lambertiana* Douglas), ponderosa pine (*P. ponderosa* C. Lawson), incense cedar (*Calocedrus decurrens* [Torr.] Florin), and black oak (*Quercus kelloggii* Newberry). Uncommon associates in the mid-story included Pacific dogwood (*Cornus nuttallii* Audubon ex Torr. & A. Gray), canyon live oak (*Q. chrysolepis* Liebm.), Scouler's willow (*Salix scouleriana* Barratt ex. Hook.), and California nutmeg (*Torreya californica* Torr.).

Fire and forest management history varied among each of the study groves (Table 1). The

Table 1. Management and fire history in the Bearskin, Black Mountain, Case Mountain, and Redwood Mountain groves in the southern Sierra Nevada, California.

Grove	Management treatment[a]	Wildfire severity[b]	Wildfire year
Bearskin	Retention harvest, burning, planting	None	Before 1900
Black Mountain	Retention harvest, burning, planting	Low	2008
Case Mountain	None	Moderate	1987
Redwood Mountain	None	High	1987

[a] Retention harvest included removal of all trees except 6 to 10 large diameter giant sequoia (one unit was clearcut in Bearskin grove) followed by prescribed or pile burning. Focal species for planting included giant sequoia in Bearskin grove and ponderosa pine in Black Mountain grove.
[b] Fire severity class is based on tree mortality in the study area: low (<25% mortality), medium (25% to 75%), and high (>75%).

76 ha Bearskin grove was predominantly unlogged with virtually no evidence of wildfire since 1900 (Kilgore and Taylor 1979, Miller and Safford 2008). In 1983 to 1985, two units (each approximately 6.5 ha) were heavily thinned using a retention harvest system in the Bearskin grove, leaving approximately 6 to 10 large diameter (>100 cm dbh) giant sequoia trees per hectare. A third unit (1.2 ha) was clearcut during the same time period with many large giant sequoia trees retained on the edges of the unit. All three units were broadcast or pile burned one year following tree harvest. Within two years following burning, approximately half (51%) of the area of each unit (100% in the clearcut unit) was planted with giant sequoia seedlings with 3 m spacing, allowing for edge buffers and substantial gaps between plantings based on soil depth and microsite suitability (average of 788 seedlings per hectare).

The 1340 ha Redwood Mountain grove is primarily located within Kings Canyon National Park, with approximately a third of the grove (420 ha) located in the Giant Sequoia National Monument. The national monument portion of Redwood Mountain grove has no recent evidence of wildfire since at least 1905 (Miller and Safford 2008), with the exception of the 440 ha Pierce Fire of 1987, which burned approximately 20 ha of the grove, primarily at high severity (>75% basal area mortality one year after fire; Miller and Safford 2008). A limited portion of the Redwood Mountain grove was clearcut prior to 1915, and approximately 25 ha (6%) of the grove was heavily thinned in the mid-1980s. We focused our sampling of the Redwood Mountain grove outside the heavily thinned or clearcut portions.

Approximately 90% of the 180 ha Case Mountain grove was burned in two overlapping wildfires: the 1760 ha Case Fire (1987) and an unnamed 9600 ha wildfire in 1928 (L. H. Jump, Bureau of Land Management, unpublished report). The Case Fire burned primarily at moderate severity (25% to 75% basal area mortality one year after fire) with some high severity patches within the Case Mountain grove. We focused our sampling in the two largest units (Case grove subunit, 51 ha; Nutmeg subunit, 53 ha) that were located on the Case Fire perimeter (i.e., contained both burned and unburned areas) and retained a significant number of large giant sequoias following heavy logging in the grove in the 1940s and 1950s. Additionally, our control sampling was restricted to areas unburned by the 1928 or 1987 wildfires.

Nearly half of the 1060 ha Black Mountain grove burned in an unnamed wildfire in 1928 and an additional 110 ha (~12% of grove) burned in the Solo II Fire (2008) in a separate area of the grove. Fire severity of the Solo II

Fire was primarily low (<25 % basal area mortality one year after fire) owing to the late seasonality (early December) of this wildfire. Small patches of moderate and high severity fire occurred in <10 % of the burned area, especially on steeper slopes in the grove that lacked mature giant sequoias. From 1985 to 1987, three units (3.4 ha, 5.2 ha, and 18.2 ha) were heavily thinned in the Black Mountain grove using a selective harvest system, resulting in the removal of all trees except 6 to 10 large-diameter (>100 cm dbh) giant sequoias trees per hectare. All three units were prescribed burned within two years following harvest. Within one year following burning, approximately half (51 %) of the area of each unit was planted with a mixture of ponderosa pine (~90 %), giant sequoia (<5 %), and white fir (<5 %) seedlings in clumps of three seedlings spaced every 4.6 m, allowing for edge buffers and microsite gaps (average of 1483 seedlings per hectare). Harvested units were located adjacent to (<1 km) the Solo II Fire perimeter and had not burned since the 1928 wildfire. We did not restrict control sampling of the Black Mountain grove to areas unburned by the 1928 wildfire due to limitations in sampling area within 1.5 km of wildfire and selective harvest stands (<1 % of this section of the grove remained unburned by either wildfire).

Regeneration Measurements

We surveyed 10 m wide belt transects to estimate the combined densities of giant sequoia seedlings and saplings and small trees (<30 cm dbh) within each burned, retention harvested, and control site. We placed 10 to 20 belt transects approximately 10 m to 20 m apart with no overlap between adjacent transects. Belt transects were 1.2 km to 1.8 km total length for each wildfire, retention harvest, and control unit of each grove (total sampling area of 102 ha for all groves). Belt transects allowed us to: 1) cover a relatively large area within each location, and 2) include areas within designated giant sequoia grove boundaries that were not biased by proximity to mature giant sequoias. We estimated the total density of giant sequoia regeneration within a grove and treatment (wildfire, retention harvest, control) by dividing the sum of all counted giant sequoia seedlings, saplings, and small trees by the total area sampled for all transects for that grove and treatment.

Within each of the harvested units (Bearskin, Black Mountain), wildfire areas (Redwood Mountain, Case Mountain, Black Mountain), and unburned and unharvested (control) area for each grove, we established three transects averaging 250 m in length (six transects total per grove, except Black Mountain with nine transects total). We situated each transect within an individual retention harvest unit or in an independent location of a burned grove, based on changes in topography, fire severity, and grove subunit boundaries. We established control transects within an adjacent unharvested and unburned area that was located within 250 m of a corresponding retention harvest or burn transect (harvest and wildfire transects for the Black Mountain grove used the same three paired control transects for comparison). We located transect locations >25 m from the harvest unit boundary or fire perimeter and <50 m from a mature giant sequoia (>75 cm dbh). We situated transects a minimum distance of 200 m from neighboring transects. For the Case Mountain grove control transects, we used a 100 m minimum distance due to the limited amount of unburned area within the grove.

From July through early September 2010, we placed 5 to 10 sample points located approximately every 30 m along each transect (average: 8.3 points per transect; total of 20 to 27 sample points per treatment type: retention harvest, wildfire, control). In a few cases where space was limited, we adjusted the angle of transects (using a random azimuth) to accommodate their lengths within plot and grove boundaries. We centered a 3.5 m radius (38.5 m^2) regeneration plot on the centermost giant sequoia seedling, sapling, or small tree within the plot in order to evaluate associations between the centralized giant sequoia regeneration class and measured stand and soil variables. In each regeneration plot, we counted the number of giant sequoia small seedlings and small diameter (<30 cm dbh) trees (which includes saplings). We also recorded regeneration of other conifer species and hardwoods. Each regeneration plot yielded a total sample area of 962.5 m^2 per treatment (in each grove) or 0.192 ha per grove (0.289 ha for Black Mountain Grove; 0.869 ha total in all groves). We divided regeneration plots into quadrants, and individuals of giant sequoia and other conifers were counted by size class: 5 cm to 50 cm in height (termed "small seedlings"), 50 cm to 140 cm ("large seedlings"), and >140 cm tall and <30 cm dbh ("small trees," which includes saplings) (Brohman and Bryant 2005). We measured the tallest seedling of each tree species in each quadrant. We chose 30 cm dbh as the cutoff diameter for older giant sequoia regeneration in our study because no giant sequoias <30 cm dbh were retained following harvest within retention harvest units of Bearskin and Black Mountain groves. Additionally, a dbh of 29.5 cm was the largest diameter of giant sequoia regeneration recorded within the retention harvest units of Bearskin and Black Mountain groves and the high-severity wildfire area of Redwood Mountain grove.

Microsite Measurements

Within a 7.67 m radius (185 m^2) of a regeneration plot center, we recorded all trees >5 cm dbh by species to calculate the density of small-diameter trees in a plot. We estimated basal area using a variable radius plot with a basal area factor between 5 and 40. We estimated the direct and indirect (diffuse) solar radiation for each plot using digital photographs taken at 1.2 m height with a Nikon Cool Pix 4500 camera (NikonUSA, Melville, New York, USA) and Bower 0.16× fisheye hemispherical lens (Bower, Long Island City, New York, USA). We analyzed digital images using Gap Light Analyzer version 2.0 software (Simon Fraser University, Vancouver, British Columbia, Canada). We estimated soil moisture at 25 cm depth using an Aquaterr Model TEMP-300 soil moisture meter (Aquaterr, Costa Mesa, California, USA) (Shellhammer and Shellhammer 2006). We also estimated percent cover of shrubs and herbaceous plants by species, coarse woody debris, litter, mineral soil, and rock. We measured litter depth in each regeneration plot by digging three shallow pits at the edge of each quadrat (at 0°, 120°, and 240° from the center point) and taking three depth measurements at each pit of the combined organic litter and humus layers (termed litter). We examined each harvested study site for evidence of recent burning (e.g., fire char on stumps, fire scars). We also measured slope and aspect with a handheld compass, and distance to nearest reproductive giant sequoia, distance to canopy gap edge, and gap size in each regeneration plot using a laser rangefinder. We did not estimate gap size in wildfire stands of the Redwood Mountain grove in the field due to its relatively large size (~20 ha).

Statistical Analysis

We evaluated data for normality with the Kolmogorov-Smirnov test and for homoscedasticity with Levene's test (Zar 1999). We used Mann-Whitney U tests (density data were both heteroscedastic and non-normal) to examine the effect of wildfire and retention harvest on giant sequoia regeneration (seedling, sapling, and small tree densities) in each grove. For the Black Mountain grove, we used a Kruskal-Wallis test with planned comparisons (Mann-Whitney U test) to examine whether burned or retention harvested sites had greater giant sequoia regeneration than control sites. We used a χ^2 test to examine whether giant sequoia regeneration (small seedlings, large seedlings, and saplings and small trees) were associated with canopy gaps (defined as gaps exceeding 0.05 ha; Stephenson *et al*. 1991, Stephenson 1994, Piirto and Rogers 1999) across all control and low- to moderate-severity wildfire stands. We used a single-factor analysis of variance (ANOVA) to test whether litter depth across all groves and stands was lower in plots occupied by giant sequoia seedlings (small and large seedlings) than sites without giant sequoia seedlings. We calculated summary statistics (mean and SE) for tree regeneration (excluding giant sequoia) and other vegetation, soil, and topographic variables in Table 2 based on individual plot data rather than transects in order to examine changes in these variables over relatively small spatial scales (i.e., across individual forest patches rather than among forest stands).

We used multiple regressions with a forward stepwise procedure to select independent predictors (distance to canopy gap edge or gap distance, soil moisture, and direct and indirect solar radiation; included in model if $P < 0.10$) of giant sequoia density (small and large seedlings, saplings and small trees) or height (all size classes pooled). All variables were evaluated for normality, homoscedasticity, and independence of residuals. Height of sequoia regeneration for the wildfire stands of the Redwood Mountain grove was $\log_{10}$ transformed to normalize these data. We tested for serial correlation using a Durbin-Watson statistic and multicollinearity by examining correlations between independent factors and calculating the Variance Inflation Factor for each significant factor (Statsoft, Pittsburg, Pennsylvania, USA). We used logistic regression to relate selected predictors (gap distance, soil moisture, direct solar radiation, indirect solar radiation) to the occurrence of giant sequoia seedlings or saplings and small trees in wildfire and retention harvest stands. To reduce model over-fitting, we only included significant ($P <$ 0.10) predictors in our logistic regression analysis. For each significant parameter in the logistic regression model, we calculated odds-ratios and their confidence intervals. The odds-ratio estimates were interpreted as the chance of occurrence of a giant sequoia seedling or sapling-small tree with a one unit change in a stand or soil parameter. We used a sensitivity analysis to evaluate the performance of each significant reduced logistic regression model and assess model accuracy in successfully predicting giant sequoia regeneration among sample points (Hosmer and Lemeshow 2000). For all statistical tests, we used an α level of 0.05 unless otherwise noted.

Table 2. Giant sequoia small seedling, large seeding, and sapling/small tree (<30 cm dbh) densities in retention harvest, wildfire, or control (no harvest or wildfire) stands at the Bearskin, Black Mountain, Case Mountain, and Redwood Mountain groves in the southern Sierra Nevada, California, USA. Wildfires occurred in 2008 (Black Mountain) and 1987 (Case Mountain, Redwood Mountain).

	Bearskin		**Black Mountain**[a]			**Case Mountain**[a]		**Redwood Mountain**[a]	
Size class	**Harvest**	**Control**	**Harvest**	**Fire**	**Control**	**Fire**	**Control**	**Fire**	**Control**
Small seedlings (no. per 100 m)	1.0*	0.0	0.5	0.3	0.0	24.0*	0.0	4.3*	0.0
Large seedlings (no. per 100 m)	4.6*	0.1	4.0	0.4	0.7	28.9*	0.0	24.8*	0.1
Small trees (no. per ha)	112.0*	0.0	150.0*	2.0	18	87.0*	3.0	289.0*	9.0

[a] Wildfire severity was primarily low in the Black Mountain grove, moderate in the Case Mountain grove, and high in the Redwood Mountain grove.
* Indicates retention harvest or wildfire stands that are significantly different ($P < 0.05$) from control stands.

RESULTS

Density of giant sequoia seedling and sapling and small tree (regeneration) densities were orders of magnitude greater in the retention harvest (Bearskin, Black Mountain) and wildfire (Case Mountain, Redwood Mountain) stands than control stands based on belt transects (Figure 2) and regeneration plots (Table 2). Density of giant sequoia regeneration was not different between the control and low-severity wildfire areas of the Black Mountain grove. Numerically, white fir and incense cedar dominated seedling and sapling and small tree (>5 cm dbh) densities in all stands and groves (Tables 2 and 3). However, densities of giant sequoia large seedlings approached or slightly exceeded densities of shade-tolerant species in the moderate- to high-severity wildfire stands of the Case Mountain and Redwood Mountain groves (Figure 3). In all sampled areas, sugar pine, ponderosa pine, and black oak were minor components of the sapling and tree densities relative to white fir and incense cedar.

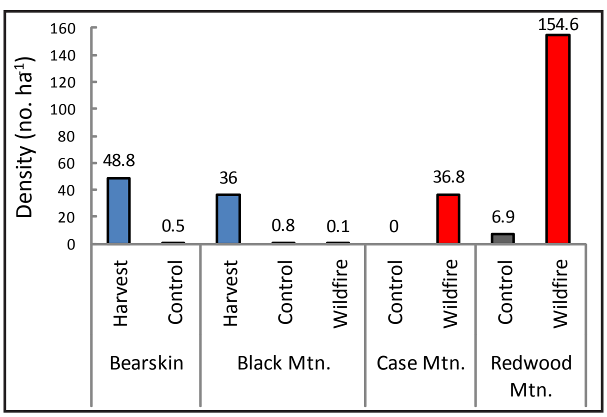

Figure 2. Density of giant sequoia regeneration (seedlings and saplings and small trees) based on belt transects in retention harvest, wildfire, and control (unharvested and unburned) stands of the Bearskin, Black Mountain, Case Mountain, and Redwood Mountain groves.

Across all control and low- to moderate-severity wildfire stands in our study groves, giant sequoia regeneration was positively associated with canopy gaps ($\chi^2_1 = 74.41$, $P < 0.001$). Natural canopy gaps with giant sequoia regeneration ranged in size from 0.015 ha to 1.6 ha in control and low- to moderate-severity wildfire stands, and 67% of these gaps were <0.4 ha (86% were <0.8 ha). Across all groves and stands, litter depth was lower in plots occupied by giant sequoia seedlings than in unoccupied sites ($F_{1,231} = 5.709$, $P = 0.018$).

In retention harvest stands, densities of large seedlings at Black Mountain grove and small trees at Bearskin grove were positively associated with gap distance (marginally significant in Bearskin), and height of giant sequoia regeneration was positively related to direct solar radiation (Black Mountain) (Tables 4, 5). In the retention harvest stands of the Black Mountain grove, the reduced logistic regression model correctly classified 67 % and 85 % of giant sequoia large seedling presence and absence, respectively. In retention harvest stands of Bearskin grove, density of giant sequoia large seedlings ($F_{1,23} = 1.549$, $P = 0.218$, $R^2_{adj} = 0.022$) and height of giant sequoia regeneration ($F_{1,22} = 1.475$, $P = 0.237$, $R^2_{adj} = 0.020$) were not related to gap distance, soil moisture, or direct and indirect solar radiation. The density of giant sequoia small trees in retention harvest stands of the Black Mountain grove were not related to microsite variables ($F_{3,21} = 1.608$, $P = 0.218$, $R^2_{adj} = 0.071$).

In wildfire stands, density of small seedlings were positively associated with gap distance (Case Mountain; marginally significant), and density of large seedlings were positively associated with soil moisture (Redwood Mountain). Density of small trees was positively associated with gap distance, soil moisture, and direct solar radiation in wildfire stands at Redwood Mountain (marginally significant for gap distance). Height of giant sequoia regeneration was positively associated with indirect solar radiation (Redwood Mountain, marginally

Table 3. Mean (±SE) seedling and tree (>5 cm dbh) densities (no. per 100 m^2 for seedlings, no. per ha for trees; excluding giant sequoia) and basal area in retention harvest, wildfire, or control (no harvest or wildfire) stands at the Bearskin, Black Mountain, Case Mountain, and Redwood Mountain groves of the southern Sierra Nevada, California. Values are based on individual plot data for each grove and treatment type (*n* = 25 in all cases except Case Mountain control: *n* = 20).

Size class	Bearskin		Black Mountain			Case Mountain		Redwood Mountain	
Tree species	Harvest	Control	Harvest	Fire	Control	Fire	Control	Fire	Control
Small seedlings (no. per 100 m^2)									
White fir	10.0 (3.0)	35.0 (10.0)	5.8 (2.5)	48.0 (10)	14.0 (3.4)	59.0 (10.0)	12.0 (3.0)	8.4 (2.1)	44.0 (19.0)
Sugar pine	0.3 (0.2)	3.7 (0.9)	0.1 (0.1)	0.0	0.0	2.7 (0.9)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)
Incense cedar	1.0 (0.5)	7.5 (3.8)	5.8 (3.2)	2.3 (1.1)	1.7 (1.0)	5.1 (3.4)	2.2 (0.9)	6.9 (1.8)	2.1 (1.2)
Black oak	1.5 (0.7)	4.5 (1.0)	1.7 (0.8)	6.4 (1.9)	3.6 (0.9)	5.7 (1.9)	12.0 (3.0)	0.7 (0.4)	1.3 (0.4)
Large seedlings (no. per 100 m^2)									
White fir	5.7 (1.9)	1.5 (0.5)	4.8 (1.3)	1.6 (0.7)	0.9 (0.3)	33.0 (8.0)	2.6 (0.9)	10.9 (3.6)	8.2 (2.6)
Sugar pine	0.3 (0.2)	1.4 (0.6)	0.1 (0.1)	0.0	0.1 (0.1)	0.4 (0.2)	0.5 (0.3)	0.5 (0.3)	0.2 (0.1)
Incense cedar	0.8 (0.4)	0.0	2.4 (0.9)	1.1 (0.9)	0.7 (0.4)	0.7 (0.3)	2.7 (0.6)	8.3 (2.0)	2.8 (1.3)
Black oak	0.1 (0.1)	0.0	0.5 (0.3)	0.0	0.1 (0.1)	0.2 (0.2)	1.3 (0.8)	0.3 (0.2)	0.0
Trees (no. ha^{-1})									
White fir	25.0 (11.1)	276.6 (34.5)	64.9 (14.0)	276.8 (31.7)	235.2 (39.8)	142.8 (24.0)	376.0 (65.6)	6.5 (3.6)	149.3 (31.3)
Sugar pine	12.5 (6.1)	62.1 (17.3)	2.2 (2.2)	6.2 (3.5)	16.6 (5.0)	30.3 (11.3)	27.1 (7.3)	6.5 (4.8)	10.8 (7.0)
Incense cedar	54.1 (18.8)	24.0 (8.8)	6.5 (4.8)	99.9 (17.5)	70.8 (20.5)	28.1 (13.7)	94.7 (24.5)	13.0 (7.2)	101.7 (31.3)
Black oak	6.2 (4.7)	0.0	0.0	62.4 (17.5)	8.3 (4.9)	8.7 (6.8)	8.1 (4.4)	2.2 (2.2)	2.2 (2.2)
Ponderosa pine	4.2 (2.9)	0.0	86.6 (24.4)	0.0	0.0	4.3 (3.0)	5.4 (5.4)	17.3 (8.1)	0.0
All trees[a]	210.0 (34.0)	370.7 (39.0)	303.0 (33.6)	457.8 (39.1)	380.8 (48.0)	305.2 (38.9)	527.5 (64.1)	320.3 (68.9)	316.0 (42.6)
Basal area (m^2 ha^{-1})									
All stems	13.2 (1.2)	53.1 (5.5)	35.7 (4.2)	34.9 (2.8)	51.9 (5.1)	60.9 (7.3)	56.8 (6.9)	24.5 (2.6)	43.7 (5.2)

[a] All tree species includes giant sequoia and infrequently encountered mid-story tree species (Pacific dogwood, canyon live oak, Scouler's willow, and California nutmeg).

Figure 3. Giant sequoia regeneration in a wildfire stand of the Redwood Mountain grove, Giant Sequoia National Monument, California. Photo was taken approximately 23 years post-fire.

significant for Case Mountain) and soil moisture (Redwood Mountain). For wildfire stands of the Case Mountain grove, the reduced logistic regression model correctly classified 94 % and 56 % of giant sequoia small seedling presence and absence, respectively. The reduced logistic model of wildfire stands in the Redwood Mountain grove correctly classified 75 % and 77 % of giant sequoia large seedling presence and absence, respectively. Based on the reduced logistic regression model, the probability of occurrence of giant sequoia seedlings at the Redwood Mountain grove was not associated with gap distance (χ^2_1 = 2.598, P = 0.107).

DISCUSSION

Giant sequoia regeneration in our study benefited from high- and moderate-severity wildfire but not low-severity wildfire. In giant sequoia groves of Sequoia and Kings Canyon national parks, the frequency of giant sequoia seedling clusters was substantially greater in prescribed burned areas of high and moderate fire severity than in neighboring control and low severity burned sites (Mutch and Swetnam 1995). In Redwood Mountain grove of Kings

Table 4. Best linear multiple regression models for direct and indirect solar radiation, soil moisture, and gap distance in relation to giant sequoia small tree (<30 cm dbh) densities (including saplings) and height in retention harvest (Bearskin, Black Mountain) and wildfire (Case Mountain, Redwood Mountain) stands of sequoia groves in the southern Sierra Nevada, California.

Grove Variable	Predictors	Coefficient estimate	Coefficient standard error	Predictor *P*	Partial *R*	Overall regression R^2_{adj}	Overall regression *P*
Bearskin							
Sequoia small tree density	Gap distance	2.2	1.2	0.072	0.37	0.10	0.072
Black Mountain							
Sequoia ht	Direct solar radiation	21.8	9.1	0.036	0.58	0.28	0.036
Case Mountain							
Sequoia ht	Indirect solar radiation	16.2	8.6	0.073	0.39	0.11	0.073
Redwood Mountain							
Log_{10}(Sequoia ht)	Indirect solar radiation	0.126	0.030	<0.001	0.69	0.48	0.001
	Soil moisture	0.019	0.008	0.040	0.44		
Sequoia small tree density	Soil moisture	21.4	6.7	0.005	0.57	0.41	0.003
	Direct solar radiation	46.5	22.1	0.047	0.42		
	Gap distance	3.9	2.0	0.061	0.40		

Table 5. Results of logistic regression models indicating stand variables associated with the occurrence of giant sequoia seedlings in retention harvest (Black Mountain) and wildfire (Case Mountain, Redwood Mountain) stands of sequoia groves in the southern Sierra Nevada, California.

Grove Size class	Independent variable	Estimate (SE)	χ^2	Odds ratio[a] (95% CI)	*P*
Black Mountain					
Large seedlings	Gap distance	0.05 (0.02)	5.869	1.06 (1.01-1.11)	0.015
Case Mountain					
Small seedlings	Gap distance	0.07 (0.04)	2.860	1.15 (0.99-1.18)	0.091
Redwood Mountain					
Large seedlings	Soil moisture	0.20 (0.09)	4.883	1.22 (1.01-1.48)	0.027

[a] Effect of a one unit increase in gap distance (m) or soil moisture (%).

Canyon National Park, giant sequoia seedling densities were 8 to 11 times greater several years following fire on intensively burned substrates than on unburned sites (Hartesveldt *et al*. 1975). Survival of giant sequoia regeneration in the same study sites was nearly 7 times greater in heavily charred soils than unburned substrates approximately 35 years following prescribed fire (Shellhammer and Shellhammer 2006). These results emphasize the importance of periodic high- and moderate-severity fire for giant sequoia regeneration and long-term recruitment (Swetnam 1993, Stephenson 1994).

Giant sequoia was a major contributor to seedling and sapling and small tree densities in stands exposed to high- and moderate-severity wildfire. In contrast, tree regeneration in retention harvest stands, low-severity wildfire stands of Black Mountain grove, and control stands in all sampled groves was dominated overwhelmingly by shade-tolerant white fir, and to a lesser degree, incense cedar. White fir dominates the understory of fire-excluded giant sequoia groves and mixed-conifer stands of the southern Sierra Nevada (Rundel 1971, Hartesveldt *et al*. 1975, Stephenson 1999, van Mantgem *et al*. 2006). Both white fir and incense cedar are shade-tolerant and relatively fire-sensitive species that benefit from low understory light, thick litter layers, and relatively high soil moisture of fire-suppressed Sierra Nevada forests (Gray *et al*. 2005, Meyer *et al*. 2007).

In Bearskin and Black Mountain groves, giant sequoia regeneration benefited from retention harvest followed by prescribed burning (both groves) and giant sequoia planting (primarily Bearskin grove). Giant sequoia regeneration is greatly increased following intensive tree harvest and logging that removes a significant portion of the forest overstory, especially in conjunction with post-harvest burning of understory fuels (Stohlgren 1993, Stephenson 1996). Benson (1986) found that in the nearby Mountain Home grove, giant sequoia regeneration increased dramatically following retention harvest but declined in subsequent years, possibly due to increased competition and desiccation. Group selection openings at Mountain Home did not enhance giant sequoia regeneration two years following thinning and burning treatments, likely due to below average precipitation following treatments (Stephens *et al*. 1999).

Density and occurrence of giant sequoia regeneration were positively associated with or related to canopy gaps. Across all control and low- to moderate-severity wildfire stands, giant sequoia regeneration was positively associated with canopy gaps, especially small-sized (<0.4 ha) gaps. Similarly in wildfire and retention harvest stands, density of giant sequoia regeneration was positively associated with distance to gap edge in all groves but not all size classes. Giant sequoia seedlings and saplings have been demonstrated to be largely associated with canopy gaps (Harvey *et al*. 1980, Stephenson *et al.* 1991, Demetry 1995), particularly in gaps exceeding 0.3 ha to 0.8 ha (Piirto and Rogers 2002). In the central and southern Sierra Nevada, canopy gap creation (0.1 ha to 1 ha in size) using group selection treatments followed by pile burning and sequoia planting resulted in increased growth of giant sequoia seedlings and saplings (York *et al*. 2004, 2011).

Density, occurrence, and height of giant sequoia regeneration were positively associated with or related to direct and indirect solar radiation, soil moisture, and thinner litter layers. Giant sequoia sapling height growth is positively correlated with both understory light and soil water supply (Stark 1968, York *et al*. 2003, Shellhammer and Shellhammer 2006). These two factors often interact to limit the occurrence and growth of seedlings or saplings, although light availability may become more important with gap infilling and stand development (Shellhammer and Shellhammer 2006). In contrast, soil moisture may exhibit relatively greater control over growth and survivorship in early stages of seedling development (Stark 1968, Hartesveldt *et al*. 1975), effectively constraining giant sequoia recruitment and the distribution of grove boundaries to areas of relatively greater soil moisture and groundwater supply (Rundel 1972). The presence of thick litter may also constrain giant sequoia seedling survivorship and growth, especially during early seedling development stages (Kilgore and Biswell 1971, Harvey *et al*. 1980). Our results corroborate previous research demonstrating that giant sequoia seedlings require bare mineral soil patches or areas of reduced surface litter for successful establishment.

Our study results have several implications for the management and restoration of giant sequoia groves. First, use of wildland fire (i. e., wildfire or prescribed fire) to enhance giant sequoia recruitment must be of sufficient intensity and resultant severity to create canopy gaps, increase understory light, and remove surface litter. Low-severity fire, while beneficial for other reasons (e.g., surface and ladder fuel reduction, nutrient cycling), may not adequately facilitate natural giant sequoia regeneration or canopy gap creation. Second, intensive retention harvest (e.g., shelterwood and seed tree harvest, clearcutting) followed by burning and possibly giant sequoia planting as observed in this study does increase giant sequoia regeneration. However, these benefits likely vary with the size and frequency of created canopy gaps, density of vegetation surrounding the gaps, and availability of solar radiation and soil moisture within gaps (York *et al*. 2003, 2011). Additionally, the benefits of intensive retention harvest or high-severity fire for giant sequoia regeneration are offset by potential negative impacts to resting and nesting habitat for late-seral dependent wildlife species in the southern Sierra Nevada, such as the Pacific fisher (*Martes pennanti*) (Spencer *et al*. 2008) and California spotted owl (*Strix occidentalis occidentalis*) (Roberts *et al*. 2011). A more prudent strategy is to apply a flexible ecosystem management approach that balances multiple ecological objectives (Piirto and Rogers 2002, North *et al*. 2010). For example, enhancing regeneration of giant sequoias and other fire-resilient species (e.g., pines, oaks) while minimizing impacts to sensitive wildlife habitat can be accomplished using a strategy that focuses on the promotion of small-size (<0.4 ha) gap creation, stand heterogeneity, resiliency to fire and drought, and key habitat structures such as large-diameter trees and snags (North *et al*. 2010). At the landscape scale, this strategy can be accomplished via prudent combinations of wildland fire, strategic forest thinning, and prescribed fire. This and other adaptive and integrated strategies will be critical for the management of sequoia groves in an era of amplified wildfire activity (Westerling *et al*. 2006), increasing fire severity (Miller *et al*. 2009), and rapidly changing climate (Stephens *et al*. 2010).

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