
Regeneration Response to Restoration in Aspen-Conifer Stands around the Lake Tahoe Basin



Final Report prepared for Aspen Community Restoration Pile Burning Monitoring Project

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MAJOR FINDINGS AND IMPLICATIONS FOR MANAGEMENT

- ✓ Current restoration practices of cutting, piling, and burning of smaller conifers are enhancing aspen regeneration while conifer regeneration is declining (but still abundant).
- ✓ Burning cut conifer wood in piles leaves blackened patches of ground (termed 'burn scars'), some of which were being recolonized by aspen, conifer, and understory vegetation. After 2-4 years, herbaceous cover was 35-71% of that adjacent to burned piles.
- ✓ Aspen were more likely to regenerate inside burn scars where fewer of the surrounding trees were firs. Conifers were more likely to regenerate in burn scars where surrounding conifer (pine or fir) trees were more common than aspen.
- ✓ Regenerating firs have much slower early growth than aspen regenerating after restoration treatments. They take an average of 18-22 years to attain 1.37 m (4.5 ft) height. Eliminating small young conifers while they are still growing slowly and don't represent much fuel loading may be an economical way to prolong restoration treatment longevity.

INTRODUCTION

Removal of conifers encroaching aspen stands is being practiced in the Lake Tahoe Basin (EIP Project #10080: Aspen Community Restoration Projects). Restoration techniques have included mechanically removing conifers or hand thinning, piling, and burning cut conifers in and adjacent to aspen-conifer stands. For land managers, the ecological consequences of these restoration efforts (e.g., regeneration following treatments) are of particular concern and not well understood. For example, a study in aspen stands following restoration treatments in the eastern Sierra Nevada reported mixed results for aspen regeneration and residual trees (Krasnow et al. 2012). One of their conifer removal sites showed no significant increases in aspen regeneration and significant overstory mortality while the other sites showed significant increases in some size classes of regeneration. Currently, there are no published studies that document regeneration following aspen restoration treatments in the Lake Tahoe Basin.

Permanent monitoring plots have been installed at nine study sites in aspen-conifer stands around the Lake Tahoe Basin (SNPLMA Science Round 10 and 12: Stocking Guidelines for Aspen Restoration, Ecosystem Response to Aspen Restoration). Aspen trees ≥ 10 cm DBH and conifer trees ≥ 20 cm DBH were mapped, measured, and their health status assessed pre-treatment. The removal of encroaching conifers has been completed at 6 sites. Cut conifer wood, branches, and debris were piled for burning, and piles burned at 4 sites. Post-treatment assessments (including sites that were not treated) have occurred repeatedly, tracking changes in tree health, survival, growth, and regeneration.

This report describes regeneration response at the nine study sites. Additionally, we report patterns of recent diameter growth for small conifers in aspen-conifer stands from around the Lake Tahoe Basin.

The objectives were to:

- (1) Quantify conifer and aspen regeneration and examine the relationship of regeneration by treatment
- (2) Quantify regeneration (conifer, aspen, and herbaceous vegetation cover) within the footprint of burned piles (hereafter referred to as burn scars) and adjacent to burn scar locations
- (3) Examine the influence of pile size on regeneration
- (4) Determine growth rates of young conifers establishing within aspen-conifer stands

We hypothesized that aspen and conifer regeneration was: (i) more common in stands where smaller conifers had been cut, piled, and burned; (ii) affected by stand characteristics; and (iii) more likely to be found in smaller burn scars (i.e., smaller burn piles that comprised less cut conifer biomass). We also hypothesized that young conifer tree growth: (i) differed among species, geographic locations and elevations; (ii) correlated with tree and crown size; and (iii) decreased at higher stand densities and in the presence of conifer trees as opposed to aspen.

METHODS

Study area

The Lake Tahoe Basin covers more than 134,000 ha in the Sierra Nevada Mountains of California and Nevada, USA. The majority of soils are formed in parent materials derived from igneous intrusive rocks (typically granodiorite) and igneous extrusive rocks (typically andesitic lahar). Soils derived from metamorphic rock are present but uncommon (NRCS 2007). A Mediterranean continental climate brings cold winters, and summers with cool nights and warm days. Precipitation generally increases with elevation and from east to west, and varies between years and seasons; most comes as snow or rain during winter months. Occasional summer thunderstorms bring short periods of rain (<http://www.wrcc.dri.edu>). Mixed aspen-conifer stands are scattered around Lake Tahoe. The average stand area is currently less than 2 ha, although a few stands are much larger. They are typically located alongside creeks or other water sources such as seeps and springs (Shepperd et al. 2006).

Regeneration and herbaceous cover

Regeneration was assessed in a systematic grid of 0.004-ha circular subplots within the 1-ha main plot area at the nine study sites in an attempt to sample the range of conditions within each site (>10% subsample). Subplots were spaced 10 m apart along transect lines spaced 25 m apart for a total of 27-30 subplots per site (Berrill and Dagley 2014). Within subplots, a count of each species was recorded for all trees ≤ 10 cm DBH. Herbaceous vegetation cover was ocularly estimated within a 1 m² quadrat centered within the 0.004-ha circular subplots.

At sites where conifers were cut and piled for restoration purposes, burn piles were mapped and measured. Pile size was deliberately varied for research purposes. Pile measurements included height, width, length, and pile shape description. Additionally, we estimated fuel size-class composition by volume and packing ratio. Pile biomass and gross volume were estimated using the Piled Fuels Biomass and Emissions Calculator (Hardy 1996 and Wright et al. 2009). In 2015, a count of aspen and conifer regeneration inside each burn scar was collected. Herbaceous cover was ocularly estimated within and adjacent to each burn scar.

We constructed models to examine the effects of treatment and stand variables on the presence of conifer and aspen regeneration. The first analysis looked at change in density of aspen and conifer regeneration pre- versus post-treatment within subplots at all nine study sites. We examined the effects of variables unique to each subplot including treatment type, vicinity stand density index (SDI), basal area (BA), species composition, and thinning intensity (post-treatment BA/pre-treatment BA). The second analysis looked at presence of regeneration inside burn scars (i.e., four study sites) and examined the effects of explanatory variables including burn pile characteristics (e.g., volume, biomass, area), presence of herbaceous cover, and vicinity SDI, BA, and species composition. For both analyses, vicinity SDI, BA, and species composition were calculated from stem map data in ArcGIS. We used ArcGIS to query each stem location map and derive stand density and species composition in the vicinity of each subplot and burn pile. This was achieved by creating a buffer of 11.28 m radius around each subplot and burn pile and clipping tree data in each buffer, giving tree data for a series of 0.04-ha circular plots surrounding each subplot and burn pile. Tree data from each 0.04-ha plot were summarized, giving BA per hectare and SDI for the aspen and conifer stand components, and other hardwoods when present. SDI was calculated by summing individual tree SDI because the DBH data were not normally

distributed: $SDI = \sum (0.04 DBH_i)^a$ where DBH_i = DBH in cm of the i^{th} tree in the plot, and $a = 1.605$ (Shaw 2000). Species composition in each plot was calculated as the proportion of aspen, fir, and pine in terms of BA. Models were fitted using PROC GLIMMIX in SAS (SAS Institute 2004). We accounted for differences among sites by specifying "Site" as a random effect in the mixed model. The selection of variables for inclusion in the final models was based on likelihood ratio tests comparing the full model against reduced models in terms of model chi square.

Retrospective data and analysis of young conifer growth

We selected aspen-conifer stands for sampling on the basis of differences in elevation and location around the Lake Tahoe Basin, and absence of major recent disturbance. Sampling was intended to generate data covering a 'matrix' of possible stand conditions and tree sizes for regression analysis of young conifer growth. We sampled a total of 29 aspen-conifer stands where young conifers (< 20 cm DBH) were present and we found no evidence of recent major disturbance. In each stand we sampled one 'small' young conifer (from 1.37-2.0 m height) and one 'large' young conifer (>2 m height) of each species. After sampling the first healthy young conifer of each species encountered, we sought an additional representative of each species, if present, in the other size class which was farthest away inside the same stand. Selected conifers were measured for DBH, tree height, and live crown base height.

For each young conifer sampled, we counted annual rings on a breast height increment core, giving breast height age. Increment cores with at least five growth rings were measured for radial growth over the most recent full five years of growth (2011, 2012,...2015 growing seasons). Measurements were taken to the nearest 0.01 mm using digital calipers. Using only five growth rings was a compromise between using more rings to better account for inter-annual variations versus using only the most recent rings that were more likely to reflect growth within the existing stand structure and not a former structure altered by a disturbance during the growth measurement period. A second increment core was taken at ground line and rings counted for total tree age. Subtracting breast height age from total age revealed time taken for each young conifer to reach 1.37 m breast height. We restricted sampling to four conifer species commonly found in aspen-conifer stands around Lake Tahoe: lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *murrayana* (Balf.) Engelm.) Jeffrey pine (*P. jeffreyi* Grev. and Balf.), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), and red fir (*A. magnifica* A. Murr.).

An estimate of stand density (in terms of basal area) and species composition in the neighboring vicinity of each young conifer sampled was obtained by separately tallying aspen, conifer, and hardwood stems within the critical radius of a $9.18 \text{ m}^2 \text{ ha}^{-1}$ basal area factor variable radius plot centered on the conifer stem being cored. Neighboring conifer tallies including lodgepole pine, Jeffrey pine, white fir, red fir, Sierra juniper (*Juniperus occidentalis* ssp. *australis*), and western white pine (*Pinus monticola* Dougl. Ex D. Don) were separated into groups for pine, fir, and juniper. The hardwood group included mountain alder (*Alnus incana* ssp. *tenuifolia*) and various willows (*Salix* spp.). Combining prism plot tallies for all species groups gave an estimate of stand density, termed "vicinity BA", which included BA of the young conifer stem at plot center. Species composition in the vicinity of each young conifer sampled was calculated as the proportion of BA in either: aspen, conifer, or other hardwoods. Each site was categorized by its location with respect to Lake Tahoe (North, South, East, or West side of the lake). Sample stand elevation was recorded with a handheld GPS.

We used generalized linear regression analysis to test for effects of tree-, stand- and site variables on growth of young conifers establishing within aspen-conifer stands. The first analysis tested for variables correlated with young conifer growth in terms of time taken to reach breast height in years. The second analysis tested for variables correlated with DBH increment (average of most recent five years DBH growth) for young conifers that were at least 1.37 m tall five years before sampling. Vicinity BA was log-transformed to reduce data distribution skewness. We used PROC GLMSELECT in SAS (SAS Institute 2004) with Mallow's C(p) model selection where

candidate variables and their interactions enter model at $\alpha=0.15$ level and exit at $\alpha=0.20$ level of significance. If the categorical 'species' variable was selected for inclusion in the model, indicating significant differences among species, we also developed individual species-specific models. Performance of these individual species-specific models was compared against the global model by calculating the root mean square error (RMSE) for predictions from all individual models and for the global model. Finally, we plotted model predictions of expected (modeled average) growth rates for young conifers across the range of values for measured variables.

RESULTS

The influence of forest restoration treatments on regeneration

Aspen and conifer regeneration was prolific and highly variable at the nine study sites (Table 1). Pre-treatment aspen densities ranged from 305-6,445 stems ha^{-1} while conifer ranged from 867-25,473 stems ha^{-1} . Differences between pre-and-post-treatment aspen density showed increases at 6 of the 9 study sites (Table 2, Figure 1). At sites where aspen density decreased, the change was statistically significant (at 95% level of confidence) and occurred at sites where no treatment was implemented. Differences between pre-and-post-treatment conifer density indicated that regenerating conifers were declining in numbers over the evaluation period. Counts of regenerating conifers declined at all nine study sites with significant differences occurring at four sites over the evaluation period (Table 2). These four sites represented all treatment types, suggesting that a significant declining trend had occurred independent of treatment type.

Table 1: Mean values and standard deviation for aspen and conifer regeneration density throughout nine 1-ha study sites surrounding Lake Tahoe, California and Nevada, USA. Data collected pre-treatment in summer 2009 or 2010 and post-treatment in summer 2015. Cut + Burn = cut smaller conifers and pile and burn cut material. Cut = cut smaller conifers and pile cut material. No cut = no restoration treatment.

Site	Prescription	Pre-treatment				Post-treatment			
		Aspen		Conifer		Aspen		Conifer	
		Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
BC20	Cut + Burn	833	1411	8472	16682	2045	3428	3674	9858
NC03	Cut + Burn	4046	6363	1953	2229	4348	6135	979	1415
SHC01	Cut + Burn	305	803	19561	77527	1308	2795	459	622
WA38	Cut + Burn	2696	2581	25473	120777	3436	2743	8685	12727
CV05	Cut	4051	4044	4154	3348	4755	4514	1006	1425
CV06	Cut	3815	3039	1815	2181	6002	4799	260	425
BP2	No Cut	1757	1815	1971	2177	1363	1893	1796	2429
SSP24	No Cut	3967	3113	867	907	3292	2743	725	674
TC01	No Cut	6445	7266	3179	4393	1297	1388	1904	2971

Prior to analysis, logarithmic transformations of regeneration density were applied to improve their normality. For both aspen and conifer, changes in density (from pre-to post-treatment) were associated with conifer composition, thinning intensity, and treatment (Appendix S1). The analysis revealed a significant increase in aspen density following CUT + BURN and CUT treatments. Additionally, within subplots at treated sites where a greater proportion of vicinity BA was cut, aspen regeneration increased. Aspen regeneration density declined at the NO CUT sites. When conifers represented a greater proportion of the trees surrounding a subplot, we found slightly less aspen regeneration. Conifer seedling densities were much lower in subplots where a high intensity of cutting had occurred and at sites receiving CUT or CUT + BURN treatments. When conifers represented a greater proportion of the trees surrounding a subplot, we predicted slightly less conifer regeneration.

Table 2: Change in density (stems ha⁻¹: pre-treatment – post-treatment) for aspen and conifer regeneration throughout nine 1-ha study sites surrounding Lake Tahoe, California and Nevada, USA. Data collected pre-treatment in summer 2009 or 2010 and post-treatment in summer 2015. Cut + Burn = cut smaller conifers and pile and burn cut material. Cut = cut smaller conifers and pile cut material. No cut = no restoration treatment.

Site	Prescription	Aspen			Conifer		
		Diff	Pr> t	95% CI [LL, UL]	Diff	Pr> t	95% CI [LL, UL]
BC20	Cut + Burn	1212	0.0472	16.4 2406.9	-4798	0.1724	-11828.7 2231.4
NC03	Cut + Burn	302	0.5069	-617.5 1221.9	-974	0.0010	-1518.9 -429.2
SHC01	Cut + Burn	1003	0.0458	20.2 1987.2	-19102	0.2038	-49194.4 10991.4
WA38	Cut + Burn	740	0.1698	-336.3 1816.0	-16788	0.4764	-64483.3 30907.6
CV05	Cut	704	0.3543	-829.0 2237.6	-3148	<0.0001	-4303.3 -1991.5
CV06	Cut	2187	0.0098	573.6 3800.4	-1555	0.0010	-2413.6 -696.8
BP2	No Cut	-394	0.0182	-717.0 -72.3	-175	0.5765	-808.7 458.7
SSP24	No Cut	-675	0.0510	-1353.1 3.1	-142	0.1241	-324.6 41.3
TC01	No Cut	-5148	0.0002	-7622.3 2673.6	-1275	0.0014	-2007.2 -542.6

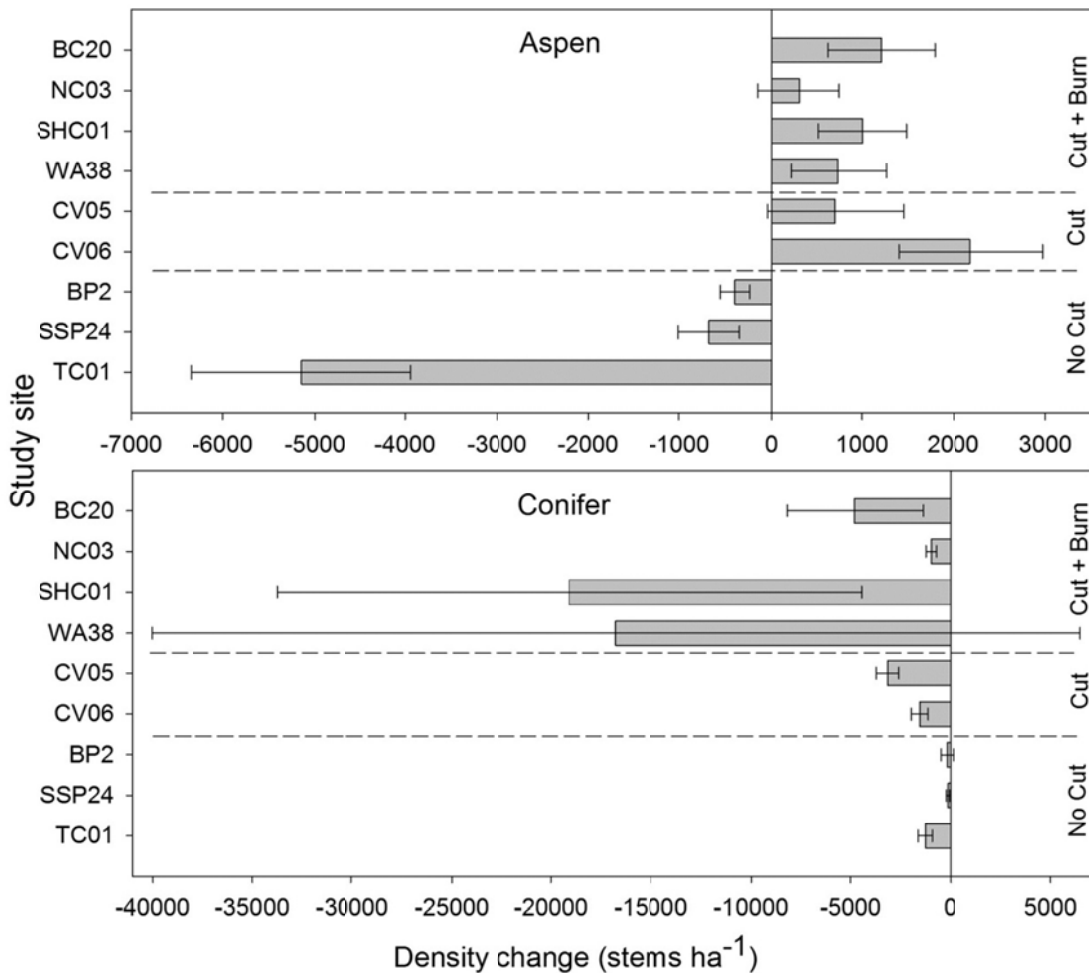


Figure 1: Change in aspen and conifer regeneration density for nine study sites surrounding Lake Tahoe, California and Nevada, USA. Differences based on data collected in 2009 (WA38, CV05, CV06 and SSP24) and 2010 (BC20, NC03, SHC01, BC20, TC01) and post-treatment in 2015.

The influence of pile burning on regeneration and herbaceous cover

Piles were larger at one site (BC20) where they comprised slash after mechanical harvest of merchantable conifer logs (Table 3). At other sites, smaller trees were cut and hand piled in a range of pile sizes. Of the 262 burn piles sampled across four study sites, 250 piles were burned. Of these 250 piles, new aspen regeneration had developed inside 16% (n=40) of burn scars. In contrast, 48% (n=121) of burn scars had new conifer regeneration present. Summary data for these four CUT + BURN sites showed differences in mean pile volume, herbaceous cover, regeneration density and height of the tallest regenerating aspen or conifer. With the exception of aspen density, Ward Creek (WA38) exhibited greater responses to pile burning than the other sites which may be due to the earlier treatment date. After two or more years, herbaceous cover inside burn scars was 35-71% of that adjacent to burn scars.

Table 3: Summary data for burn piles and recovery of burn scar areas in four 1-ha study sites at Lake Tahoe, California and Nevada, USA. Herbaceous cover (inside and adjacent), and tree regeneration density and height measurements assessed in summer 2015.

Site	BC20	NC03	SHC01	WA38
Treatment date	2013/14	2011/12 or 2012/13	2012/13	2011/12
Number of burn piles sampled	18	72	48	124
Mean burn pile volume (m ³)	26.29	1.99	8.67	5.59
Herbaceous cover adjacent (%)	65.83	28.34	46.10	71.54
Herbaceous cover inside (%)	38.89	7.74	20.43	41.70
Herbaceous cover (inside/adjacent)	0.58	0.35	0.56	0.71
Conifer regeneration inside (stems ha ⁻¹)	721	187	2106	37751
Aspen regeneration inside (stems ha ⁻¹)	363	730	318	442
Height of tallest conifer inside (cm)	10.20	4.80	8.63	13.53
Height of tallest aspen inside (cm)	28.25	49.00	30.38	64.87

Regression analysis revealed that the occurrence of aspen and conifer regeneration inside burn scars was related to pile area and fir or conifer composition, for aspen and conifer, respectively (Appendix S2). An alternate, plausible regression model was a simpler reduced model where only fir or conifer composition was used as predictors of the presence of aspen and conifer, respectively, regeneration inside burn scars. Likelihood ratio tests favored the reduced models for aspen and conifer ($p \leq 0.05$). This supported the development of a final model which included 23 more observations in which we had composition data but were missing pile size data (Table 4). We excluded vicinity SDI and herbaceous vegetation from the aspen and conifer regeneration models because they were not significantly affecting their occurrence. A negative coefficient for fir tree composition indicated that the occurrence of aspen regeneration decreased as vicinity fir composition increased. The probability of the occurrence of aspen regeneration was low, ranging from 0.2 to 0.11 with increasing fir composition (Figure 2). The final model for conifer regeneration indicated that conifer regeneration was more likely to be found in burn scars surrounded by conifers as opposed to aspen (i.e., higher vicinity conifer composition (Table 4). The probability of the occurrence of conifer regeneration was higher than that of aspen, ranging from 0.11 to 0.53 (Figure 2).

Table 4: Logistic regression models for probability of occurrence of aspen and conifer regeneration inside burn scars 2-4 years after pile burning (n=249 piles) at four study sites at Lake Tahoe, California and Nevada, USA.

Species	Parameter	Estimate	Std. error	t Value
Aspen $\chi^2= 248.75$	Intercept	-1.3657	0.28	-4.87
	Fir composition	-0.6969	0.57	-1.23
Conifer $\chi^2= 233.49$	Intercept	-2.0634	0.84	-2.44
	Conifer composition	2.1871	0.57	3.81

Std. error = standard error for coefficient; d.f. = degrees of freedom; n = number of observations; χ^2 = generalized chi-square for model.

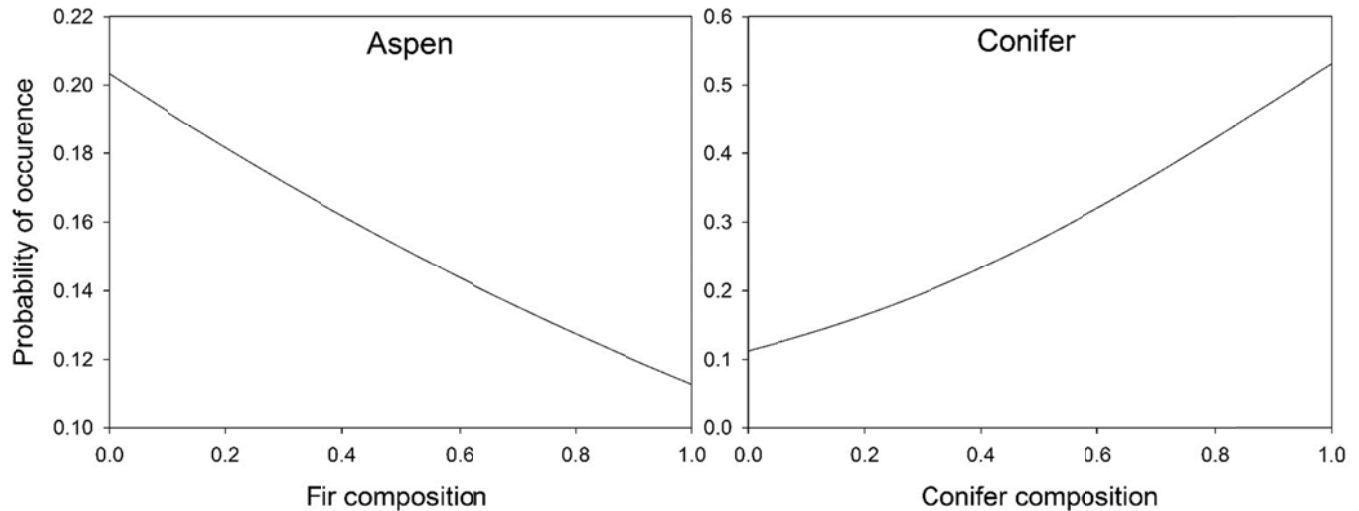


Figure 2: Regeneration inside burn scars: modeled probability of occurrence of aspen and conifer regeneration in response to varying levels of fir and conifer tree composition around each burn pile. Note: different scales on y-axis.

Growth of young conifers

The generalized linear model predicting time to reach breast height for all conifer species (RMSE = 5.51 years) outperformed individual models for each species (Overall RMSE = 6.13 years). This time was slightly longer (i.e., slower growth) at higher elevations, and was prolonged by overstory competition in terms of higher vicinity BA (Table 5). On average, the most rapid ascension to 1.37 m height ranked Jeffrey pine = lodgepole pine > white fir > red fir (Figure 3).

Table 5: Generalized linear model for young conifer growth in terms of years taken to reach 1.37 m (breast height) as a function of elevation (m) and vicinity basal area (BA; m² ha⁻¹) in prism plot centered on each sample tree (n=123) at 28 sites throughout the Lake Tahoe Basin, California and Nevada, USA.

Parameter	Estimate	Std. Error	t Value
Intercept	-5.632634	7.63	-0.74
Elevation	0.008072	0.00	3.00
Ln(vicinity BA)	1.791390	1.19	1.51
Species: Jeffrey pine	-3.840508	1.50	-2.56
Species: lodgepole pine	-3.926845	1.47	-2.67
Species: red fir	1.934610	1.46	1.33
Species: white fir	0.000000	-	-

Coefficients from Table 5 can be implemented in species-specific prediction equations as follows:

$$\text{YearsBH}_{jp} = -5.632634 + 0.008072 * \text{Elev} - 3.840508 + 1.79139 * \text{Ln}(\text{BA}+1)$$

$$\text{YearsBH}_{lp} = -5.632634 + 0.008072 * \text{Elev} - 3.926845 + 1.79139 * \text{Ln}(\text{BA}+1)$$

$$\text{YearsBH}_{rf} = -5.632634 + 0.008072 * \text{Elev} + 1.93461 + 1.79139 * \text{Ln}(\text{BA}+1)$$

$$\text{YearsBH}_{wf} = -5.632634 + 0.008072 * \text{Elev} + 0.0 + 1.79139 * \text{Ln}(\text{BA}+1)$$

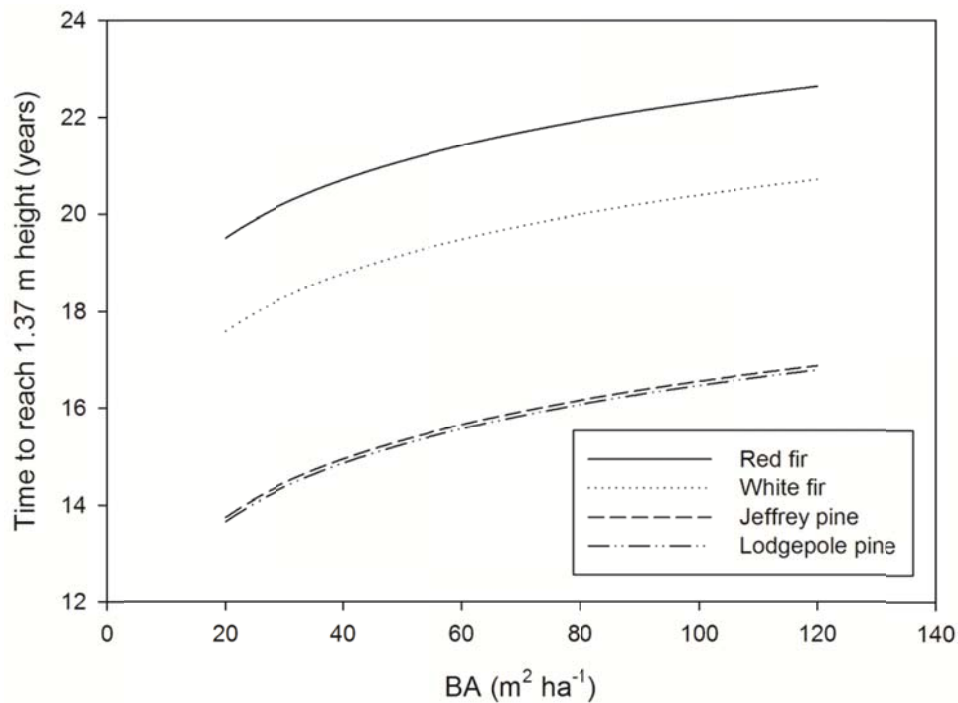


Figure 3: Predicted time taken for conifers to reach 1.37 m breast height at average sampled elevation according to basal area (BA) in the vicinity of each young conifer (n=123) sampled in 28 aspen-conifer stands around Lake Tahoe Basin, California and Nevada, USA.

The generalized linear model predicting DBH increment for all conifer species (RMSE = 0.51 mm yr⁻¹) outperformed individual models for each species (overall RMSE = 0.88 mm yr⁻¹). Once above 1.37 m height, young conifers grew slightly more rapidly at higher elevations, and on South and West sides of Lake Tahoe (Table 6). Dbh increment was impacted by overstory competition in terms of higher vicinity BA which itself was not correlated with sample tree crown ratio, another influential predictor of young conifer growth. Unlike white fir where DBH increment remained approximately constant across the range of trees sizes sampled, growth was more rapid in larger Jeffrey pine, lodgepole pine, and red fir. On average, young conifer DBH increment ranked white fir > Jeffrey pine > lodgepole pine ≈ red fir (Figure 4).

Table 6: Generalized linear model for young conifer growth in terms of DBH increment (mm yr^{-1}) as a function of sample tree DBH (mm) and crown ratio, elevation (m), North/East versus South/West side of lake, vicinity basal area (BA; $\text{m}^2 \text{ha}^{-1}$) and proportion of conifer (range: 0-1) in prism plot centered on each sample tree (n=113) in 29 aspen-conifer stands around Lake Tahoe Basin, California and Nevada, USA.

Parameter	Estimate	Std. Error	t Value
Intercept	0.286010	1.0555	0.27
Elevation	0.000710	0.0003	2.34
North/East	-0.244495	0.1319	-1.85
South/West	0.000000	.	.
$\ln(\text{vicinity BA})$	-0.539245	0.1383	-3.90
Proportion conifer BA	-0.891601	0.2204	-4.05
Species: Jeffrey pine	-0.668681	0.5983	-1.12
Species: lodgepole pine	-1.589861	0.5082	-3.13
Species: red fir	-1.277538	0.5572	-2.29
Species: white fir	0.000000	.	.
Species \times DBH: Jeffrey pine	0.121425	0.0516	2.35
Species \times DBH: lodgepole pine	0.196427	0.0410	4.79
Species \times DBH: red fir	0.128074	0.0513	2.50
Species \times DBH: white fir	0.024233	0.0390	0.62
Crown ratio of sample tree	3.535094	0.6226	5.68

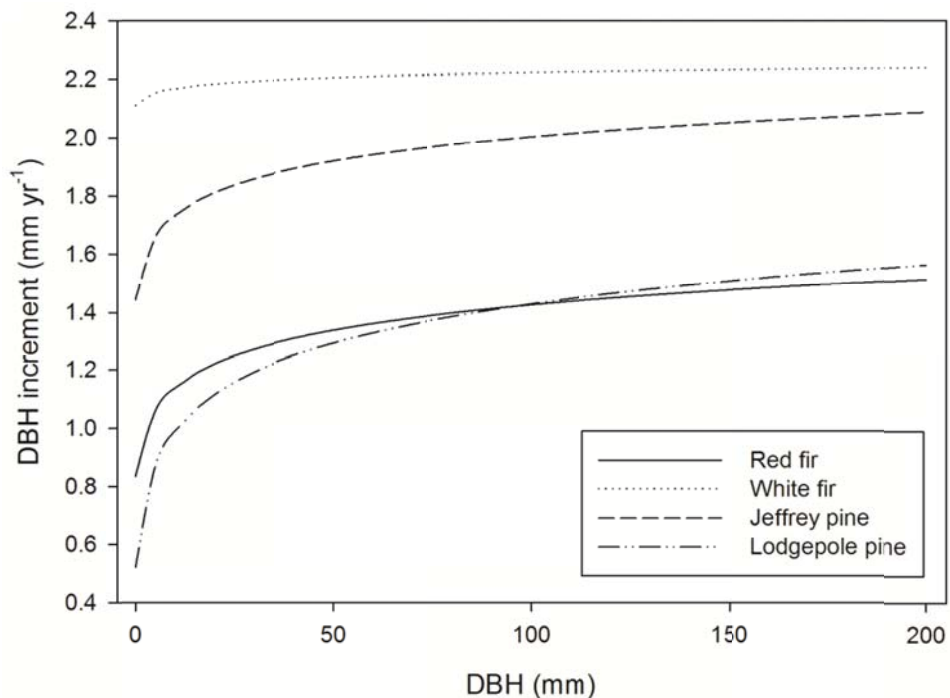


Figure 4: Predicted 5-year average DBH increment for young conifers, according to tree size (DBH), on the South/West side of Lake Tahoe, with other variables held constant at/near mean values: elevation (2200 m), sample tree crown ratio (0.8), and basal area ($50 \text{ m}^2 \text{ha}^{-1}$) and proportion of conifer (0.5) in the vicinity of each young conifer (n=113) sampled in 29 aspen-conifer stands around Lake Tahoe Basin, California and Nevada, USA.

Coefficients from Table 6 can be implemented in species-specific equations as follows:

$$DBHI_{jp} = 0.28601 + 0.00071 \times Elev - 0.244495 \times LocE - 0.539245 \times \ln(BA+1) - 0.891601 \times \%ConBA - 0.668681 + 0.121425 \times DBH^{0.5} + 3.535094 \times CR$$

$$DBHI_{ip} = 0.28601 + 0.00071 \times Elev - 0.244495 \times LocE - 0.539245 \times \ln(BA+1) - 0.891601 \times \%ConBA - 1.589861 + 0.196427 \times DBH^{0.5} + 3.535094 \times CR$$

$$DBHI_{rf} = 0.28601 + 0.00071 \times Elev - 0.244495 \times LocE - 0.539245 \times \ln(BA+1) - 0.891601 \times \%ConBA - 1.277538 + 0.128074 \times DBH^{0.5} + 3.535094 \times CR$$

$$DBHI_{wf} = 0.28601 + 0.00071 \times Elev - 0.244495 \times LocE - 0.539245 \times \ln(BA+1) - 0.891601 \times \%ConBA - 0.0 + 0.024233 \times DBH^{0.5} + 3.535094 \times CR$$

DISCUSSION

Changes in regeneration density from the CUT + BURN and CUT treatments were favorable (for aspen restoration objectives), with significant increases and decreases in aspen and conifer density, respectively. In subplots with higher thinning intensity, the treatment effects on density were significantly enhanced (i.e., more aspen, less conifer). Both models predicted the responses to be slightly larger for the CUT treatment compared to the CUT + BURN treatment. This result was unexpected. We expected fire to increase aspen regeneration because fire is known to stimulate the sprouting of aspen suckers from the roots (Perala 1990). For conifers, we hypothesized that an increase in regeneration density would follow conifer removal treatments due to the increase in understory light. To find that both the CUT and CUT+BURN treatments resulted in significantly reduced conifer regeneration was surprising but encouragingly positive for aspen restoration efforts. High variability in density of regeneration among subplots (coefficient of variation for aspen: 0.78-2.63, conifer: 0.81-4.74) was indicative of spatial variability (Table 1). This is consistent with the aggregated spatial pattern of aspen and white fir regeneration reported by Pierce and Taylor (2010).

The ecological consequences of pile burning are a concern for land managers interested in maintaining and/or restoring native understory plant diversity. Extreme temperatures and the long duration from burning high fuel loads can be lethal to soil biota and seed reserves and alter physical, chemical, and biological soil properties (Busse et al. 2014). Additionally, some studies have shown the establishment of non-native plant species to be favored inside burn scars (Haskins and Gehring, 2004, Korb et al. 2004). At all four of our CUT+ BURN sites, there was still visible evidence of burn scars (i.e., 2+ years post-burn). Herbaceous cover inside burn scars was 35-71% of that adjacent to the burn scars. We did not find non-native plants within burn scars. The recovery of vegetation in burn scars from a study in the Colorado Front Range showed similar results with total native plant cover at 33 and 73 percent of that measured in unburned areas after 1 and 2 years, respectively (Rhoades et al. 2015). Longer term studies have shown no significant differences in plant cover inside and outside burn scars 7 years after burning and very little or no invasions from non-native plants after pile burning treatments (Creech et al. 2012, Halpern et al. 2014).

We hypothesized that larger burn piles would have less regeneration than smaller piles because of greater heating and/or longer duration time of burning. However, since the initiation of our study, Busse et al. (2013) published a report on the effects of pile burning in the Lake Tahoe Basin and found no significant relationship between pile size and maximum soil temperature or heat duration for piles ranging from 1.8-6.1 m (6-20 ft)

diameter. Similarly, our piles ranged from 1.3-6.6 m diameter, and we found that pile size was not a significant factor in regressions predicting regeneration. There were significant differences in regeneration occurrence inside burn scars according to composition of trees surrounding each burn pile (Figure 3). For conifer, regeneration increased when surrounding trees were conifer. For aspen, fir composition was more influential than similar descriptors of neighbor tree species composition (i.e., percent aspen or conifer), and aspen occurrence declined with increasing vicinity fir tree composition. This result was also found for regenerating aspen growth rates (Berrill et al., in prep). In addition, Berrill et al. (in prep) found understory light was significantly less useful than vicinity fir tree composition in predicting growth of young aspen. Similarly, we found vicinity SDI (a measure of competition and surrogate for understory light) to be a less useful predictor of regeneration than fir composition in our study. These findings suggest: (i) true firs (having more leaf area than pines or aspen of similar size) cast more shade, and/or that (ii) firs may change soil properties and/or exert more influence below ground, and/or that (iii) in areas where firs are more common, microsite conditions may be poorer than those where aspen or pine are found.

Vicinity BA was an important predictor variable negatively correlated with early height growth and DBH growth of young conifers (Table 5 & 6). The young Jeffrey pine we sampled were found in areas with vicinity BA below $92 \text{ m}^2 \text{ ha}^{-1}$. The other conifers were found in progressively denser areas: lodgepole pine was found below $111 \text{ m}^2 \text{ ha}^{-1}$, red fir below $120 \text{ m}^2 \text{ ha}^{-1}$, and white fir below $138 \text{ m}^2 \text{ ha}^{-1}$ (Appendix S4). This matches our expectations for ranking of JP < LP < WF < RF having progressively greater shade tolerance and ability to withstand higher stand densities with the exceptions of the firs (Reineke 1933). Dbh increment model predictions for a 10 cm DBH white fir at mid-elevation on the West/South side of Lake Tahoe indicated that diameter growth was: 1.50 mm yr^{-1} in a stand with $100 \text{ m}^2 \text{ ha}^{-1}$ of which 90% was conifer; 2.22 mm yr^{-1} in a stand with $50 \text{ m}^2 \text{ ha}^{-1}$ of which 50% was conifer, and 3.06 mm yr^{-1} in a stand with $20 \text{ m}^2 \text{ ha}^{-1}$ of which 10% was conifer. In comparison, young aspen in similar stand conditions took an average of 4-6 years to attain 1.37 m height, after which time they exhibited DBH increments of 3.0-4.5 mm with the most rapid growth in low-density aspen-dominated stands (Berrill and Dagley, in prep). Regenerating pines take an average of 14-16 years to reach 1.37 m height, and regenerating firs averaged 18-22 years to reach 1.37 m in aspen-conifer stands (Figure 3). We saw the same pattern inside burn scars; regenerating aspen were approximately 4× taller than the tallest conifer seedlings (Table 3). If their removal can be accomplished efficiently, treatment longevity would be extended at low cost and without excessive fuel loading. Otherwise, regenerating conifers are expected to be numerous, take up growing space, and be a big part of the restored stand over time (Berrill et al. 2016).

Growth of regenerating conifers up to 1.37 m height did not differ according to location (North, South, East, West sides of lake), but was slower at higher elevation. Trees taller than 1.37 m had more rapid DBH growth on the West and South sides of Lake Tahoe, and at higher elevations, where snowpack and precipitation are greater. One explanation could be that growth of small conifers covered in snow over winter begins later in the season, as opposed to growth on drier sites which ceases earlier in the season when soil moisture becomes scarce. Then, once the conifers surpass 1.37 m, they may be less affected by snow cover and benefit from snowpack-enhanced soil moisture as opposed to being slowed by scarcity of soil moisture on drier sites on the North and East sides of the lake. This study took place during a period of above average snowpack (winter 2010/11) followed by a multi-year drought (2012-2015). Under different climatic conditions, we might expect different regeneration occurrences, density, herbaceous cover, and overall growth rates for young conifers than those reported in this study. Therefore, we recommend continued monitoring of regeneration inside and outside burn scars in our large permanent plots surrounding Lake Tahoe.

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APPENDIX

Table S1: Logistic regression models and associated fit statistics for changes in aspen and conifer density (from pre-to post-treatment) at nine study sites around Lake Tahoe, California and Nevada, USA. Model predicts $(\ln(\text{Density}_{\text{post}}) - \ln(\text{Density}_{\text{pre}}))$

Model	Parameter	Coefficient	s.e.	d.f.	t-Value	Pr> t
Aspen	Intercept	-0.1587	0.2960	6	-0.54	0.6111
	Thinning Intensity	1.4093	0.7040	245	2.00	0.0464
	ConComp	-0.0466	0.3471	245	-0.13	0.8933
	Cut + Burn	0.5588	0.3057	245	1.83	0.0688
	Cut	0.6422	0.3431	245	1.87	0.0624
	No Cut	0				
Conifer	Intercept	-0.1004	0.7343	6	-0.14	0.8957
	Thinning Intensity	-3.5505	1.6383	245	-2.17	0.0312
	ConComp	-0.3697	0.5781	245	-0.64	0.5230
	Cut + Burn	-1.1677	0.9034	245	-1.29	0.1974
	Cut	-3.2227	1.0328	245	-3.12	0.0020
	No Cut	0				

Table S2: Candidate logistic regression models and associated fit statistic -2 Log Likelihood (-2LL) for probability of occurrence of aspen and conifer regeneration inside burn piles at four study sites at Lake Tahoe, California and Nevada, USA.

Species	n	Model	-2LL
Aspen	227	$1/(1 + \text{EXP}(-(-0.7326 * \text{Fircomp})))$	1117.66
	227	$1/(1 + \text{EXP}(-(-1.7835 - 0.8655 * \text{Fircomp} + 0.0491 * \text{PileArea})))$	1128.97
Conifer	227	$1/(1 + \text{EXP}(-(-2.1586 + 2.1693 * \text{Concomp})))$	1121.68
	227	$1/(1 + \text{EXP}(-(-3.0907 + 2.0795 * \text{Concomp} + 0.08790 * \text{PileArea})))$	1144.04

Fir and conifer composition ranges from 0-1. Pile area (m^2).

Regeneration Response to Restoration in Aspen-Conifer Stands

Table S3: Summary data for burn piles in 1-ha plots within four aspen-conifer stands at Lake Tahoe, California and Nevada, USA.

Variable	n	Mean	Std. Dev.	Minimum	Maximum
<i>BC20</i>					
Vicinity SDI	18	502.97	307.23	41.53	971.75
Conifer vicinity BA (%)	18	81	32.63	0.00	100.00
Fir vicinity BA (%)	18	59	40.57	0.00	100.00
Aspen vicinity BA (%)	18	19	32.63	0.00	100.00
Pile area (m ²)	18	20.85	12.21	4.37	48.65
Conifer regen. presence (%)	18	28	46.09	0.00	100.00
Aspen regen presence (%)	18	22	42.78	0.00	100.00
<i>NC03</i>					
Vicinity SDI	95	759.53	289.02	270.42	1604.64
Conifer vicinity BA (%)	95	45	7	19.00	50.00
Fir vicinity BA (%)	95	30	11	7.00	50.00
Aspen vicinity BA (%)	95	55	7	50.00	81.00
Pile area (m ²)	72	3.48	2.31	1.23	20.23
Conifer regen. presence (%)	75	7	25.11	0.00	100.00
Aspen regen presence (%)	75	17	38.11	0.00	100.00
<i>SHC03</i>					
Vicinity SDI	48	527.83	347.56	27.00	1462.50
Conifer vicinity BA (%)	48	59	38.73	0.00	100.00
Fir vicinity BA (%)	48	32	35.11	0.00	100.00
Aspen vicinity BA (%)	48	41	38.72	0.00	100.00
Pile Area (m ²)	48	12.94	5.76	2.28	29.47
Conifer regen.presence (%)	40	40	49.61	0.00	100.00
Aspen regen presence (%)	40	20	40.51	0.00	100.00
<i>WA38</i>					
Vicinity SDI	124	618.42	334.72	0.00	1487.24
Conifer vicinity BA (%)	124	81	28.26	0.00	100.00
Fir vicinity BA (%)	124	53	33.62	0.00	100.00
Aspen vicinity BA (%)	124	18	26.36	0.00	100.00
Pile Area (m ²)	124	6.47	2.02	2.99	14.52
Conifer Presence (%)	117	81	39.24	0.00	100.00
Aspen Presence (%)	117	13	33.58	0.00	100.00

Regeneration Response to Restoration in Aspen-Conifer Stands

Table S4: Summary data for young conifers sampled for growth in aspen-conifer stands (n=29) around Lake Tahoe, California and Nevada, USA.

Variable	n	Mean	Std. Dev.	Minimum	Maximum
<i>Jeffrey pine</i>					
DBH (mm)	27	73.81	48.43	0.00	160.00
Height (m)	27	4.32	2.27	1.37	9.30
Height:Diameter ratio	26	70.16	29.01	38.29	155.17
Crown ratio	27	0.77	0.10	0.55	0.94
Time to breast height (years)	25	14.12	3.73	9.00	21.00
DBH increment (mm yr ⁻¹)	22	2.24	1.11	0.58	4.37
Vicinity BA (m ² ha ⁻¹)	27	45.91	21.19	18.37	91.83
Conifer vicinity BA (%)	27	60	28	14	100
Elevation (m)	27	2080.32	198.52	1901.95	2430.48
<i>Lodgepole pine</i>					
DBH (mm)	33	74.55	49.07	0.00	189.00
Height (m)	34	4.51	2.64	0.36	10.12
Height:Diameter ratio	31	71.45	28.06	44.82	165.95
Crown ratio	34	0.82	0.11	0.43	0.99
Time to breast height (years)	29	14.83	6.79	5.00	37.00
DBH increment (mm yr ⁻¹)	29	2.26	0.79	0.84	3.68
Vicinity BA (m ² ha ⁻¹)	34	43.48	19.26	13.77	110.19
Conifer vicinity BA (%)	34	67	27	14	100
Elevation (m)	34	2228.54	213.56	1904.39	2430.48
<i>Red fir</i>					
DBH (mm)	34	67.38	38.61	0.00	167.00
Height (m)	34	3.65	1.70	1.37	8.60
Height:Diameter ratio	31	55.13	10.74	37.54	87.09
Crown ratio	34	0.77	0.10	0.55	0.93
Time to breast height (years)	33	22.30	6.84	13.00	38.00
DBH increment (mm yr ⁻¹)	31	1.72	0.65	0.66	3.58
Vicinity BA (m ² ha ⁻¹)	34	59.01	23.82	18.37	119.38
Conifer vicinity BA (%)	34	48	27	8	100
Elevation (m)	34	2332.84	125.73	1939.14	2467.97
<i>White fir</i>					
DBH (mm)	37	66.86	47.94	0.00	166.00
Height (m)	39	4.03	2.36	0.73	9.11
Height:Diameter ratio	36	80.76	41.82	42.63	213.36
Crown ratio	39	0.81	0.08	0.60	0.96
Time to breast height (years)	36	18.75	5.23	9.00	30.00
DBH increment (mm yr ⁻¹)	31	2.00	0.61	0.81	3.56
Vicinity BA (m ² ha ⁻¹)	39	59.33	27.19	18.37	137.74
Conifer vicinity BA (%)	39	57	28	11	100
Elevation (m)	39	2130.70	208.34	1904.39	2430.48