CONVERTING COAST REDWOOD/DOUGLAS-FIR FORESTS TO MULTIAGED MANAGEMENT: RESIDUAL STAND DAMAGE, TREE GROWTH, AND REGENERATION

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ABSTRACT

CONVERTING COAST REDWOOD/DOUGLAS-FIR FORESTS TO MULTIAGED MANAGEMENT: RESIDUAL STAND DAMAGE, TREE GROWTH, AND REGENERATION

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There is increased interest in multiaged management as a silvicultural and restoration tool in redwood forests of California. The effect of varying residual densities and spatial arrangements on residual stand damage, tree growth and regeneration was studied in a multicohort silviculture experiment on Jackson Demonstration State Forest. Four treatments varying in residual stand density or spatial arrangement were replicated at four sites. The experiment provided 4-year periodic growth measurements of residual trees and annual measurements of redwood and tanoak sprout height increments. Residual trees were more likely to sustain bole scarring when retained at higher densities. Crown damage was more likely to be sustained by smaller trees. From 2-6 years after partial harvesting, redwood trees grew faster than Douglas-fir or tanoak following harvest. The height increment of dominant redwood stump sprouts was much greater than dominant tanoak sprouts across all treatments and the growth of both species was directly correlated to understory light. No differences were detected for any dependent variables between dispersed and aggregated retention. No differences in sprout growth were detected when retaining a residual tree on the same root system as sprouting redwood stumps when compared against sprouts growing on a root system after all redwood stems were cut. Overall, these results suggest that managers have flexibility to manage multiaged redwood stands at different densities, and that retention of low densities of large trees will provide a good balance between overstory tree growth and understory development in multiaged stands while reducing incidences of residual stand damage.

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INTRODUCTION

Societal pressures and a modern understanding of forest ecology have led to increased interest in alternatives to traditional even-aged forestry. Multiaged forest management involves a silvicultural system in which two or more age classes, or cohorts, of trees are permanently retained in a stand (O’Hara 2014). This type of management, also frequently called selection forestry, is becoming an increasingly popular way of ensuring sustainable timber production while maintaining some continuity of canopy cover and protecting non-timber resources (Rosenvald and Lõhmus 2008; Lindenmayer et al. 2012). Early attempts at multiaged silviculture in North America were based on a perceived correlation of tree diameter to tree age; this led to “high graded” forests and left forest managers skeptical about its application (O’Hara 2002). A renewed interest in this style of management calls for critical thought about the quality of trees that should be retained as well as how the residual overstory affects regeneration.

Variable retention harvesting (VR) has emerged as an effective way to initiate or maintain multiple cohorts in a variety of ecosystems (O’Hara 1998, Mitchell and Beese 2002; Aubry et al. 2009). The system has been tested throughout the northwestern USA, and has been dubbed “ecological forestry” because it can mimic natural disturbance patterns (Franklin et al. 2018). Variable retention treatments can be used to create a patchwork of different residual overstory densities and spatial arrangements (Berrill et al. 2018a). The residual stand can have areas that are roughly evenly spaced (dispersed retention) or areas where trees are retained in groups or ‘clumps’ (aggregated retention;

Ashton and Kelty 2018). Aggregated retention leaves more space between groups of trees to move equipment and logs and may allow more light to reach the ground. A VR-like approach that defines different spatial arrangements, as well as densities, of residual stands to meet different objectives may have practical application in the conversion of coast redwood (*Sequoia sempervirens*) forests to multiaged management.

Redwood forests are capable of exhibiting very high levels of leaf area (Berrill and O'Hara 2007a; Van Pelt et al. 2016) and can be extraordinarily productive under multiaged management regimes (Berrill and O'Hara 2014). Trees in redwood forests have been shown to respond to various levels of precommercial thinning (O'Hara et al. 2015), commercial thinning (Oliver et al. 1994, Webb et al. 2017), group selection and single-tree selection (Berrill and O'Hara 2014, 2016), and restoration treatments (O'Hara et al. 2010; Dagley et al. 2018). The effects of VR treatments on residual tree growth in multiaged redwood stands have been simulated (Berrill and O'Hara 2007b) but not yet measured directly. These simulations showed that a higher density of retention enhanced stand growth and harvest of large-diameter redwoods. However, there were no data to validate the model predictions of understory tree growth rates beneath aggregated or dispersed overstories.

Growth and yield or value of the residual stand may also be affected by damage resulting from harvest operations (Han and Kellogg 2000; Vasiliauskas 2001). Severity and extent of damage can vary with harvest intensity, arrangement, and harvesting system. Moore et al. (2002) found that lower levels of retention resulted in a higher proportion of damaged trees. However, other research has indicated that basal area reductions of more than 15% had little effect on incidence of damage (Jonkers 1987). Hartsough (2003) found similar results for damage sustained during felling activity but damage sustained during skidding was more likely in higher levels of retention. Bole scarring has been shown to be more common in tractor logged units and crown damage more likely in cable and helicopter yarding systems (Han and Kellogg 2000). Identifying tree characteristics and harvesting systems that make a tree more likely to be damaged will assist forest managers in selecting trees to retain and cut.

Residual stand densities and spatial arrangement also affect regeneration (Maguire et al. 2006; O'Hara and Berrill 2010). Redwood is shade tolerant with a unique ability among western North American conifers to sprout from the stump or root collar after harvest or natural disturbance (Baker 1945; Roy 1966; Olson et al. 1990). These characteristics suggest that redwood forests may be well adapted to regenerating under an existing overstory, but the growth rates of new cohorts depend on availability of growing space (O'Hara et al. 2007; O'Hara and Berrill 2010). Tanoak (*Notholithocarpos densiflorus*) is a common associate of redwood that is also capable of regenerating by basal sprouting after disturbances and competes with redwood for growing space in the understory (Tappeiner et al. 1990). Berrill et al. (2018b) identified positive relationships between both understory light and parent tree stump diameter and stump sprout growth in this forest type, and provided equations to predict understory light from residual stand density. These relationships suggest that stump sprouts quickly transition from reliance on carbohydrate reserves within the stump and root system to growth controlled by light availability. The transition from dependence on carbohydrate reserves to dependence on understory light may affect sprout growth over time.

As sprouts age their growth may also be affected by the structure of the residual stand. It is possible that high growth efficiency of large residual trees will allow them to grow more leaf area and, therefore, cast more shade upon the understory (Berrill and O'Hara 2007b). More information is needed on how the ongoing expansion of residual crowns into growing space made available by partial harvesting impacts the growth of new cohorts in multiaged stands.

The purpose of this study was to determine the effect of multiaged treatments on regeneration, residual stand damage, and residual tree growth. Understanding these relationships will assist forest managers in creating effective silvicultural prescriptions and tree marking guidelines. The following questions regarding regeneration will be analyzed: (1) How do the growth rates of redwood and tanoak sprouts vary in the first six years after treatment under different overstory densities and spatial arrangements?; (2) Does the removal of all redwood trees within a clump versus retention of one or more trees within a clump affect growth of new stump sprouts sharing the existing root system?; (3) How do the relationships between sprout growth and leaf area index (LAI), and understory light change over the first six years of sprout growth? Residual stand damage was also assessed to (1) determine if any correlation exists between incidents of damage and tree growth rates, and (2) examine whether treatment and a tree's physical characteristics makes it more likely to sustain damage. Additionally residual trees were assessed for possible relationships between post-harvest diameter growth and tree size, vigor, crown position, harvest damage, or density and spatial pattern of the residual stand.

MATERIALS AND METHODS

Site Description

The study was conducted in a replicated experiment located on Jackson Demonstration State Forest (JDSF) between the cities of Fort Bragg and Willits in Mendocino County, California, USA (39.3756, -123.6590). This forest land is owned by the state and managed by the state agency Cal Fire. The area has a typical climate for the coast redwood range with cool wet winters and warm dry summers. The four experimental replicates are located between about 16 to 24 kilometers from the Pacific Ocean and experience frequent fog. The stands have a history of logging and are now second-growth stands that have been re-entered either once or twice (Berrill et al. 2018b). Redwood dominates most of the area but tanoak and Douglas-fir are common. There is also a minor component of grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), Pacific madrone (*Arbutus menziesii*), and red alder (*Alnus rubra*).

Experimental Design

In 2012, four treatments were replicated at four sites to create a randomized complete block design. The treatments were group selection (GS), high-density dispersed retention (HD), high-density aggregated retention (HA), and low-density dispersed retention (LD). Appendix A illustrates the desired structure of stands after treatment. LD treated units were harvested to a target of 13% relative density and HA and HD treatments both had targets of 21% relative density. These densities were expected to reach 30% and 50% relative density at the time of the next partial harvest (Berrill and O’Hara 2009). These “low” and “high” densities were chosen as reasonable prescriptions to represent the range of density management zones suitable for multiaged stands with understory cohorts expected to maintain vigor throughout the entire cutting cycle. Growth and yield model simulations indicated that the low-density prescription would favor growth in the new cohort over stand volume production, as opposed to the high-density prescription favoring stand production while allowing for some reduced level of understory growth (Berrill and O’Hara 2009). The targeted species composition in each unit was 70-75% redwood, 20-25% Douglas-fir, and 0-5% tanoak. Each treatment was applied to 2 hectare (ha) units. At the center of each treatment unit, one 0.2 ha plot was established. All residual trees in a plot were tagged and marked with a white stripe at breast height (1.37 meters). A tag and pin flag were placed at the base of roughly 25 sprouts each of tanoak and redwood. The white marks and pin flags were used to facilitate precise re-measurements of residual tree diameter and sprout height, respectively. The experimental units were nested with plots, specifically: individual trees, and entire clumps of stump sprouts sharing a root system.

Data Collection

Residual tree measurements included DBH, height, and live crown base height. These measurements were first taken in the spring of 2014 and subsequent measurements were taken in winter 2017/2018, resulting in post-harvest 4-year periodic average DBH increment. The basal area of each tree was calculated from both sets of measurements and the difference between the two was used to calculate the periodic annual basal area increment (BAI). Incidences of damage to the tree crown or scarring of the tree bole attributed to the harvesting operation were noted. Residual basal area (BA; m^2 ha^{-1}) and stand density index (SDI; Reineke 1933) of each plot were calculated from 2014 tree data. The summation method was used to calculate SDI (Shaw 2000). Treatment intensity in terms of percent and absolute BA reduction was calculated by subtracting the 2014 post-harvest BA from pre-harvest inventory data for each plot in each replicate.

Annual height measurements of the dominant redwood or tanoak sprout in each clump were conducted at three of the four replicates each year since the winter of 2013/2014. The fourth replicate was first measured in 2012/2013 because it was harvested a year earlier than the others. The tallest sprout in each clump was measured for total height above ground level at the pin flag. Although different sprouts within the clump could be taller in different years, due to damage or differences in growth, the height measurement consistently represented the height of the experimental unit, the sprout clump. Sprouts were measured in the first winter after harvest and subsequently each year until the sixth measurement. The first measurement was subtracted from the second measurement to calculate the year 2 height increment. Year 3 and year 6 height increments were calculated using the same method with subsequent measurements. Measurements of the fourth replicate were not taken in the fourth year after harvest. For this reason, year 4 and year 5 height increments were replaced by a periodic annual height increment for years 4 and 5 combined, calculated from growth between year 3 and year 5 sprout height measurements.

Hemispherical photos were taken directly above a subset of redwood and tanoak sprouts in summer 2014; data from these photos was first presented in Berrill et al. (2018b). The photos were used to calculate two canopy variables (4-ring leaf area index (LAI) and percent canopy openness (1- % canopy cover)) and two understory light variables (total (direct + diffuse) light transmitted to the understory over the 2014 growing season (March 15th to September 15th) in mols m^{-2} day^{-1}, and percent above canopy light (PACL)).

Data Analysis

Examining a tree's probability of experiencing damage to the crown or scarring of the bole from logging operations involved generalized linear mixed-effect modeling. A binomial log-likelihood (logLik) distribution and the following equation were utilized to model probability:

$$\hat{p}(damage) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 + \beta_2 x_{2+\cdots+\beta_n x_n})}}$$

Where *damage* refers to either crown damage or bole scarring, and $\beta_{0\cdots}\beta_n$ are coefficients returned from the logLik model. X-variables tested for correlation to the logLik of damage included DBH, height, crown ratio, treatment, species, and a categorical variable indicating whether the unit was harvested using cable or tractor systems.

Residual tree growth was modeled using the periodic annual basal area increment as the response variable for each species: redwood, Douglas-fir, and tanoak. Either DBH or height, and crown ratio (CR) were tested as explanatory variables representing tree size and vigor. Presence of damage to the crown, scarring of boles, and whether or not a tree was suppressed (defined as a tree growing directly under the canopy of another tree) were tested as categorical variables for explaining variations in post-harvest residual tree growth. Treatment (categorical variable), plot BA, plot SDI, and treatment intensity were also tested as predictors of sprout height increment. Treatment intensity was the proportion of BA remaining after harvest relative to the pre-harvest BA (calculated from variable radius point sampling using a systematic grid and separated by treatment block).

Redwood and tanoak sprout height increments were analyzed using generalized linear mixed effect models. Models were fit to three alternate measurements representing residual overstory structure and/or density: a categorical variable representing treatment type (GS, LD, HD, HA), residual BA, and residual SDI. In models where either BA or SDI were used to represent stand density, the influence of aggregated retention was investigated by also incorporating a binary variable (i.e., HA yes/no). Sprout growth was analyzed in terms of annual increments (repeated measures) and also for total height at age 5 (required input parameter for a regional growth and yield model). There were negative height increments for some years due to damage or loss of the dominant sprout in a clump. Therefore, before transforming the height increment data to improve normality (reduce skewness), a scalar was applied to make all height increment data positive. The repeated measurements of height increment were analyzed simultaneously by incorporating ‘year’ (i.e., 2, 3, 4/5, 6) as a categorical variable and sprout number as a random effect to account for the temporal autocorrelation of sprout growth. In these models a categorical variable was tested representing whether or not the existence of a residual redwood tree sharing the root system with a clump of new sprouts influenced growth of these sprouts (e.g., resource sharing).

Linear mixed-effects regression was also used to test for relationships between sprout growth and four measures of canopy or understory light for a subset of tanoak and redwood sprouts which had hemispherical photos taken directly above them in 2014. The models also incorporated the repeated measurements of height increment where ‘year’ was tested as a categorical variable.

In mixed-effects regressions, ‘replicate’ was tested as a random effect to account for variation among replicates. An additional random effect for ‘plot’ was tested in models where plot-level variables (treatment, BA, and SDI) were not found to be significant fixed effects. Generalized linear mixed-effect models were fit using the ‘lme4’ package in R statistical software. Post-hoc comparisons of means and slopes were conducted using the Tukey method in the ‘emmeans’ package. Likelihood ratio tests were used to determine significance of random and fixed effects. An alpha value of 0.05 was used as the standard for significance in pairwise comparisons and likelihood ratio tests. In models where no random effects were found to be significant, variables were included when they lowered the model AIC by at least 2 points. Analyses of residuals were conducted to determine if transformations of the independent and dependent variables were necessary to create a normal distribution. Models were compared using Akaike information criterion (AIC) weights (probability of a model being the ‘best’; Akaike 1973; Burnham and Anderson 2002; Symonds and Moussalli 2010).

RESULTS

Residual Stand Damage and Tree Growth

The majority of the residual stand under all treatments was composed of redwood (Table 1). Douglas-fir and tanoak together represented a minor component of each plot with some plots containing one without the other. Relative to the 2500 SDI upper limit for redwood (Reineke 1933), post-harvest densities for LD, HD, and HA plots averaged 13%, 21% and 22% relative density, respectively. The dominant height and diameter (i.e., average height and DBH of the largest 100 trees ha^{-1}) at each site ranged from 33-41 m, and 56-65 cm DBH, respectively (Appendix B).

Across all treatments, 9% of residual trees sustained bole scarring and 11.7% sustained crown damage. Probability of bole scarring varied among treatments and was positively correlated to stand density (Figure 1; Table 2). The LD treatment was estimated to have a significantly lower probability of bole scarring when compared to either of the high density treatments. Mean probability of bole scarring was 12% in the HA treatment, 11% in the HD treatment, and 2% in the LD treatment, and did not differ among species. Incidences of crown damage were more common in plots where cable harvesting was utilized and among smaller trees (Figure 1).

Table 1. Ranges of residual stand density and composition by treatment: low-density dispersed (LD), high-density dispersed (HD) and high-density aggregated (HA).

	Treatment		
	LD	HD	HA
Density (trees ha^{-1})	70-185	125-210	160-240
BA (m2 ha-1)	19-24	36-42	36-45
SDI (metric)	298-354	509-564	524-590
Redwood BA (%)	74-96	66-94	62-96
Douglas-fir BA (%)	0-25	3-31	0-38
Tanoak BA (%)	0-18	1-5	0-12

Table 2. Coefficients and fit statistics for models predicting the probability of a tree sustaining bole scarring according to treatment, BA, or SDI, or crown damage according to DBH and harvest system (HS): ground-based or cable yarding (n=382 trees).

	Bole Scarring			Crown Damage
	Treatment	BA	SDI	DBH + HS
Intercept	-1.969	-6.091	-6.675	-0.925
Treatment HD	-0.092	-	-	-
Treatment LD	-2.029	-	-	-
BA or SDI	-	0.105	0.009	-
DBH	-	-	-	-0.021
Ground-based	-	-	-	-1.105
AIC	222.76	219.68	221.00	264.33
AIC weight	0.12	0.58	0.30	-

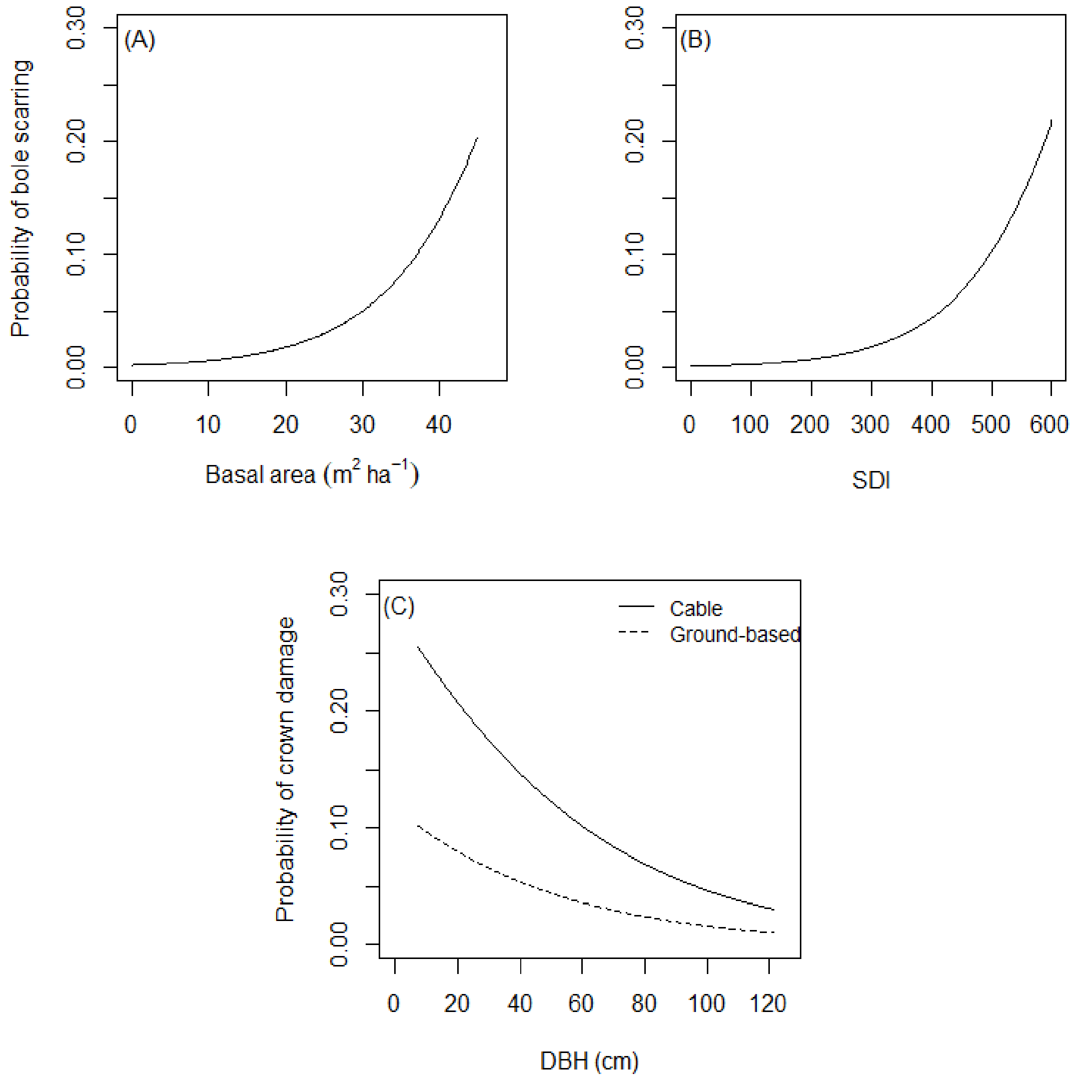

Figure 1. The relationships between probability of bole scarring and stand density (A, B), and between probability of crown damage and DBH by harvest system (C).

There was no correlation between BAI and stand density, treatment, or treatment intensity. The following equation was used to model redwood annual BAI:

$$BAI = (-2.424 + 0.612\sqrt[3]{DBH_i} + 2.572\sqrt[3]{CR_i} - 0.254\,x_1 - 0.208\,x_2)^4 - 1$$

where x_1 is 1 for trees with damaged crowns and 0 for undamaged trees, and x_2 is 1 for suppressed trees and 0 for trees that are not suppressed. Bole scarring did not result in a discernable decrease in post-harvest tree growth. Conversely, redwood trees sustaining crown damage exhibited significantly lower BAI (25.6 cm^2 year^{-1}) than undamaged trees of the same DBH (39.3 cm^2 year^{-1}). Redwood trees retained in suppressed crown positions had significantly lower post-harvest BAI (Table 4). Douglas-fir trees were largest on average, and exhibited the highest average BAI (Table 3). After accounting for the effect of tree size on post-harvest tree growth, the analysis revealed that the smallest trees of all species grew slowly, but otherwise redwood trees had greater BAI than tanoak and Douglas-fir of the same DBH (Figure 2).

Table 3. Mean tree diameter at breast height (DBH) , height (HT), crown ratio (CR), and post-treatment periodic annual BAI in with standard errors for the four year period between 2014 and 2018 for redwood (n=335), Douglas-fir (n=26), and tanoak (n=21).

	DBH (cm)		HT (m)		CR		BAI (cm^2 year^{-1})	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Redwood	41.94	1.24	27.80	0.74	0.49	0.01	49.80	2.72
Douglas-fir	67.33	2.55	45.19	1.57	0.43	0.12	57.74	7.58
Tanoak	29.27	2.75	18.77	1.55	0.60	0.06	27.47	5.99

Table 4. Tree basal area increment (BAI, cm^2 year^{-1}) model coefficients and fit statistics for redwood (BAI+1)$^{0.25}$, and Douglas-fir or tanoak (BAI+1)$^{0.33}$). DBH coefficients for redwood are fit to (DBH + 1)$^{0.33}$ transformations.

	Redwood		Douglas-fir		Tanoak	
	coef.	S.E.	coef.	S.E.	coef.	S.E.
Intercept	-2.425	0.601	2.571	0.309	2.504	0.307
DBH	0.612	0.038	0.017	0.008	0.017	0.008
CR$^{0.33}$	2.572	0.488	-	-	-	-
Crown damage	-0.254	0.064	-1.245	0.512	-1.245	0.511
Suppressed	-0.208	0.057	-	-	-	-
AIC		314.38	-		-	
Marginal R^2		0.54	-		-	
Conditional R^2		0.64	-		-	
Adjusted R^2	-			0.39		0.39

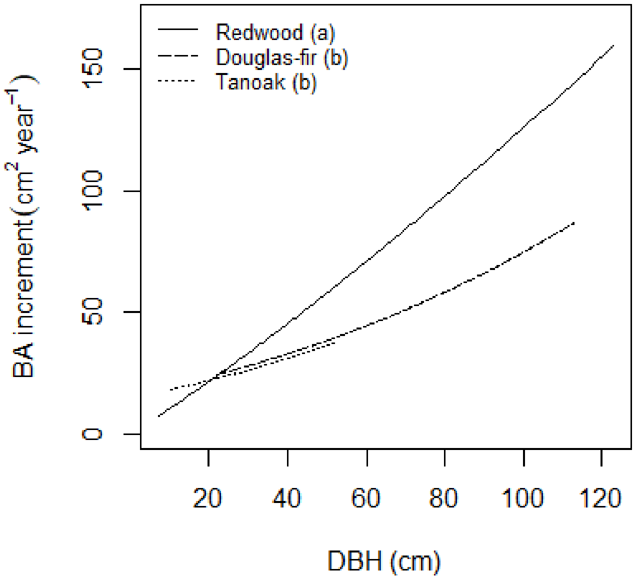

Figure 2. Predicted redwood (n=335, marginal R^2=0.54, conditional R^2=0.64), Douglas-fir (n=26, R^2=0.43), and tanoak (n=21, R^2=0.43) BAI as a function of DBH. Common letters in parentheses indicate least-squares mean BAI that were not significantly different.

Development of Stump Sprouts

After six years of growth, heights of dominant redwood sprouts ranged from 0.61 m up to 11.00 m and tanoak sprouts ranged from 0.46 m to 6.92 m. Annual height increments ranged from a low of -45 cm to as high as 246 cm for redwood and from -35 cm to 121 cm for tanoak (Table 5). Redwood sprout growth varied more among the treatments than according to residual SDI or BA. Conversely, SDI was a better predictor of tanoak sprout growth than residual stand BA or treatment type (Table 6). Sprout height increments were consistently superior in group selection openings (Figure 3). Redwood sprout growth appeared to decline in dispersed retention treatments with advancing age, and exhibited significant inter-annual variability (Figure 4).

Table 5. Range of height increments (cm year^{-1}) for dominant redwood (n=382) and tanoak (n=392) sprouts by year and treatment.

		Year 2		Year 3		Year 4/5		Year 6	
Species	Treatment	Min	Max	Min	Max	Min	Max	Min	Max
Redwood	GS	-18	230	12	233	22.5	195	11	246
	HA	-45	175	-13	153	3	167	0	227
	HD	1	200	-36	139	-28	198	-35	172
	LD	2	191	-2	184	-7	181	0	200
Tanoak	GS	-5	101	1	121	-27	104	-35	93
	HA	-1	113	-16	74	2	87	-8	110
	HD	-3	103	-23	75	-27	79	-10	121
	LD	-14	120	-6	99	2.5	106	0	99

Redwood stump sprouts were more sensitive to stand density than tanoak sprouts (Figure 5). The relationship between tanoak sprout height increment and overstory density changed over time (interaction between year and overstory density). Tanoak sprout height increment was relatively insensitive to stand density in year 2 and exhibited highest sensitivity in year 3. Both redwood and tanoak exhibited significantly lower average sprout height increment in year 3 and year 6 (Figure 5). These differences appeared to be age-related as opposed to climate-year-related because, for example, year 3 data represent the 2015 growing season at three sites and 2014 season at the fourth site.

Table 6. Coefficients (with standard errors in parantheses) and fit statistics for models of dominant redwood (n=382) and tanoak (n=392) sprout height increment (HTI) response variables: $(HTI + 46)^{0.5}$ for redwood or $(HTI + 36)^{0.5}$ for tanoak.

	SESE			Tanoak		
Model	Treatment	BA	SDI	Treatment	BA	SDI
Intercept	11.982 (0.280)	12.095 (0.279)	12.1575 (0.2530)	8.880 (0.154)	8.811 (0.119)	8.8406 (0.1464)
treatment HA	-1.815 (0.266)	-	-	-0.452 (0.180)	-	-
treatment HD	-1.520 (0.270)	-	-	-0.415 (0.182)	-	-
treatment LD	-0.387 (0.273)	-	-	-0.431 (0.184)	-	-
overstory BA	-	-0.042 (0.004)	-	-	-0.010 (0.004)	-
overstory SDI	-	-	-0.0031 (0.0003)	-	-	-0.0008 (0.0003)
Year 3	-0.221 (0.201)	-0.552 (0.103)	-0.5523 (0.1025)	0.584 (0.155)	0.555 (0.144)	0.5537 (0.1464)
Year 4/5	0.080 (0.201)	-0.106 (0.103)	-0.1061 (0.1025)	0.306 (0.155)	0.387 (0.144)	0.3704 (0.1460)
Year 6	-0.345 (0.201)	-0.432 (0.103)	-0.4322 (0.1027)	-0.281 (0.157)	-0.155 (0.145)	-0.1937 (0.1472)
HA:Year 3	-0.008 (0.283)	-	-	-1.029 (0.218)	-	-
HD:Year 3	-0.638 (0.287)	-	-	-1.435 (0.220)	-	-
LD:Year 3	-0.731 (0.290)	-	-	-0.826 (0.223)	-	-
HA:Year 4/5	0.350 (0.282)	-	-	-0.429 (0.218)	-	-
HD:Year 4/5	-0.324 (0.287)	-	-	-0.726 (0.220)	-	-
LD:Year 4/5	-0.844 (0.291)	-	-	-0.126 (0.222)	-	-
HA:Year 6	0.490 (0.283)	-	-	-0.115 (0.220)	-	-
HD:Year 6	-0.215 (0.286)	-	-	-0.298 (0.221)	-	-
LD:Year 6	-0.688 (0.292)	-	-	0.162 (0.224)	-	-
BA or SDI:Year 3	-	-	-	-	-0.031 (0.005)	-0.0022 (0.0004)
BA or SDI:Year 4/5	-	-	-	-	-0.016 (0.005)	-0.0011 (0.0004)
BA or SDI:Year 6	-	-	-	-	-0.008 (0.005)	-0.0004 (0.0004)
Marginal R^2	0.14	0.12	0.13	0.12	0.11	0.11
Conditional R^2	0.54	0.54	0.53	0.37	0.36	0.36
AIC	5923.71	5937.62	5929.98	5049.46	5046.26	5040.50
AIC weight	0.96	0.00	0.04	0.01	0.05	0.94

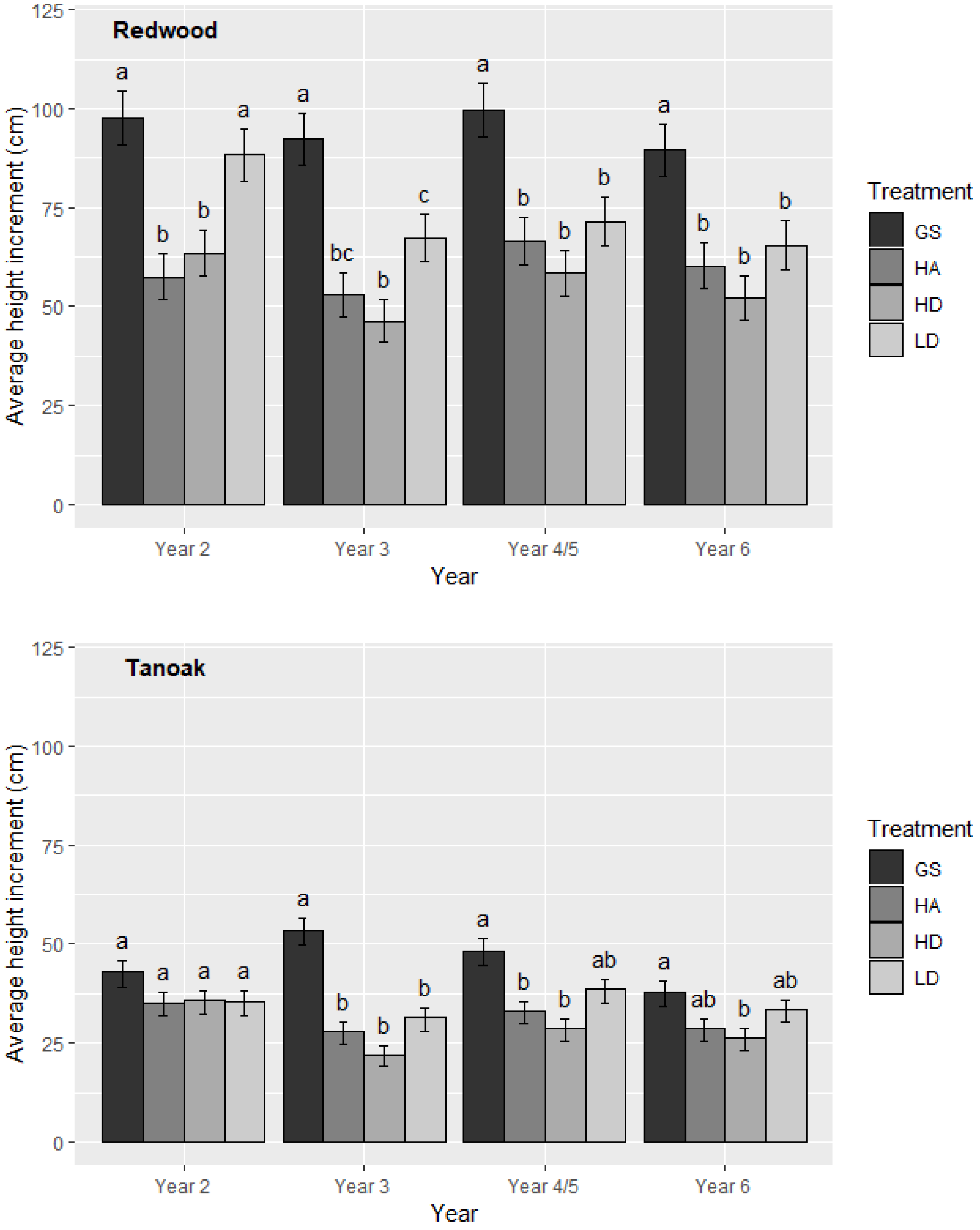

Figure 3. Dominant redwood and tanoak sprout growth by treatment – least-square-mean height increment with standard error bars for each treatment by year. Common letters denote increments that are not significantly different among treatments within each time period.

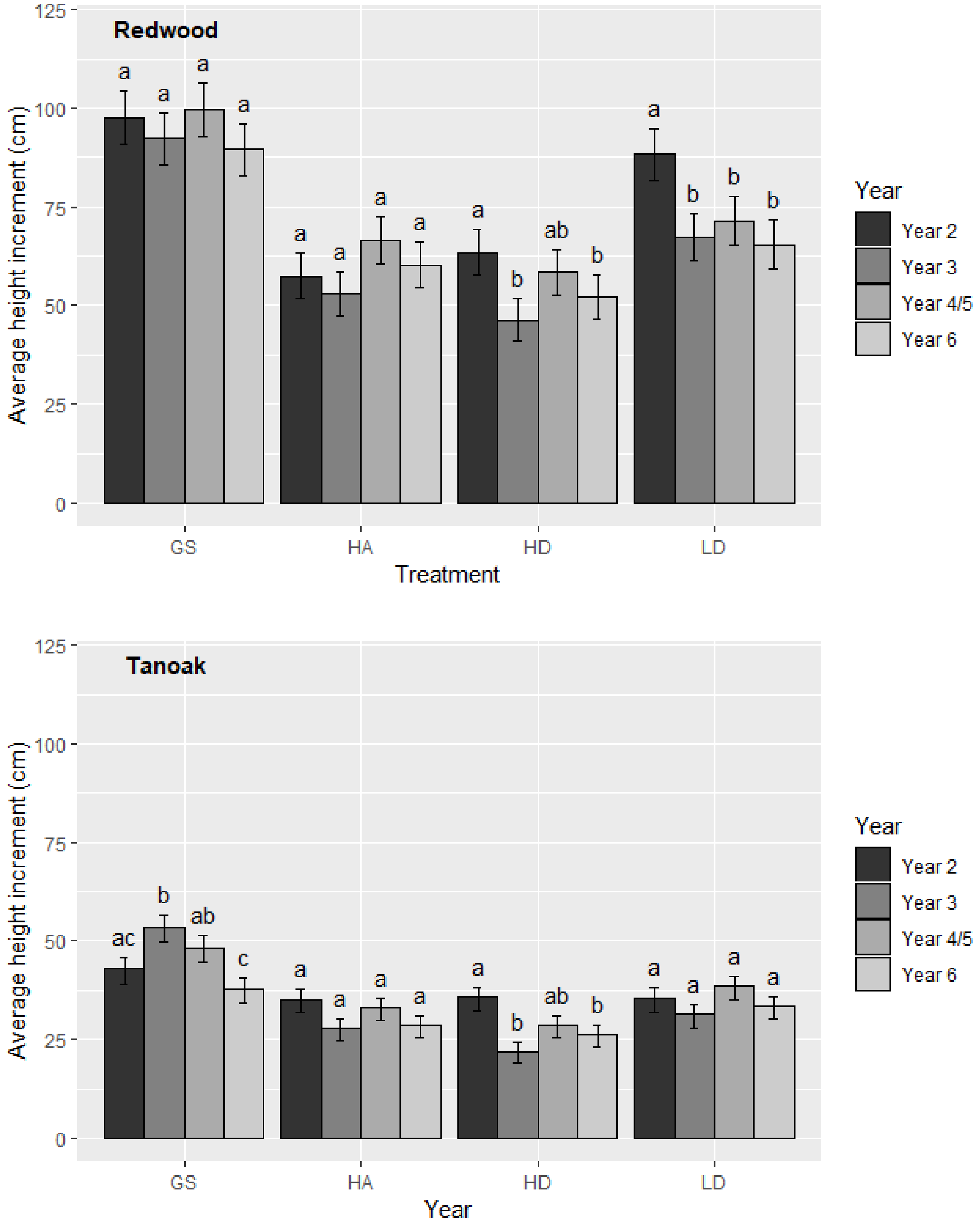

Figure 4. Dominant redwood and tanoak sprout growth over time – least-square-mean height increment with standard error bars for each year by treatment. Common letters above error bars denote increments that are not significantly different among years within each treatment type.

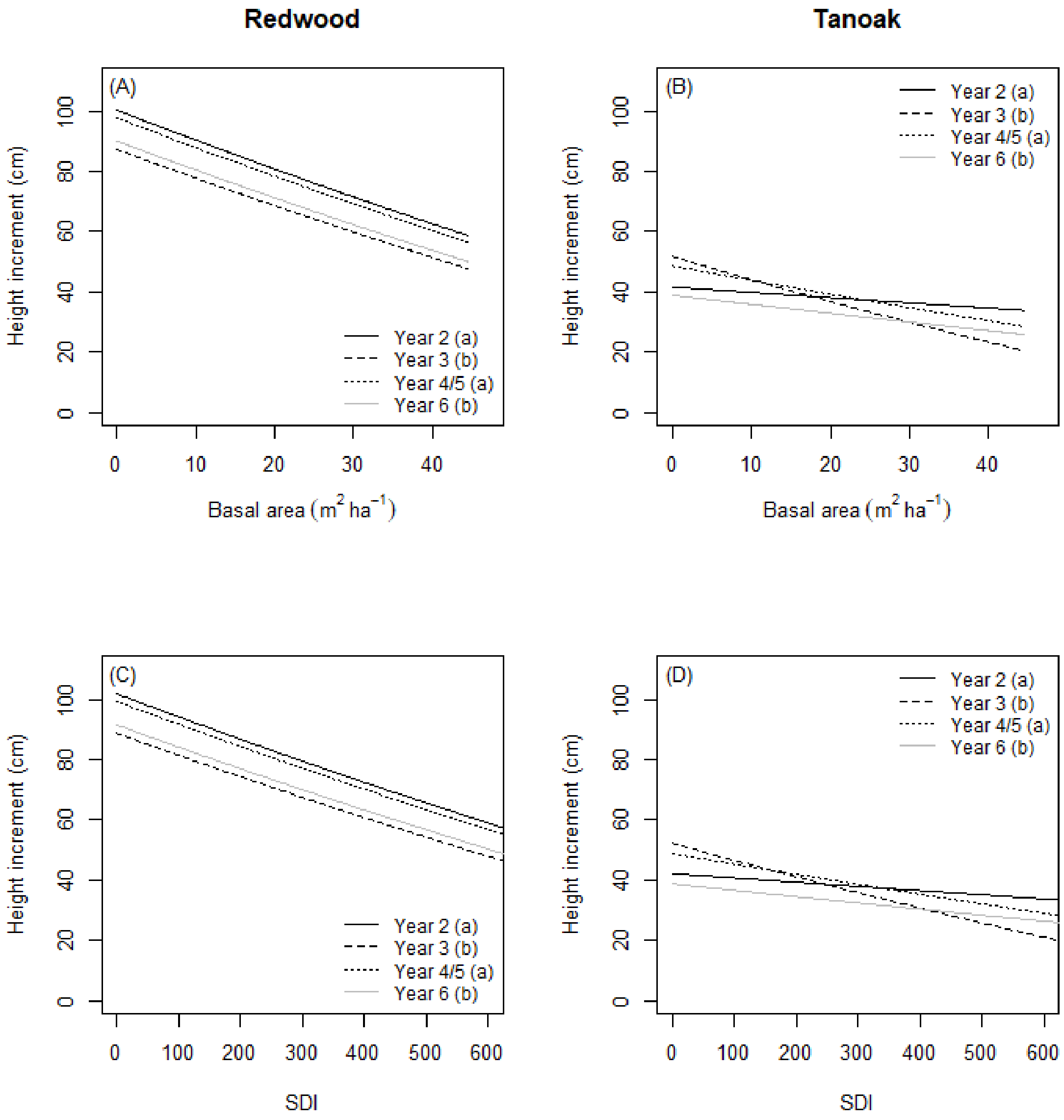

Figure 5. Stand density and sprout growth – relationships between height increment of dominant redwood and tanoak sprouts and residual stand BA (A, B) or metric stand density index (SDI; C, D). Tukey letters in legends indicate significant differences among time periods.

Models fit to the age-5 height of sprouts revealed a significant negative correlation to both BA and SDI (Figure 6). Redwood sprouts were significantly taller than tanoak across the range of stand density. Age 5 sprout heights ranged from 0.54 to

9.81 m for redwood and from 0.55 to 5.48 m for tanoak. SDI was the best predictor of age-5 sprout height for both redwood (AIC weight = 0.83) and tanoak (AIC weight = 0.57). The following equations were found to result in the most normal distribution of residuals:

$$\hat{y}_{RW} = \beta_0 + \beta_1 x^2 + \beta_2 x$$

$$\hat{y}_{TO} = (\beta_0 + \beta_1 x^2 + \beta_2 x)^2$$

where $\hat{y}_{RW}$ and $\hat{y}_{TO}$ refer to the sprout height at 5 years for redwood and tanoak respectively and x is overstory BA or SDI (Table 8). The categorical variable for presence/absence of a residual tree on the fairy ring was not significantly correlated to sprout growth in any model.

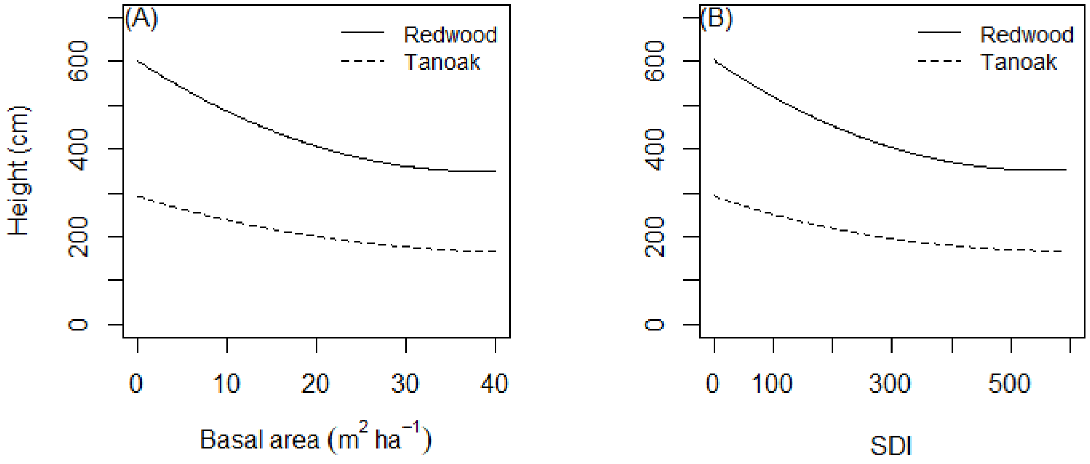

Figure 6. Inverse exponential relationship between age-5 sprout height and BA (A) or SDI (B).

Table 7. Coefficients (with standard errors in parentheses) for models predicting height of dominant sprouts after five years of growth by basal area or scaled variable: SDI/100.

	Redwood		Tanoak	
Model	BA	SDI	BA	SDI
Intercept	600.936 (29.880)	603.177 (28.622)	17.122 (0.3140)	17.138 (0.319)
BA^2 or SDI^2	0.173 (0.037)	8.382 (2.453)	0.002 (0.0005)	0.116 (0.036)
BA or SDI	-13.178 (1.651)	-91.76 (13.934)	-0.200 (0.0237)	-1.394 (0.203)
Marginal R^2	0.33	0.34	0.40	0.41
Conditional R^2	0.41	0.41	0.44	0.44
AIC	4292.33	4288.45	1476.60	1475.10
AIC weight	0.12	0.88	0.32	0.68

Sprouts and Understory Light

Among variables collected from hemispherical photos, LAI was the best predictor of redwood sprout height increment (Table 8). Tanoak sprout growth was best predicted by understory light. For both species, PACL was the second best predictor of sprout growth. Percent canopy openness and diffuse light were also significantly correlated to the height increment of both species.

Overall trends of sprout height increment showed a negative correlation to LAI and positive correlations to total understory light and PACL for both species (Figure 7). Redwood sprout growth was more sensitive (i.e., steeper regression slope) to LAI and understory light in year 6 than in year 2. Tanoak sprout growth did not show a significant change in sensitivity to light after year 2 when height increment was insensitive to light or LAI (Figure 7).

Table 8. Canopy or understory light (β_1) models of sprout growth – coefficients and fit statistics for five candidate models explaining height increments ((HTI+11)$^{0.5}$ for redwood and (HTI+8)$^{0.5}$ for tanoak) with data collected from hemispherical photos taken above dominant redwood (n=143) and tanoak (n=138) sprouts: percent above canopy light (PACL), light transmitted to the understory (mols m^{-2} day^{-1}) 2014 over the growing season, 4-ring leaf area index (LAI), percent canopy openness, and diffuse light (mols m^{-2} day^{-1}). (Continued on Next Page)

	ln(PACL)				*ln*(Total Light (mols m^{-2} day^{-1}))				LAI			
	Redwood		Tanoak		Redwood		Tanoak		Redwood		Tanoak	
Parameter	coef	S.E.	coef	S.E.	coef	S.E.	coef	S.E.	coef	S.E.	coef	S.E.
Intercept	4.088	3.472	5.720	3.135	5.982	2.575	5.433	2.257	9.443	0.526	6.359	0.404
Year 3	-4.762	2.613	-9.149	3.461	-3.866	1.923	-6.829	2.472	-0.186	0.378	0.497	0.378
Year 4/5	-3.462	2.605	-7.583	3.491	-3.104	1.906	-5.045	2.482	0.234	0.376	0.813	0.376
Year 6	-8.476	2.609	-8.983	3.481	-6.194	1.908	-5.989	2.485	0.393	0.378	0.699	0.378
β_1	1.123	0.845	0.160	0.752	0.898	0.847	0.308	0.729	-1.071	0.631	0.045	0.631
Year 3: β_1	1.026	0.639	2.037	0.833	1.095	0.638	1.998	0.804	-0.538	0.475	-1.846	0.475
Year 4/5: β_1	0.823	0.637	1.827	0.840	0.999	0.633	1.644	0.807	-0.467	0.472	-1.262	0.472
Year 6: β_1	1.918	0.639	2.104	0.838	1.846	0.634	1.869	0.808	-1.437	0.473	-1.476	0.473
marginal R^2		0.07		0.08		0.07		0.08		0.08		0.07
conditional R^2		0.68		0.37		0.68		0.37		0.68		0.37
AIC		2199.69		1973.02		2201.41		1972.83		2197.93		1974.21
AIC weight		0.20		0.36		0.08		0.40		0.48		0.20

Table 8. (Continued)

	ln(canopy openness)(%)				*ln*(diffuse light (mols m^{-2} day^{-1}))			
	Redwood		Tanoak		Redwood		Tanoak	
parameter	coef	S.E.	coef	S.E.	coef	S.E.	coef	S.E.
Intercept	4.385	4.067	8.743	3.499	6.497	2.005	7.135	1.863
Year 3	-3.205	3.051	-11.749	3.753	-2.221	1.530	-6.324	2.024
Year 4/5	-3.939	3.020	-8.950	3.756	-2.085	1.502	-4.128	2.026
Year 6	-10.023	3.031	-8.758	3.729	-5.208	1.507	-4.132	2.016
β_1	1.109	1.044	-0.597	0.887	0.981	0.886	-0.323	0.804
Year 3: β_1	0.679	0.787	2.817	0.956	7.741	0.684	2.456	0.881
Year 4/5: β_1	0.991	0.779	2.281	0.957	0.892	0.673	1.800	0.882
Year 6: β_1	2.423	0.783	2.167	0.949	2.054	0.676	1.692	0.877
marginal R^2		0.06		0.06		0.06		0.05
conditional R^2		0.68		0.37		0.68		0.36
AIC		2200.77		1979.58		2200.84		1977.94
AIC weight		0.12		0.01		0.11		0.03

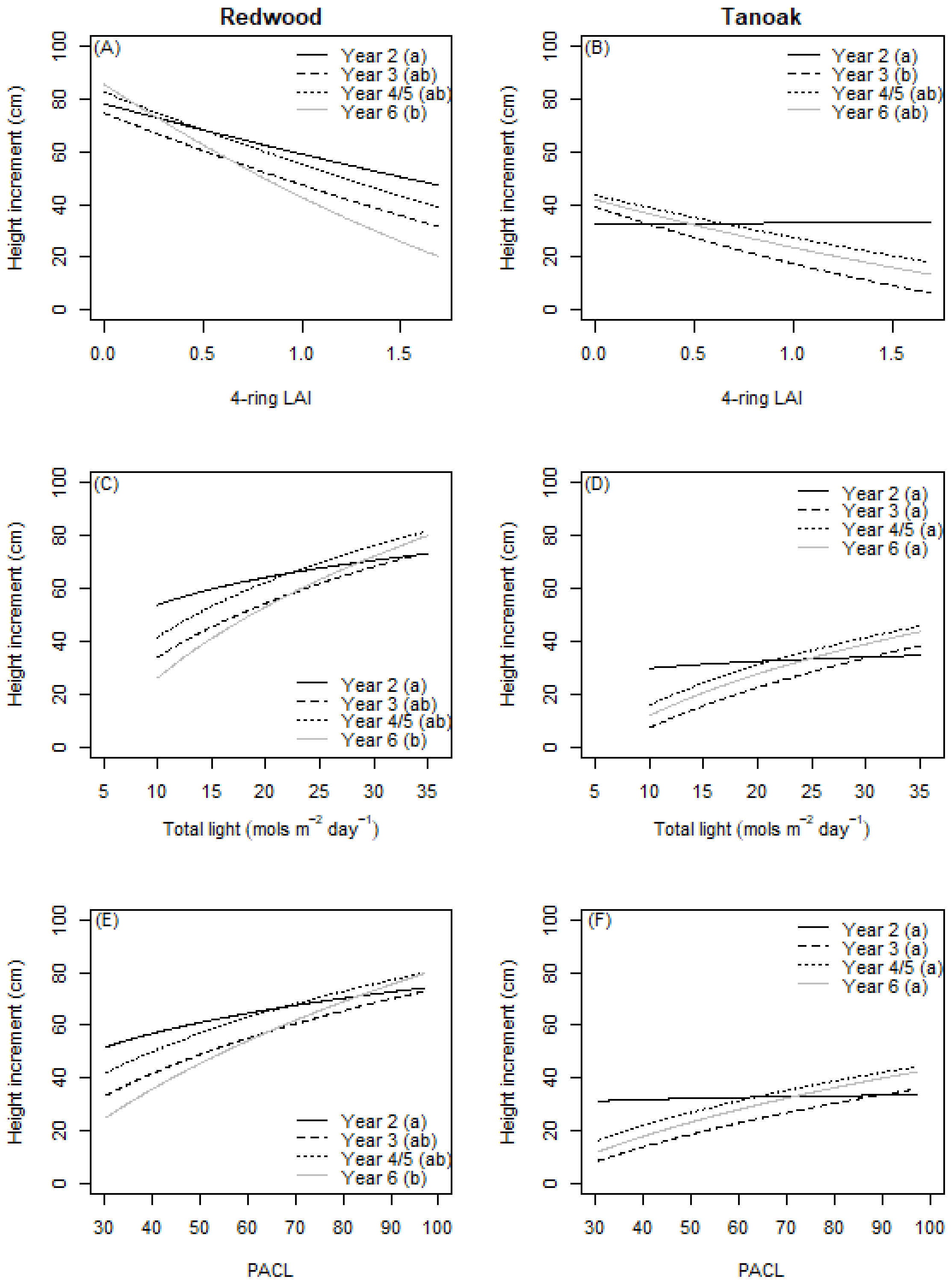

Figure 7. Sprout growth and canopy or understory light – redwood (A,C,E) and tanoak (B, D, F) sprout height increment relationships to 4-ring LAI (A,B), total transmitted light (C,D), and PACL (E,F) obtained from hemispherical photos. Common letters in legends indicate slope coefficients that are not significantly different.

DISCUSSION

Residual Stand Damage and Tree Growth

Analyses of residual trees indicated that larger trees were less likely to sustain crown damage. Our finding that smaller trees were more vulnerable to crown damage is similar to previous findings in other ecosystems (Jonkers 1987; Hartsough 2003). Jonkers (1987) suggested that larger trees are purposely avoided when cutting a neighboring tree while small trees are often ignored. Small stature and stem slenderness may also factor into this increased susceptibility especially higher up on the stem on slender trees grown at high densities (Berrill et al. 2012). Trees in the three replicates where cable yarding harvest systems were utilized were more likely to be damaged than those in the fourth replicate that was harvested using a ground-based system; this relationship has also been observed after commercial thinning in Douglas-fir stands (Han and Kellogg 2000). This suggests that smaller trees are susceptible to crown damage from the felling of neighboring trees and from yarding activities.

The direct relationship between probability of bole scarring and residual stand density identified in this study is contrary to previous findings in Douglas-fir forests of northwest Oregon and Southwest Washington where it was found that damage was more prevalent under higher treatment intensities (Moore et al. 2002). Alternately, Jonkers (1987) proposed a lack of correlation found between incidence of residual tree injury and BA removal in tropical hardwood forests of Suriname was due to the crowns of falling trees being more likely to fall into already existing gaps as more trees are harvested. The lower proportions of bole scarring in low residual density stands may be because it is easier to avoid injuring more widely-spaced trees during falling and yarding/skidding activities. After retention trees are damaged during harvest operations, it is common practice to cut them in lieu of cutting trees of similar size originally marked for harvest. This process, referred to as "swapping out" damaged trees for marked trees, is designed to leave the prescribed residual stand density while removing damaged trees. There is more opportunity to swap out damaged trees when more trees are cut; this could explain why fewer damaged trees were left after harvest in stands with lower residual density. It is important to note that our study does not report the total number of trees sustaining damage. Instead we reported the number of damaged trees remaining in the residual stand after harvest operations had concluded.

Our data on stand damage is limited for two reasons. The first reason is we are unable to account for variability in skill of the logging crews and distances from skid trails or cable yarding corridors. The four replicate sites were harvested by three different contractors and each contractor may have had different crews working on the experimental harvests. Differences in damage between cable and ground based harvesting systems could be confounded by operator skill. For example, an inexperienced skidder operator may cause more damage than a highly experienced cable yarding crew. Damage is also more likely to occur in closer proximity to skid trails and cable corridors; this relationship may have confounded the models presented in this study

(Howard 1996; Froese and Han 2006). The second reason is that there were three replicates treated using cable yarding systems but only one replicate that utilized a ground-based harvesting system. Additional replication would be needed to test whether ground-based harvesting systems lower the probability of crown damage.

Analysis of residual tree growth was limited by a lack of a no-cut control against which to compare response to treatment. However, it is already well known that redwood exhibits higher BAI after a variety of precommercial thinning treatments (O'Hara et al. 2010, 2015; Dagley et al. 2018) and commercial thinning or partial harvest treatments (Oliver et al. 1994; Webb et al. 2017). Response to partial harvesting is greater on better sites and along the edge of openings (Berrill and O'Hara 2014, 2016). Our finding that post-harvest BAI was greater among larger redwoods with higher crown ratio is consistent with findings that larger redwoods had higher volume growth efficiency (Berrill and O'Hara 2007b) and consistent with Berrill and O'Hara (2014) who reported that redwood of similar age and size sustained rapid DBH growth over a 20 year period after partial harvesting to a range of densities. In this forest type, conifers exhibiting rapid DBH growth after precommercial thinning are more likely to sustain bear damage (Perry et al. 2016). Additionally, after partial harvesting, conifers may respond with excessive branch development creating large knot sizes that negatively impact wood quality (Kirk and Berrill 2016). However, if rapid DBH growth is an objective of management, the analyses of residual stand damage and tree growth models presented in this study favor selecting larger trees for retention at low densities. This strategy would minimize the negative effects of harvest damage by retaining widely-spaced fast-growing trees.

Development of Stump Sprouts

The relationships identified in this study between sprout growth and overstory stand density indicated that sprouts compete with the residual overstory for growing space, including soon after major reductions in stand density. Similar results have been observed in mixed conifer regeneration after variable retention harvest (Maguire et al. 2006). Presence of a residual tree on the fairy ring did not have a discernable effect on redwood sprout growth. The management implication is clear: managers can cut some or all stems in a fairy ring without concern for growth rates of the new sprouts arising after treatment, provided that enough understory light is available for sprout clumps to survive and become “self-sustaining” (O’Hara et al. 2007). However, it is still unclear if there is resource sharing between stems and new sprouts sharing the same root system, or if any advantage of sharing is being negated by other factors such as the added competition for light among sprouts near a residual stem and crown.

Redwood sprouts were growing faster than tanoak sprouts across the range of residual stand densities in our experiment. This result only applies to similar situations where forest managers “level the playing field” by cutting all tanoaks at the time of harvest so that they resprout around the same time as redwood sprouts arising after commercial harvest. Under these conditions, redwood sprouts outperform tanoak sprouts. Our findings do not apply to the historical practice of harvesting conifer and leaving tanoak untreated which left tanoak in an advantageous position outsizing and shading redwood regeneration. Our findings also do not apply where tanoak has been eliminated or had densities reduced by herbicide treatment. Here, we would expect the same or slightly more rapid growth of conifer regeneration without competition from resprouting hardwoods (Berrill et al. 2018a).

Reduced sprout height increment in year 6 may be attributed to the depletion of carbohydrate reserves from the parent tree root system (Wiant and Powers 1966) and the expansion of overstory crowns into canopy openings (O’Hara et al. 2007). Reduced growth in year 3 was originally suspected to be due to variance in climatic factors among calendar years. However, when the data from the four replicates were grouped by calendar year of harvest and modeled separately the analysis produced similar results: slower sprout growth in the third growing season. Slower height growth in year 3 may be attributed to physiological factors not accounted for in this study, possibly related to the transition from use of stored carbohydrates to becoming a self-sustaining organism (O’Hara et al. 2007). The decline in redwood sprout growth from year 3 to year 6 was more apparent in dispersed retention treatments than in the HA or GS treatments. This suggests that that the larger gaps created for sprouts to grow in aggregated retention treatments may help to offset the increased shade from expanding residual crowns.

Age-5 sprout heights also exhibited a significant inverse relationship to residual stand density and revealed a similar disparity between species. Predicted redwood sprout height at the maximum overstory basal area observed (39 m^2 ha^{-1}) was 3.50 m which is substantially lower than averages of about 5.70 m observed by O’Hara et al. (2007) at similar densities on a fertile alluvial flat in Humboldt County. However, the age-5 modeled averages at our sites on JDSF in Mendocino County are much higher than heights of redwood seedlings 6 years after planting in clearcut redwood stands on JDSF (Jameson and Robards 2007). Models presented in this study predicting age-5 sprout heights have a practical application in the regional FORSEE growth and yield model. FORSEE requires an input representing the height of regeneration at this age to serve as a starting value for subsequent growth projections.

The results indicate that the density of a residual stand has a substantial effect on the newly established cohort. Analysis of aggregated vs. dispersed retention did not reflect any difference in sprout growth. It is possible that the structural differences among different spatial arrangements must be quantified (i.e. surface area of gaps between aggregates) for an effect to be seen. It is also possible that effects of spatial arrangement will be evident further along in the regeneration process. Future research is needed to study the effects of residual density and arrangement on further development of the new cohort and the recruitment of the stump sprouts into the canopy.

Sprouts and Understory Light

Relationships between sprout height increment and understory light identified by this study have been reported previously (O’Hara et al. 2007, O’Hara and Berrill 2010, Berrill et al. 2018b). In our study, the changes in sensitivity to canopy cover and understory light from year 2 to year 6 were different for tanoak and redwood. Tanoak sprout growth was reduced and most sensitive to LAI in year 3 which may indicate a depletion of carbohydrate reserves from the parent tree (Wiant and Powers 1966). Just as LAI impacted tanoak sprout growth in year 3, increased sensitivity of tanoak sprout growth to understory light in year 3 was also expected but not found. Hemispherical photos were taken only once in year 2 (year 3 for one replicate) so changes in understory light over time have not been accounted for. However, it is possible that the rapid growth of redwood sprouts has resulted in a changing light environment for the tanoak sprouts. They were being shaded by redwood sprouts and, therefore, unable to access all of the understory light detected soon after harvesting.

Redwood sprouts increased in sensitivity to understory light and canopy cover from year 2 to year 6. This is counter to our finding that the relationship between redwood sprout growth and stand density did not change with advancing age. We hypothesize that this may be because hemispherical images were taken above individual sprout clumps, capturing more detailed information on a spatially variable phenomenon such as understory light, as opposed to stand density where one value represents the density across the entire plot. Therefore while stand density has proven to be a useful predictor of sprout development, it appears that direct assessment of understory light allowed us to detect a change in the pattern of redwood sprout growth with advancing age: specifically that they become more dependent on available light as they age. This steady increase in sensitivity suggests a slower depletion of carbohydrate reserves provided by the parent tree. This slower depletion may be explained by the relationship between stump size and early redwood sprout growth reported by Berrill et al. (2018b). Mature redwood trees typically have much larger diameters than tanoak when the two species are found in association. Therefore, redwood stump sprouts may have access to a larger supply of carbohydrates that help sustain them longer than the supplies available to tanoak sprouts.

CONCLUSION

Converting to multiaged management from an even-aged stand requires consideration of both the residual overstory and the establishment of a new cohort. The relationships identified in this study for residual stand damage, tree growth, and regeneration should be used to inform silvicultural prescriptions and marking guidelines. The analyses of residual stand damage and tree growth indicate that large trees will be more productive and less susceptible to crown damage; and, when retained at lower densities, will be less likely to experience bole scarring while providing more growing space for regeneration. Redwood stump sprouts outcompeted tanoak sprouts through post-harvest year six. This suggests that cutting tanoak around the time of conifer harvest is a viable strategy to give redwood sprouts a competitive advantage. Lower levels of overstory retention promoted faster stump sprout growth, especially among redwood sprouts.

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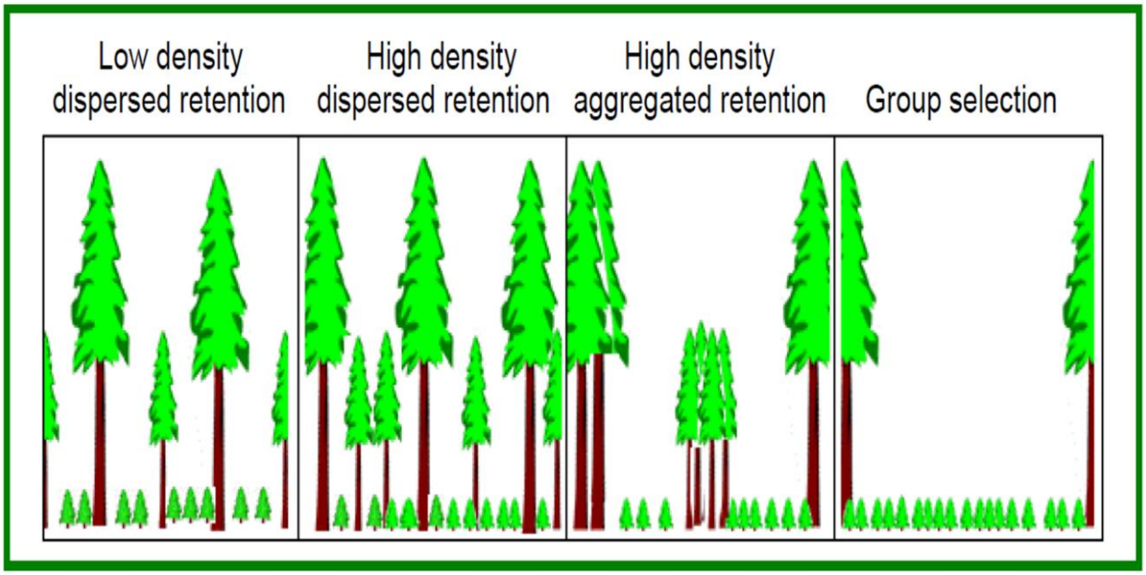
APPENDIX A

Appendix A. Schematic diagram of the desired stand structure following the four treatments prescribed at each replicate.



APPENDIX B

Appendix B. Average, minimum (Min.), maximum (Max.), and standard deviation (SD) of DBH and height (HT) for the 100 largest trees ha^{-1} in all plots at each replicate.

	DBH (cm)				HT (m)			
Site	Average	Min.	Max.	SD	Average	Min.	Max.	SD
Camp 6	55.8	35.3	90.7	14.9	32.4	20.4	52.2	7.5
Waldo North	56.9	16.8	121.9	27.4	33.5	10.6	57.5	13.3
Waldo South	60.4	28.1	123.2	21.0	38.1	7.9	56.7	12.3
Whiskey Springs	51.4	21.3	113.4	16.7	36.2	16.3	57.7	10.2