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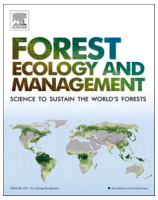

Dynamics of stump sprout regeneration after transformation to multiaged management in coast redwood forests

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ABSTRACT

There is considerable interest in multiaged management as a silvicultural and restoration tool in redwood forests of California. For multiaged silviculture to be successful, a new cohort of trees must first be able to regenerate underneath the residual overstory. We used annual re-measurement data from a replicated manipulative experiment in coastal northern California to determine how understory light, stand density, and spatial arrangement of residual trees affected coast redwood (*Sequoia sempervirens*) and tanoak (*Notholithocarpus densiflorus*) stump sprouts regenerating after partial harvest of conifers and felling-to-waste of tanoak. Four treatments (group selection, aggregated retention, low-density dispersed retention, and high-density dispersed retention) were applied at each replicate on redwood-dominated sites. Height growth of redwood sprouts was 49% greater than tanoak sprouts across all treatments. Redwood and tanoak sprouts were sensitive to overstory density. Redwood sprouts were marginally taller under high-density aggregated versus dispersed overstory trees at the same residual stand density (39.5 m^2/ha BA). Sprout growth correlated with understory light; redwood sprouts exhibited a significant increase in sensitivity to light availability from year 2 to year 6. No differences in redwood sprout growth were detected when retaining a residual tree on the same root system versus sprouts growing on a root system where all redwood stems were cut. Our finding that cutting unwanted hardwoods in tandem with partial harvesting of merchantable conifers can maintain a competitive advantage for redwood sprouts versus tanoaks is an important consideration for maintaining redwood dominance when transitioning to multiaged management.

1. Introduction

Forest management is increasingly focused on a broad suite of non-timber related ecosystem services that are vital components of ecological sustainability such as carbon sequestration, wildlife habitat, and water quality (Franklin et al. 2018). Concurrently, societal pressures often discourage even-aged forest management focused exclusively on wood production and extraction. An alternative is multiaged management, which aims to retain at least two cohorts of trees within a stand. This type of management is also called selection forestry or retention forestry (Lindenmayer et al. 2012; O'Hara 2014). Various forms of multiaged silviculture have long been practiced throughout central Europe and the United States but with mixed results (O'Hara 2002; Kenefic et al. 2021).

Altering the amount and spatial pattern of overstory retention has been an important avenue of study into multiaged forest management approaches (O'Hara, 1998; Mitchell and Beese 2002; Aubry et al. 2009). Multiaged management can fit within an ecological forestry framework when it emulates natural disturbance patterns (Long 2009; Franklin et al. 2018) and promotes biodiversity conservation (Beese et al. 2019). Managers can retain different overstory densities and spatial arrangements within stands to promote growth of residual trees, regeneration, and structural heterogeneity (O'Hara 2014; Berrill et al. 2018a). The residual stand can include evenly spaced trees (dispersed retention) and/or trees retained in groups (aggregated retention; Ashton and Kelty 2018). Aggregated retention leaves more space between groups of trees,

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thus allowing more sunlight to reach the ground (Berrill et al. 2018b) but aggregates can also have an edge effect that inhibits the growth of new cohorts (Whyte and Halpern 2019).

Multiaged management may be especially valuable in coastal redwood forests. Coast redwood (*Sequoia sempervirens*) occurred naturally across approximately 810,000 ha, along a narrow strip of land within 8–56 km of the Pacific coast of North America, from Monterey County, California to the Chetco River watershed in Oregon just north of the California border (Roy 1966). Only approximately five percent of California's pre-European settlement old-growth coast redwood forests remain (Sawyer et al. 2000), highlighting the need to not only conserve existing old-growth forests, but also restore and sustainably manage forests. Coast redwood is an important commercial species for wood products and rural economies throughout much of its range (Henderson et al. 2017). By implementing multiaged silvicultural systems that vary in levels and spatial arrangement of overstory retention as described above, it may be possible to maintain a forest structure and disturbance regime closer to the historic range of variability. Historically, coastal redwood forests had frequent low-severity fire regimes, that have been largely absent over the past century via the loss of indigenous cultural burning and broad fire exclusion policies (Brown and Swetnam 1994; Stephens and Fry 2005). The historical fire regime played a critical role in the competitive dynamics of these forests, promoting multiaged structures and redwood dominance on upland sites (Lorimer et al. 2009; Ramage et al. 2010). Assuming that such disturbances removing individual trees and/or creating gaps leading to multiaged conditions are more desirable than stand-replacing disturbances, multiaged management has the potential to serve as a surrogate for historic disturbances while maintaining some continuity of ecosystem components and services in redwood forests and simultaneously providing a sustainable supply of valuable timber.

In contrast to even-aged management where artificial regeneration, with regular spacing and management of competing vegetation, is relatively free to grow rapidly in the absence of shade, regeneration in multiaged systems is strongly influenced by the density and spatial arrangement of the residual stand (Maguire et al. 2006; O'Hara et al., 2007). Redwood is tolerant of shade and its primary mode of regeneration reflects the 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). The characteristics of shade tolerance and reliable vegetative reproduction suggest that redwood forests may be well suited to multiaged management. However, redwood trees exhibit lower growth efficiency in heavier shade and higher growth efficiency in dominant and emergent crown positions and within canopy gaps (Berrill and O'Hara 2007; Sillett et al. 2020). Therefore, lower residual stand densities may be preferable when the goal is to promote survival and recruitment of regenerating redwood stump sprouts into the upper canopy (O'Hara et al. 2017). Lower stand densities may also promote the development of tanoak (*Notholithocarpus densiflorus*), a common associate of redwood that is also tolerant of shade, sprouts prolifically after disturbance, and competes with redwood in the understory of multiaged stands (Tappeiner et al. 1990; Berrill et al. 2020).

The growth of redwood and tanoak stump sprouts correlates with understory light, and redwood sprout growth is also positively associated with size of the parent tree stump (Berrill et al. 2018b). These relationships suggest that stump sprout growth is a function of both current and past conditions, specifically: available light reaching the understory and carbohydrate reserves remaining in the root systems of the harvested trees (Wiant and Powers 1966; O'Hara et al. 2017). As carbohydrate reserves from the parent tree stump and root system are depleted, growth of sprouts may become increasingly dependent on understory light which can be spatially heterogeneous in stands dominated by clumps of re-sprouting conifers and hardwoods (Berrill et al. 2018b). Increasingly complex aggregations of redwood stems arise following repeat harvesting and sprouting events that create sprout clumps developing in/around so-called 'fairy rings' of second-growth stumps encircling large old-growth redwood stumps (O'Hara et al. 2017).

The spatiotemporal relationships between light resources and carbohydrate reserves for tanoak and redwood sprouts regenerating after partial harvesting are not well understood (O'Hara et al. 2017). Information on the relationship between overstory retention and understory development would assist forest managers in creating effective multiaged silvicultural prescriptions in redwood forests (O'Hara 2014). Our approach was to analyze fine-scale data on growth of stump sprout regeneration. The following questions regarding regeneration were analyzed: (1) How did growth rates of redwood and tanoak sprouts compare in the first six years after treatment under different overstory densities and spatial arrangements?; (2) Did 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 did the relationships between sprout growth and post-harvest stand conditions change over the first six years of sprout growth? We hypothesized that the development of the dominant sprout on each clump of re-sprouting redwood and tanoak stumps: (1) was greatest in the center of a group selection opening where rapid sprout growth would be sustained, and lowest under high-density dispersed retention where the growth of sprouts would gradually decline; (2) would not differ among dominant sprouts arising from root systems with/without one or more residual redwood stems retained; and (3) over time become progressively more sensitive to (i.e., their growth more strongly influenced by) canopy openness and understory light conditions created by partial harvesting. In addition to studying stump sprout dynamics, we developed predictive models for total height of five-year-old redwood and tanoak stump sprout clumps to allow for future comparison of our results with published studies or for use in calibration of growth and yield model simulations.

2. Methods

2.1. Site description

Our study occurred at the Jackson Demonstration State Forest (JDSF) near Fort Bragg, California, USA. JDSF is located near the geographic center of the redwood range. The redwood-dominated portion of JDSF where the study was conducted was initially railroad logged between 1870 and 1930, resulting in stands dominated by the new cohort arising in response to the major harvest disturbance. Since the state took ownership in 1947, a range of different stand-level silvicultural prescriptions were applied by the California Department of Forestry and Fire Protection, creating a mosaic of different structures available for observational studies or implementation of manipulative experiments. Prior to installation of our experiment, the four stands chosen as experimental replicates were well stocked 80 to 100-year-old redwood-dominated second-growth that had received either no or one partial harvest.

The area has a typical climate for the redwood range with cool wet winters and warm dry summers. Coastal fog is less frequent and annual rainfall increases with rising elevation as one moves further inland, away from the Pacific Ocean. Rainfall at nearby North Fork Caspar averages 1200 mm per year (Dahlgren 1998). The four study sites are located between 16 and 24 km from the Pacific Ocean at 1800 to 2400 m elevation. Site quality is classified as Site Class II, representing 'moderate to good' quality (Lindquist and Palley 1963; Webb et al. 2012). Soils are sandstone derived and well drained. Topography and aspect differ among sites, from a gentle broad ridgeline at one site to steep sites facing south, north, and north-east at the other three sites. Prior to installation of the experiment, redwood was intermingled with tanoak and coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*).

2.2. Experimental design

The study utilized a randomized complete block design, where four treatments were replicated once each at four sites, giving four replicates per treatment. The treatments were group selection (GS), high-density dispersed retention (HD), high-density aggregated retention (HA), and low-density dispersed retention (LD). Each GS treatment resulted in complete removal of the overstory throughout a 1-ha circle and light commercial thinning of < 33% of basal area in the surrounding matrix which extended roughly 50 m or at least one tree height in all directions. In the other three treatments, retention was prescribed in terms of relative densities, based on the maximum stand density index (SDI) of 2470 stems/ha for redwood (Reineke 1933). The HD and HA treatments were both harvested to a target of 21% relative density (SDI = 520), and LD treatments were harvested to a target of 13% relative density (SDI = 320). These residual stand densities were chosen based on the expectation that, roughly 20 years later, stands would reach the prescribed upper limits of 30% and 50% relative density respectively when partial harvesting would again initiate a new cohort (Berrill and O'Hara 2009). Prior growth and yield model simulations indicate maintaining stand density below 30% in the LD treatment favored individual tree growth with modest sacrifice in stand volume production, while maintaining stand density below 50% in the HD and HA treatments favored stand volume production without major sacrifice of individual tree growth within subordinate cohorts in multiaged redwood stands (Berrill and O'Hara 2009). The targeted species composition for retention after partial harvesting was 70–75% redwood, 20–25% Douglas-fir, and 0–5% tanoak.

Each treatment was applied throughout 2-hectare (ha) treatment units except the 1-ha circular GS opening which was placed at the center of a 2-ha treatment unit. After harvesting, one 0.2 ha plot was established in the center of each treatment unit in order to minimize edge effect on growth measurements. Within each plot, approximately 25 sprout clumps each of redwood and tanoak were marked for yearly measurement. These clumps were selected systematically to be well dispersed across the plot, and for redwoods to represent one of two conditions: stump sprouts sharing a root system with one or more residual redwoods, or after complete removal of residual trees from the resprouting root system.

2.3. Data collection

The height of the tallest individual sprout represented the height development of the entire clump. Annual height measurements of the dominant redwood or tanoak sprout in each selected clump were used to calculate annual height increment. The tallest sprout in each clump was measured for total height with a height pole placed on a spot marked by a pin flag and numbered tag each year to ensure precise annual remeasurements during winter after growth had ceased for the year. Although the dominant sprout in a clump could be a different individual from year to year due to damage or differences in growth, measurements consistently represented the height of the experimental response variable, the tallest sprout. Height measurements were taken the first six years following harvest with one exception: the year 4 measurement was missed at the first site to be treated, where sprout heights were measured in winter 2012/13, 13/14, 14/15, [missed: 15/16], 16/17, and 17/18. The other three replicates were harvested a year later (2012) during the same season as the prior summer growing season harvest (2011), and heights were measured annually in winter 2013/14, 14/15, 15/16, 16/17, 17/18, and 18/19. Due to the missing measurement, year 4 and year 5 height increments were replaced by a 2-year periodic annual height increment (i.e., year 4/5) representing the average annual height growth over the fourth and fifth growing seasons. Therefore, we calculated height increment for year 2, year 3, year 4/5, and year 6.

Hemispherical photos were taken pre-dawn or post-dusk in the absence of direct sunlight above nine sprout clumps each of redwood and tanoak per plot using a Sigma SD15 camera with a 4.5 mm 180° fisheye lens mounted on a tripod (Berrill et al. 2018b). The photos were used to calculate percent canopy openness (PCO; 1- % canopy cover), which represented canopy density, as well as the percent of above canopy light (PACL) using Gap Light Analyzer (GLA) software (Frazer et al. 1999).

The diameter at breast-height (DBH) was measured for each residual tree within a plot and used to calculate residual basal area (BA; $m^2\,ha^{-1}$) and SDI using the summation method (Shaw 2000). A note was made for each residual redwood tree sharing a root system with a stump sprout clump, allowing for comparison of sprout growth after complete versus partial cutting of redwood stems growing in clumps with shared root systems.

2.4. Data analysis

All statistical analyses were conducted in the R statistical environment version 3.4.3 (R Development Core Team 2017). Using the lme4 package in R (Bates et al. 2015), generalized linear mixed-effect models were used to analyze sprout height growth in relation to treatment type and residual stand density. To answer our research questions, we sought to identify the best predictors of sprout growth by analyzing three candidate models. Model 1 incorporated density and aggregation effects through use of one categorical fixed-effect variable representing treatment type (GS, LD, HD, HA). Model 2 included residual BA as a continuous fixed-effect variable representing density, and a binary (yes/no) fixed effect for aggregation (yes = HA; no = GS, LD, HD). Similarly, Model 3 included residual SDI as a continuous fixed-effect variable representing density, and a binary (yes/no) fixed effect for aggregation. Sprout growth, was modeled in terms of annual height increments, and also for total height at age 5. The repeated measurements of height increment were analyzed simultaneously by incorporating 'year' (i.e., year 2, 3, 4/5, 6) as a categorical fixed effect and also testing for interactions of time × treatment or time × residual stand density. A unique identifier for each sprout clump was included as a random effect to account for the temporal autocorrelation of sprout growth. In these models, an additional binary fixed effect was included that tested whether the retention of a residual tree(s) in a fairy ring affected the growth of new sprouts. Finally, a fourth and fifth model of sprout height increment were developed. Linear mixed-effects regression via the lme4 R package (Bates et al. 2015) was used to model the relationship between sprout height increment and either PCO or PACL for the tanoak and redwood sprouts which had hemispherical photos taken directly above them in 2014. These models also incorporated the repeated measurements of height increment where 'year' was tested as a categorical variable.

Analyses of residuals were conducted to determine if transformations of the independent and dependent variables were necessary to create a normal distribution. The sprout height increment response variable was based on difference in heights of the tallest sprout within each clump in each measurement year, not necessarily the tracking of height for each individual sprout over time. Nevertheless, top damage or loss of the dominant sprout in a clump occasionally resulted in some negative growth measurements. Therefore, before transforming the height increment data to improve normality, a scalar was applied to make all height increment data positive.

In mixed-effects regressions, a categorical random effect representing differences among replicates was tested to account for variation among sites. The models testing understory light and canopy density as variables included a random effect representing the plot. Likelihood ratio tests were used to determine significance of random and fixed effects at the alpha = 0.05 level. Post-hoc comparisons of means and slopes were conducted using the Tukey method with the R package emmeans (Lenth et al. 2019). Models with similar independent variables (i.e. residual plot BA or SDI) were compared using Akaike information criterion (AIC) weights (probability of a model being the 'best'; Akaike

1973; Burnham and Anderson 2002). Model goodness-of-fit was described in terms of marginal R^2 representing the variance explained only by fixed effects, and conditional R^2 representing the variance explained by both fixed effects and random effects.

3. Results

3.1. Development of stump sprouts

Residual stand density ranged from zero within GS openings up to similar levels in both the HA and HD treatments which averaged (±s.e.): 38.8 ± 2.2 and 39.5 ± 1.4 m^2/ha BA, and 546 ± 15 and 532 ± 11 SDI, respectively. The LD residual stands averaged 22.4 ± 1.2 m^2/ha and 325 ± 13 SDI across the four replicates. After six years, heights of redwood sprouts ranged from 61 to 1100 cm and heights of tanoak sprouts ranged from 46 to 692 cm. Annual height increments were highly variable, ranging from −45 to 246 cm for redwood and −35 to 121 cm for tanoak; where negative increment resulted from mortality or damage to the tallest sprout in the clump making it shorter and occasionally outgrown by a different sprout which was then measured as tallest sprout in the clump. Among the 3308 height increment data representing four time periods, there were 11 negative increments for redwood and 27 negative increments for tanoak sprout clumps. Loss of height was more common at younger ages, and most often attributed to animal browsing, followed by dead tops and broken tops more commonly noted with advancing sprout age. Models describing sprout height increment consistently had modest conditional R^2 and low marginal R^2 indicating low predictive ability of fixed effects, and random effects accounted for much of variation in sprout growth. Among the models tested, the most parsimonious model describing redwood sprout growth included the categorical treatment variable. Conversely, the most parsimonious model describing tanoak sprout growth included the continuous variable SDI representing post-harvest residual stand conditions (Table 1). Redwood and tanoak sprout growth was highest in group selection openings (Fig. 1). In dispersed treatments (LD, HD) redwood exhibited significant decline in height increment after their second growing season. Conversely, redwood sprouts maintained consistent height increment in the HA and GS plots (Fig. 1C).

Redwood stump sprouts exhibited a higher sensitivity to residual stand density than tanoak sprouts, as indicated by a greater slope of modelled height increment in relation to stand density (Fig. 2). The sensitivity of tanoak sprouts to stand density was found to vary among years; 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 (Fig. 2). These differences appeared to be age-related as opposed to climate-year-related: when analyzed separately, the height increments from the site harvested a year earlier than the others exhibited a similar pattern.

Both redwood and tanoak sprout heights at age 5 were variable, and lower at higher levels of stand BA and SDI. Heights ranged from 54 to 981 cm for redwood and from 55 to 548 cm for tanoak. Redwood sprouts were significantly taller than tanoak across the range of stand density (Fig. 3). SDI was a better predictor of age-5 sprout height than BA for both redwood and tanoak (AIC weight = 0.99; Table 2). The variable representing whether a residual redwood tree was present on the same fairy ring as a sprout was not significant in either the age-5 height models or the annual height increment models. The model predicting redwood height at age 5 using SDI was improved by including the aggregation variable. This model resulted in an AIC value 2.4 points lower than the simpler model (not shown). At higher residual densities, redwood sprouts in aggregated retention plots were taller on average than those in dispersed treatment areas (Fig. 3).

3.2. Stand density and understory light

Overall trends of sprout height increment showed a positive correlation to both percent of above canopy light (PACL) and percent canopy openness (PCO) (Fig. 4). Pairwise comparisons of slope indicated that redwood sprout growth was more sensitive to understory light and canopy openness in year 6 than in year 2. Sensitivity of tanoak annual height increment to measurements of understory light (PACL) did not

Table 1
Coefficients (with standard errors in parentheses) 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, as a function of meaurement year and its interactions with alternate predictor variables treatment type, basal area (BA), or stand density index (SDI); where treatment is group selection (GS; the latent variable), high-density aggregated (HA), high-density dispersed (HD), or low-density dispersed (LD) retention.

	Redwood			Tanoak		
Parameter	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

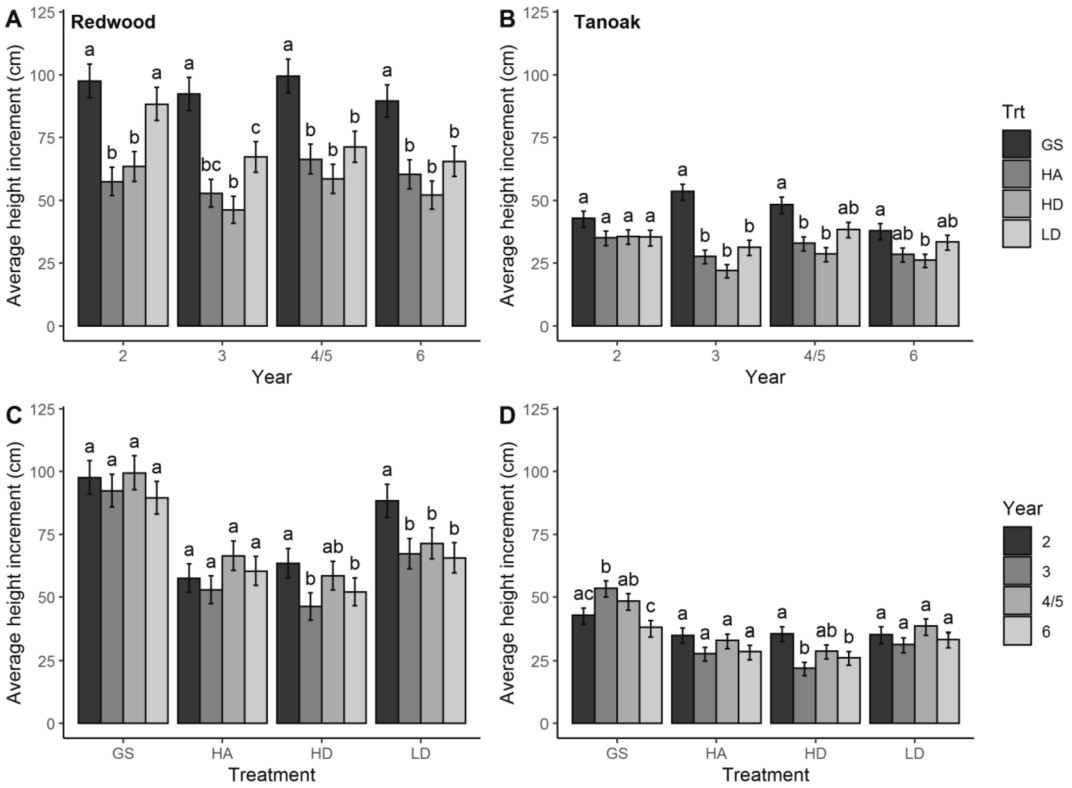

Fig. 1. Height increment of dominant redwood and tanoak sprouts, respectively, each year (A, B) with Tukey letters representing differences among treatment types (Trt) within each year, and for each treatment type (C, D) with Tukey letters representing significant differences among measurement years within each treatment type: group selection (GS), high-density aggregated (HA), high-density dispersed (HD), and low-density dispersed (LD) retention. Error bars represent standard error of the least-squares means.

change from post-harvest year 2 through year 6, but tanoak sprout growth exhibited an increase in sensitivity to PCO from year 2 to year 3 (Fig. 4). However, low marginal R^2 indicated that neither of these variables were strong predictors of sprout growth in part due to variability within plots and among sites (Table 3).

4. Discussion

This study revealed how understory light, stand density, and spatial arrangement of residual trees affected height growth of redwood and tanoak stump sprouts regenerating after different multiaged silviculture treatments. Growth of redwood stump sprouts outpaced tanoak sprouts across all treatments, was highly sensitive to overstory density, and exhibited an increase in sensitivity to light availability from year 2 to year 6. Aggregated retention slightly increased height growth of redwood sprouts, and we did not detect a difference in growth between sprouts originating from sprout clumps where all redwood trees were cut compared against clumps where one or more trees were retained. These findings improve our understanding of stump sprout dynamics after partial harvesting and reaffirm the importance of stand density and understory light when regenerating multiaged redwood stands (O'Hara et al., 2007).

4.1. Development of stump sprouts

During transformation (sometimes referred to as conversion) to multiaged management, we found height growth of the newly established cohort was most sensitive to residual stand density. In particular, we found a pronounced difference between rapid growth of sprouts in group selection openings and slower growth in partial shade. While redwood sprouts were taller on average after aggregated retention treatments versus dispersed retention treatments of similar residual densities, the difference was small. It is unclear if differences in understory performance related to residual stand arrangement will be more or less evident as multiaged stands develop, with tree crowns expanding into openings, less available growing space, and intensifying competition in all but the larger canopy gaps found at low residual densities and under more highly aggregated retention patterns. O'Hara et al. (2007) reported more rapid canopy closure and reduction in understory light after thinning in a redwood plantation to retain trees in a more evenly-dispersed pattern of retention where their crowns can expand on all sides versus after row thinning to leave residual trees in close proximity within rows where tree crowns can only expand on two sides. Nevertheless, even shortly after partial harvests where stand densities were heavily reduced, redwood and tanoak sprout growth may have been constrained by resource limitations imposed by the overstory trees (Berrill et al. 2018b). Similar results are reported for sprouting hardwoods. Dinh et al. (2019) reported reduced sprout growth of two oak species under greater canopy cover soon after partial harvesting in Japan. Also consistent with our findings, Mårell et al. (2018) reported a strong positive correlation between understory light and oak stump sprout increment 2–3 years after partial harvesting in France.

In our experiment where both redwood and tanoak trees were cut and allowed to re-sprout, the resultant redwood sprouts were growing faster than tanoak sprouts across the range of residual stand densities at each study site. This is consistent with multiaged growth and yield studies in the region (Berrill and Boston 2019) and studies of sprouting hardwoods where some species consistently outperform others at different intensities of partial harvest (Keyser and Zarnoch 2014; Knapp et al. 2017). Our findings do not apply to the common historical practice of harvesting conifers and leaving hardwood trees including tanoak standing in the advantageous position where their crowns can expand and shade out conifer regeneration (Kenefic et al. 2021). Our findings also do not apply where tanoak has been eliminated or had densities

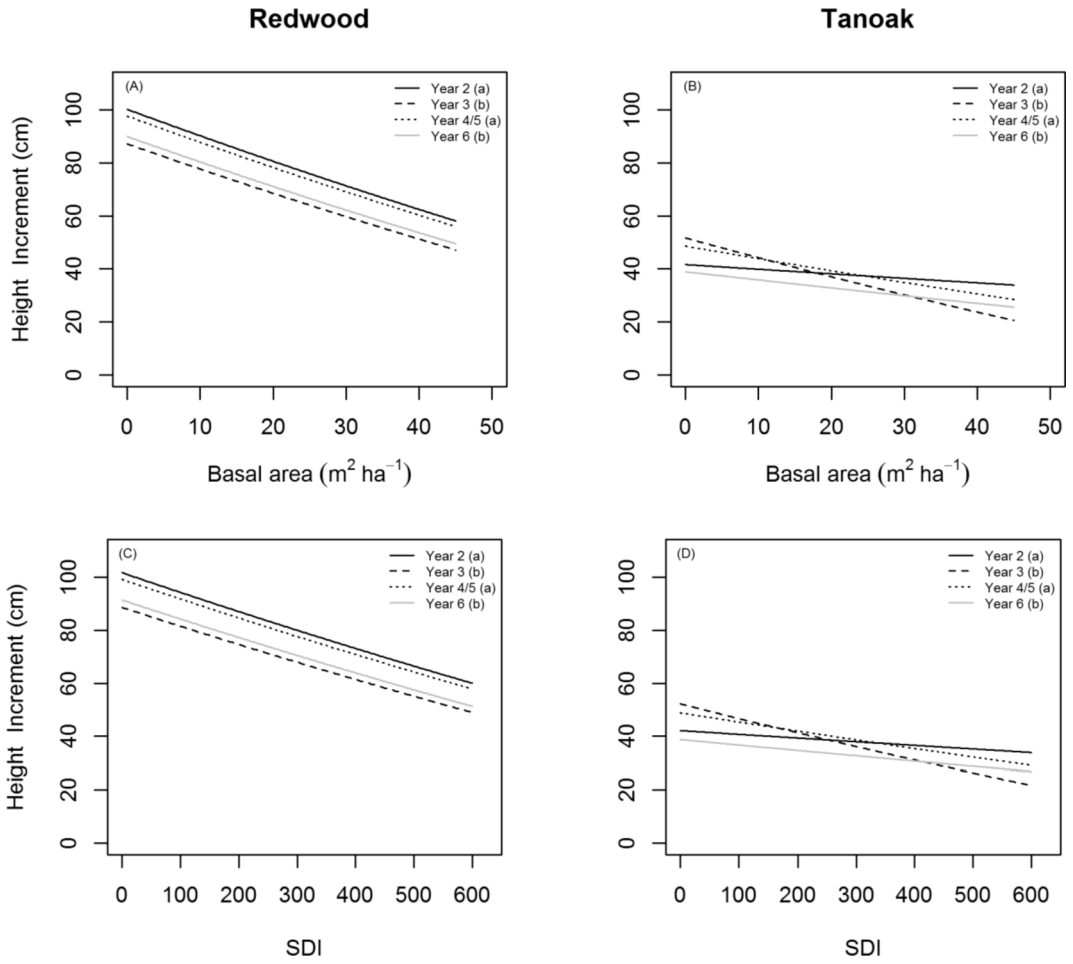

Fig. 2. Stand density and sprout growth – linear regression of the relationship between height increment of dominant redwood and tanoak sprouts and residual stand BA (A, B) or metric stand density index (SDI; C, D). Tukey letters in legends indicate significant differences of mean height increment among time periods.

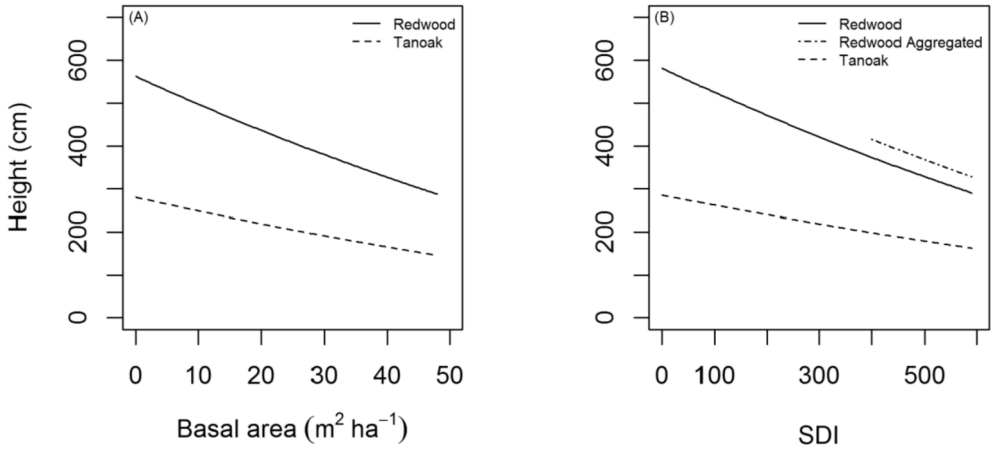

Fig. 3. Inverse exponential relationship between age-5 sprout height and BA (A) or SDI (B).

reduced by herbicide treatment (e.g., Berrill and Howe 2019). Here, we would expect the same or slightly more rapid growth of conifer regeneration without competition from re-sprouting hardwoods (Berrill et al. 2020). Since redwood is highly sensitive to changes in site quality, it is also likely that redwood sprouts have slower growth relative to tanoak sprouts on sites with lower redwood site index (O'Hara et al. 2017).

Variance in climatic factors was originally suspected to be the cause of reduced growth in year 3. Lockhart and Chambers (2007) also suspected that two years of drought affected development of young oak stump sprouts arising after different intensities of partial harvesting and may have confounded treatment effects. However, when our data from the four replicates were grouped by year of harvest and modeled separately: both groups displayed relatively slow growth in year 3 (i.e., different calendar years). It is possible that interannual variations in climate were not greatly affecting the growth of young sprouts, but more likely is that we did not have enough representation of different sprout

Table 2
Coefficients (with standard errors in parentheses) for models predicting the height$^{0.5}$ of dominant redwood sprouts and tanoak sprouts after five years of growth from either basal area (BA) or stand density index (SDI) and categorical variable denoting aggregated spatial pattern.

	Redwood		Tanoak	
Parameter	BA	SDI	BA	SDI
Intercept	23.719 (-0.841)	24.121 (0.778)	16.751 (0.338)	16.899 (0.327)
BA or SDI	−0.141 (0.012)	−0.012 (0.001)	−0.097 (0.006)	−0.007 (0.001)
Aggregated	–	1.067 (0.531)	–	–
Marg. R^2	0.25	0.29	0.37	0.38
Cond. R^2	0.35	0.37	0.41	0.42
AIC	1865.79	1851.48	1494.53	1483.7
AIC weight	<0.01	0.99	<0.01	0.99

ages growing in different climate years to assess the influence of drought on regeneration dynamics. Physiological factors, such as the transition from relying on stored carbohydrates to becoming a self-sustaining organism, may account for the phenomenon of slower sprout growth from year 3 onwards (O'Hara et al., 2007). Decreased growth in year 6 might be explained by a combination of factors: the depletion of carbohydrate reserves from the parent tree root system (Wiant and Powers 1966; Del Tredici 2001), competition among sprouts sharing a root system, and the expansion of overstory tree crowns into canopy openings (O'Hara et al. 2007). The small crowns of the sprouts may not be capable of generating enough photosynthate to maintain the expansive root system of the parent tree which could explain the slower growth in year 6. Growth of redwood sprouts in dispersed retention treatments appeared to slow from year 3 to year 6 while growth of sprouts in the HA and GS treatments remained relatively constant. The larger gaps created for sprouts to grow in aggregated retention treatments may remain open longer and help to offset the increased shade from expanding residual crowns. This is consistent with Knapp et al. (2017) who only recorded an early reduction in dominant sprout growth in clumps under higher overstory retention while sprouts sustained rapid growth at lower overstory retention.

To create a dispersed pattern of tree retention, foresters tend to retain one or few residual stems in each redwood fairy ring. Conversely, partial harvesting to create an aggregated pattern of retention leads to cutting and regenerating of entire redwood clumps between widely spaced or larger aggregates of residual trees. Presence of a residual tree on the fairy ring did not have a discernable effect on redwood sprout growth. This finding has practical relevance because it is often easier to harvest

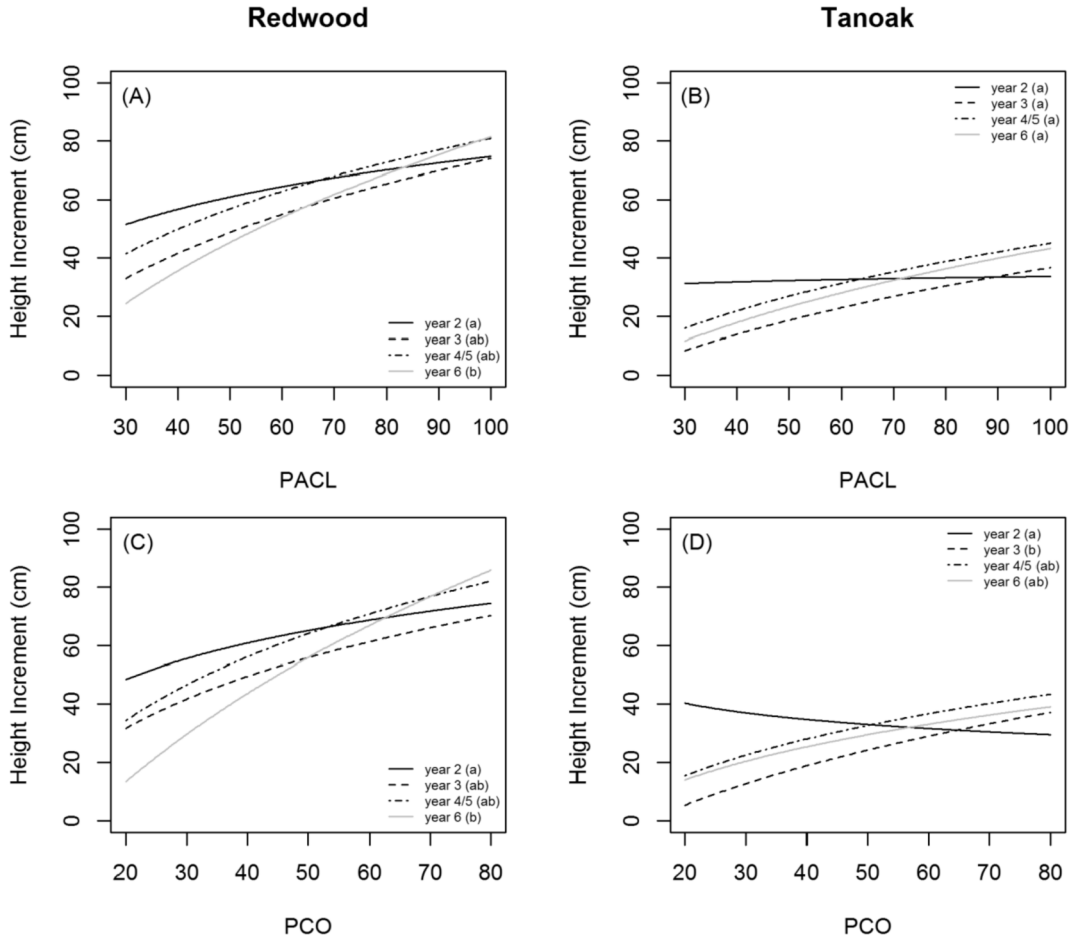

Fig. 4. Sprout growth and canopy or understory light – redwood (A, C) and tanoak (B, D) sprout height increment relationships to percent above canopy light (PACL) (A, B) and percent canopy openness (PCO) (C, D) obtained from hemispherical photos. Common letters in legends indicate slope coefficients that are not significantly different.

Table 3
Canopy or understory light (β_1) models of sprout growth – coefficients and fit statistics for two 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, and percent canopy openness (PCO).

	Redwood				Tanoak			
	ln(PACL)		ln(PCO)		ln(PACL)		ln(PCO)	
Parameter	coef	S.E.	coef	S.E.	coef	S.E.	coef	S.E.
Intercept	4.088	3.472	4.385	4.067	5.72	3.135	8.743	3.499
Year 3	−4.762	2.613	−3.205	3.051	−9.149	3.461	−11.749	3.753
Year 4/5	−3.462	2.605	−3.939	3.02	−7.583	3.491	−8.95	3.756
Year 6	−8.476	2.609	−10.023	3.031	−8.983	3.481	−8.758	3.729
PACL or PCO	1.123	0.845	1.109	1.044	0.16	0.752	−0.597	0.887
Year 3: β_1	1.026	0.639	0.679	0.787	2.037	0.833	2.817	0.956
Year 4/5: β_1	0.823	0.637	0.991	0.779	1.827	0.84	2.281	0.957
Year 6: β_1	1.918	0.639	2.423	0.783	2.104	0.838	2.167	0.949
Marginal R^2	0.07		0.06			0.08		0.06
Conditional R^2	0.68		0.68			0.37		0.37
AIC	2199.69		2200.77			1973.02		1979.58
AIC weight	0.63		0.37			0.96		0.04

an entire clump of stems than to leave one or more standing due to the high probability of residual stand damage or worker safety hazard felling stems with interconnected crowns. Managers may choose to cut all stems or only partially cut a fairy ring without concern for growth of the subsequent sprouts as long as there is enough understory light available for the sprouts to be self-sustaining (O'Hara et al. 2007). It is still unclear whether there is nutrient sharing between residual trees and sprouts on the same fairy ring. It is possible that any provision of resources to the young sprouts is negated by the increased shade from the close proximity of a large tree.

Models of sprout heights at age-5 produced similar results to annual growth increment models: heights were negatively correlated to residual stand density and there was a significant disparity between species. Five years after harvest, the new cohort of redwood sprouts averaged 290 cm height at 600 SDI dispersed retention and 320 cm height after aggregated retention of 600 SDI (24% relative density), 420 cm height after dispersed retention of 300 SDI (12% relative density), and 580 cm height in group selection openings. Predicted redwood sprout height at the maximum overstory basal area observed (48 m^2 ha^{-1}) was 280 cm which is substantially lower than averages of about 570 cm observed at similar densities on a highly-fertile alluvial flat in Humboldt County (O'Hara et al. 2007). Slower growth is expected on poorer sites (Berrill et al. 2020), and drought conditions in 2013 and 2014 may also have caused a reduction in height increment for years 3–5. Nevertheless, the age-5 modeled averages at our sites on JDSF in Mendocino County are higher than the height of redwood seedlings planted in full sun on sites of similar quality at JDSF after 6 growing seasons (Jameson and Robards 2007).

4.2. Sprouts and understory light

The relationships between sprout height increment and understory light identified in this study are consistent with findings from earlier studies of redwood stump sprouts in multiaged stands, demonstrating the importance of understory light for the development of regenerating redwoods. For example, O'Hara and Berrill (2010) reported major reductions in sprout height increment with decreasing understory light and advancing sprout age on a top-quality site. While understory light was also influential on our sites, the early growth of stump sprouts was lower overall, presumably due to slightly lower site quality (Berrill et al. 2018b). We also found high variability in the growth of redwood (R^2 = 0.06–0.07) and tanoak (R^2 = 0.06–0.08) sprouts across the range of PCO and PACL. Similarly, uncertain growth-light relationships were reported for sprout regeneration in Wisconsin USA (R^2 = 0.05–0.20; Forrester et al. 2014) and the Czech Republic (R^2 = 0.09–0.32; Adamec et al. 2017). We speculate that much of this variability can be attributed to the fine-scale variability in stand structure and microsite conditions within mixed multiaged redwood-dominated stands with inherent clumping of redwood and also different species and tree sizes present (Battaglia et al. 2002), differences in site quality within and among plots at the same site and also among sites (Berrill and O'Hara 2015), differences in aspect and slope position among sites affecting available growing space and understory light throughout the growing season (Berrill et al. 2018b), and the amount of carbohydrates stored in re-sprouting root systems of different sizes that were being exploited by the developing stump sprouts (Wiant and Powers 1966; Del Tredici 2001).

In the current study, we showed how sensitivity to light and canopy cover quickly changed. Tanoak sprout growth was insensitive to PCO and PACL in year 2, after which time sprouts within areas of greater canopy openness exhibited faster growth than sprouts under more canopy cover, which may be indicative of a depletion of carbohydrate reserves from the parent tree root system and transition to reliance on intercepted light and other resources limiting sprout growth (Del Tredici 2001). We also noted sensitivity of tanoak sprout growth to understory light beginning in year 3, however this transition (change in regression slope) was not statistically significant. 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. It is possible that the rapid growth of redwood sprouts had resulted in a changing light environment for neighboring tanoak sprouts, introducing additional variability in sprout growth. The redwood sprouts may have grown tall enough to further shade tanoak sprouts so that they did not have the same understory light environment that was detected soon after harvest.

Redwood sprout growth became increasingly more sensitive to available understory light and canopy cover from year 2 to year 6. This result is more informative than our other finding that the sensitivity of sprouts to residual stand density did not change significantly from year 2 to year 6. Hemispherical images were taken above individual clumps of sprouts, whereas values of stand density represented an entire plot. Measurements of understory light and canopy cover are more accurate representations of the conditions each individual clump was experiencing. Therefore, while stand density has proven to be a useful predictor of sprout development, it appears that assessing the light environment for individual clumps allowed us to detect a change in the pattern of redwood sprout growth with advancing age: they became more dependent on available light as they aged. This steady increase in sensitivity suggests a slow depletion of carbohydrate reserves identified as important to early sprout growth by Berrill et al. (2018b). Mature redwood trees typically have much larger diameters than tanoak when the two species are found in association (Waring and O'Hara 2008). Therefore, redwood stump sprouts originating on large cut stumps and presumably larger root systems may have access to a larger supply of

carbohydrates that help sustain them longer than more modest supplies available to many tanoak sprouts originating from relatively small cut stumps with smaller root systems (Namm and Berrill 2020). Similarly, Keyser and Loftis (2015) and Zhang et al. (2021) report larger stump sprouts originating from the stumps of relatively larger cut trees.

4.3. Limitations and recommendations for future research

Establishing and maintaining multiaged silviculture experiments is a formidable task, and the choice of treatments to include is critical. The implementation of our replicated experiment involved survey, inventory, marking, and harvesting a total of 32 ha at four sites, plus permanent sample plot establishment and annual monitoring. The replicated design allowed for rigorous analysis, however, being replicated at four relatively high-quality sites in central Mendocino County in the latitudinal center of redwood's geographic distribution may limit the scope of inference for our findings. We recommend establishing additional replicates at warmer and drier sites further inland where tanoak may outcompete redwood. We also recommend establishing sites along a north–south gradient to assess sprouting along a gradient from xeric southern sites to mesic northern sites, and adding a low-density aggregated treatment to allow testing for interactions between residual stand density and spatial pattern of retention. However, incorporating extra experimental area makes it harder to maintain uniformity of site conditions among treatment blocks because redwood site quality is highly variable at small spatial scales (Berrill and O'Hara 2015).

Managers of multiaged stands must decide whether to undertake tending in the new cohort. We did not undertake weed control, and the result was abundant natural regeneration of trees and plants. Weed control may have been beneficial and warrants further investigation in multiaged stands. At the same time, herbicide use for vegetation management can be controversial, so our results may have particular value where herbicide application is undesirable for a variety of ecological, societal, and regulatory reasons. Another consideration is timing of precommercial thinning in redwood sprout clumps. At age 6, sprouts receiving more understory light were already much taller and larger. This implies that thinning might be best scheduled according to sprout height and not age. Available information on precommercial thinning comes from even-aged stands (O'Hara et al. 2017), where heavy early thinning initiated an unwanted new cohort of redwood stump sprouts (O'Hara et al., 2015). Therefore, we recommend further research of precommercial thinning within sprout clumps of different heights and ages to help develop best management practices for tending the new cohort in multiaged stands.

5. Conclusion

The management of multiaged stands or transformation to multiaged management requires careful consideration of how a residual overstory affects the development of the new cohort. Our findings indicate that the growth of young redwood sprouts is highly sensitive to light availability and moderated by older cohorts. It was also found that redwood stump sprouts outcompeted tanoak sprouts through six years after harvest, even under the higher levels of overstory retention on our relatively productive redwood-dominated test sites. When compared against redwood sprout height five years after harvest in group selection openings, the new cohort of redwood sprouts averaged 72% of this height at 12% relative density dispersed retention and 56% or 49% height at 24% relative density aggregated retention or dispersed retention, respectively. Therefore, if the objective of management is to promote rapid development of a vigorous new cohort of redwoods, we recommend combining conifer harvest with cutting of unwanted tanoak to obtain substantial reductions in overstory density. If slower growth of regenerating redwoods is acceptable or desirable, then higher residual stand densities can be retained but managers should expect declining stump sprout growth over time.

CRediT authorship contribution statement

Robert Muma: Formal analysis, Writing – original draft. **Lynn A. Webb:** Conceptualization, Methodology, Writing – review & editing, Project administration, Resources, Funding acquisition. **Harold S.J. Zald:** Formal analysis, Writing – review & editing. **Kevin Boston:** Supervision, Writing – review & editing. **Christa M. Dagley:** Conceptualization, Methodology, Writing – review & editing. **John-Pascal Berrill:** Conceptualization, Methodology, Supervision, Project administration, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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