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Understory light predicts stump sprout growth in mixed multiaged stands in north coastal California

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Abstract Regeneration of commercial species is central to long-term success of multiaged management for wood production. We examined relationships between understory light, varying overstory tree retention, and growth of coast redwood (*Sequoia sempervirens*; commercial species) and tanoak (*Notholithocarpus densiflorus*) stump sprouts initiated by group selection and single-tree selection harvesting in 80–100 year old mixed stands at four sites. Treatments included a complete harvest in 1-ha group selection openings, low-density dispersed retention, and either aggregated or dispersed high-density retention. Post-harvest stand density index and basal area were useful predictors of understory light. Mean and maximum understory light did not differ significantly between treatments with the same density where residual trees were retained in aggregated versus dispersed spatial patterns. However, the dispersed retention had lower minimum light levels when compared to the aggregated retention treatment. Aspect appeared to influence understory light more in dispersed treatments. At all light levels, the dominant sprout within clumps of redwood stump sprouts generally grew faster than dominant tanoak sprouts within tanoak sprout clumps. Differences in sprout height growth between aggregated and dispersed treatments were minimal. Stump size had a significant effect on redwood stump sprout height growth, with sprouts on the largest stumps growing approximately twice as quickly as sprouts on the smallest stumps. In the low density dispersed treatment, redwood sprouts outperformed tanoak sprouts by the greatest margin. Regeneration of redwood and tanoak was most rapid within group selection openings.

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Introduction

Multiaged forest management is becoming a more common approach to meeting multiple objectives in many forests. Multiaged silviculture can create variable overstory tree arrangements which influence subsequent natural and artificial regeneration (O'Hara 2014). Available understory light declines with increasing overstory stand density (Palik et al. 1997; O'Hara and Berrill 2010). Spatial arrangement of the residual overstory may also affect the quantity and quality of understory light, as well as the availability of other resources for understory regeneration (Baldocchi and Collineau 1994; Brown and Parker 1994; Clark et al. 1996; Nicotra et al. 1999). For example, when comparing dispersed and aggregated patterns of retention the range of available understory light increased to higher maximum levels within a longleaf pine (*Pinus palustris*) stand where the overstory trees were aggregated (Palik et al. 2002). Growth of understory trees can be influenced by manipulation of the spatial arrangement of the overstory in multiaged stands (Oliver and Larson 1996; McGuire et al. 2001). We expect aggregation of the residual overstory to enhance understory light availability, as well as spatial and temporal variation in light. This heterogeneous light environment may also lead to increased biodiversity (Battaglia et al. 2002). Understanding how stand density and patterns of retention affect regeneration of different species may help us maximize benefits or preserve a mixture of species in mixed multiaged stands.

Multiaged silviculture is increasingly being practiced along the Coast Range of California, especially in coast redwood (*Sequoia sempervirens*) forests managed for timber. These forests typically include mid-tolerant coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), and two shade-tolerant species that re-sprout from cut stumps: redwood, a valuable merchantable conifer, and tanoak (*Notholithocarpus densiflorus*), a hardwood generally considered to be non-merchantable and over-represented in secondary forests. Tanoak competes with redwood, especially within disturbed or harvested areas where tanoak can dominate (Tappeiner et al. 1990, 1992, 2007; Berrill and O'Hara 2014, 2016). Stump sprouts often develop quickly to reoccupy growing space and comprise the majority of regenerating stems following harvest (Lindquist and Palley 1967; Tappeiner et al. 2007). Initially, stump sprouts rely on carbohydrate reserves, while the growing sprout clump begins to supply its own carbohydrates via its photosynthetic system (Wiant and Powers 1967). As the sprouts transition from using stored energy to using photosynthates they become increasingly dependent on light for leaf area development and growth (Lieffers et al. 1999). Other factors that may influence stump sprout development include site quality, insects, pathogens, and herbivory (Drever and Lertzman 2001; Gratzer et al. 2004; Stancioiu and O'Hara 2006).

Redwood is well suited to multiaged systems because of its shade tolerance (Baker 1949), but it grows best in high light (Berrill and O'Hara 2007). Stand density, species composition, and site quality vary widely over short distances in redwood forests (Berrill and O'Hara 2014, 2016; Berrill et al. 2017). Furthermore, canopy closure can occur rapidly on good sites (O'Hara et al. 2007; O'Hara and Berrill 2010). Examining the relationship between light availability to the understory and spatial pattern of the overstory will

allow us to determine how management influences the quantity and spatial variability of understory light and how these factors affect regeneration.

The goal of this study was to quantify and model the growth of redwood and tanoak stump sprouts initiated by four partial harvest treatments: group selection, and three single-tree selection prescriptions. We sought to answer the following questions: (1) How well does stand density correlate with understory light, and can understory light be predicted by stand density? (2) For a given level of understory light, which treatment maximizes growth of redwood, while minimizing growth of tanoak regeneration? (3) For a given level of stand density, which spatial pattern (aggregated or dispersed) maximizes understory light, and/or growth of new stump sprouts? (4) How does size of parent tree stump at time of harvest affect subsequent redwood sprout growth at varying levels of light? Our specific objectives were to:

1. Model understory light as it relates to:

   a. Stand density index (SDI) and basal area (BA).
   b. Spatial pattern of retention (aggregated vs. dispersed).

2. Model height growth of redwood and/or tanoak sprouts as it relates to:

   a. Understory light.
   b. Spatial pattern of retention.
   c. Size of parent tree at time of harvest (stump diameter).

Methods

Site description

Jackson Demonstration State Forest (JDSF) is located within Mendocino County, north coastal California (39°21′N 123°36′W). The 20,000 ha forest is situated along highway 20, approximately 16 km from Fort Bragg (Supplemental File, Fig. S1). The forest extends east across the Coast Range, in the middle of redwood's natural range which extends north–south along a narrow 800 km strip of coastline from southwest Oregon to central California. Most of the old-growth conifer-dominated forests on JDSF were cut, beginning as early as the 1860's, and continuing through the 1930's with fire used to remove debris to facilitate access for logging. By 1947 when the state acquired these lands, the west portion of the forest where this study took place comprised 15–60 year old even-aged stands with scattered old residuals. Subsequent management has included single-tree selection harvests with removal of individual trees or small clusters of trees, group selection, and some clearcutting. The various disturbances released tanoak trees, seedlings, and stump sprouts to grow and occupy more growing space, and even dominate in some areas where conifers had not regenerated well. Nevertheless, redwood still dominates in many areas, in association with Douglas-fir and tanoak, and occasionally grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), Pacific madrone (*Arbutus menziesii*), and red alder (*Alnus rubra*). Soils are loamy, moderately deep to deep (up to about 2 m depth), well-drained, and formed from weathered sandstone. Gentle ridges give way to steep slopes and valleys with ephemeral or permanent streams. Valley bottoms contain gravelly, deep, moderate- to

low-permeability soils. Elevation ranges from 20 m near the coast up to 700 m as the forest extends inland up to and over the crest of the Coast Range. The climate is Mediterranean with cool moist winters and warm dry summers, with coastal fog moderating summer temperature closer to the coast. Precipitation near the coast averages 1000 mm per year and 1300 mm per year further inland at higher elevations on the eastern side of JDSF.

Experimental design

The experiment was a randomized complete block design with four replicates on JDSF representing different locations and aspects. Prior to harvesting, we surveyed four 2 ha silvicultural treatment blocks side-by-side within each one of the four different 8 ha replicates (except Whiskey Springs replicate which had five plots). Within each replicate, 2 ha treatment blocks were randomly assigned one of four multiaged silvicultural treatments: low-density dispersed (LD), high-density dispersed (HD), high-density aggregated (HA), and group selection (GS) (Supplemental File, Fig. S2). The LD treatment had a designated density management zone (DMZ) of 13–30% relative density (i.e., harvest to retain 13% relative density, and schedule future harvests when stand attains 30% relative density). The HD and HA treatments had a designated DMZ of 21–50% relative density. For the redwood-dominated stands on JDSF, this translated to a prescribed post-harvest density for LD of approximately 330 SDI (metric units). For HD and HA, the same post-harvest density of approximately 530 SDI allowed for study of the effects of spatial pattern of the residual stand with density held constant. Aggregates (clumps) were created by retaining 3–4 similar sized trees in a clump. Clumps were pure redwood or a mixture of redwood, Douglas-fir, and occasionally tanoak. The goal of retention was to maintain species composition consistent among treatments at around 70–75% redwood, 20–25% Douglas-fir, and 0–5% tanoak. Pre-harvest tree size and density varied among replicates (41–48 cm quadratic mean dbh, SDI 710-1640). Harvesting with a mix of tractor and cable systems began in autumn 2011 and continued into 2012 at some replicates. There were minor final density adjustments in 2013 at one replicate. Harvesting did not take place during the wet winter months.

Field data collection

After harvest, we installed one 0.2 ha measurement plot (45×45 m) within each individual 2 ha treatment block. Residual trees in each plot were measured for DBH, height, and live crown base height. Harvest slash and advance regeneration were cut, lopped, and scattered. Next, we planted 25 redwood and 25 Douglas-fir seedlings throughout each plot as far away as possible from residual trees and stumps of sprouting species.

Within each 0.2 ha plot, 25 sprout clumps of both redwood and tanoak were measured. If there were fewer than 25 clumps on the plot, then all clumps within the plot were measured. For each of these sprout clumps, the dominant (tallest) sprout was measured for total height. Heights were recorded early in spring before the beginning of the growing season for three consecutive years after treatment (2014–2016) for all treatments except Whiskey Springs (recorded 2013–2015), which gave two consecutive annual increments: a second and third year height increment of dominant redwood and tanoak sprouts in all treatments. Stump diameter was measured on all redwood stumps having sprouts selected for measurement. Specifically, stump diameter was measured at the height where the tree was cut

(stump height) which was usually 20–30 cm above ground but sometimes higher on fused redwood stems.

Plot corners were used as survey points to map location of stump sprouts, seedlings, and residual trees. Horizontal distance and azimuth were measured with a Vertex IV Hypsometer or Impulse Rangefinder (Laser Technology Inc.) and compass or Map Star compass module (Laser Technology Inc.) from the closest plot corner. A stem location map was created for all seedlings, stump sprouts, and residual trees using ArcGIS.

Understory light

Hemispherical photos were taken throughout each plot to quantify understory light above regeneration during the summer of 2014. Photos were taken using a Sigma SD15 camera with a 4.5 mm 180° fisheye lens mounted on a tripod. Hemispherical photos were taken above approximately 25% of stump sprouts and 25% of planted seedlings, for a total of 20 photo locations per plot.

All hemispherical photos were analyzed in Gap Light Analyzer 2.0 to quantify the percent above canopy light (PACL) for a growing season (March 15th to September 15th, Bawcom et al. 1961). PACL values were imported into ArcMap 10.1 and attached to the x and y coordinates of the corresponding seedling and stump sprouts where the photos were taken. The ArcMap Geostatistical Analyst extension was used to conduct semi-variance analysis for each plot as follows: we developed a semi-variogram of PACL (assuming no directional trends), and selected the best of three fitted variogram models: exponential, spherical, and Gaussian models (Isaaks and Srivastava 1989). Visual assessment revealed that semi-variance data were generally well represented by spherical models. Therefore the spherical model for each plot was used for spatial interpolation by ordinary Kriging, to interpolate understory light between sampled point locations and create a light map for each plot. The interpolated values were then attached to corresponding seedling and stump sprout records where photos were not taken.

Analysis

Regression analysis was used to examine the relationship between the response variables and multiple candidate explanatory variables categorized as sprout-level (species, height increment, percent above canopy light (PACL), and cut redwood tree stump diameter) or plot-level (BA, SDI, mean sprout height increment, mean PACL, mean stump diameter, and aggregation (yes/no dummy variable)). Linear models and generalized linear mixed-effects models (GLMMs) were used to model PACL as well as second and third year height increment for both tanoak and redwood stump sprouts. Regression analysis was completed using open-source statistical software package R version 3.2.3 (R Core Team 2015). To determine the best combination of variables within a model, candidate models were compared in terms of AIC or AICc values. The best model was checked for errors and outliers using residual plots, normal Q–Q plots to test for normality, and Cook's distance to check for high leverage outliers. Box–Cox graphs were used to test if transformation on the response variable was needed, and the Durbin–Watson test was used to identify autocorrelations among selected explanatory variables (Faraway 2016).

At the plot level, regression models predicted mean PACL for a given SDI, BA, or multiaged treatment type. These prediction models allow users to predict PACL from basic forest inventory data (SDI, BA). Models were created predicting mean height increment for

each species, and height increment of individual redwood and tanoak sprouts for each year to compare growth between species. Diameter of the cut stump associated with each redwood sprout clump was tested along with PACL or silvicultural treatment type as explanatory variables in models of redwood height increment. The best redwood height increment-stump diameter models were selected by comparing AICc. Likelihood ratio tests between models with and without stump diameter evaluated the statistical significance of including stump diameter as a covariate in models of PACL-height increment or treatment-height increment. A derived R^2 was obtained using the r.squaredGLMM() function in the Multi-model Inference (MuMln) package in R. Graphs of modeled estimates depict the influence of explanatory variables on predictions of PACL and the height increment of dominant sprouts.

Results

Understory light

Understory light was heterogeneous within all single-tree selection treatment blocks (Fig. 1). The aggregated treatment plots had areas of high light at all sites. The dispersed treatment plots had much higher light in the south-facing replicate (Waldo North) than other replicates. At individual sites, the high density aggregated (HA) treatment appeared to have the most spatially heterogeneous light environment. Conversely, our sample plot near the center of each GS opening had a relatively homogenous light environment (Fig. 1; Supplemental File, Fig. S3).
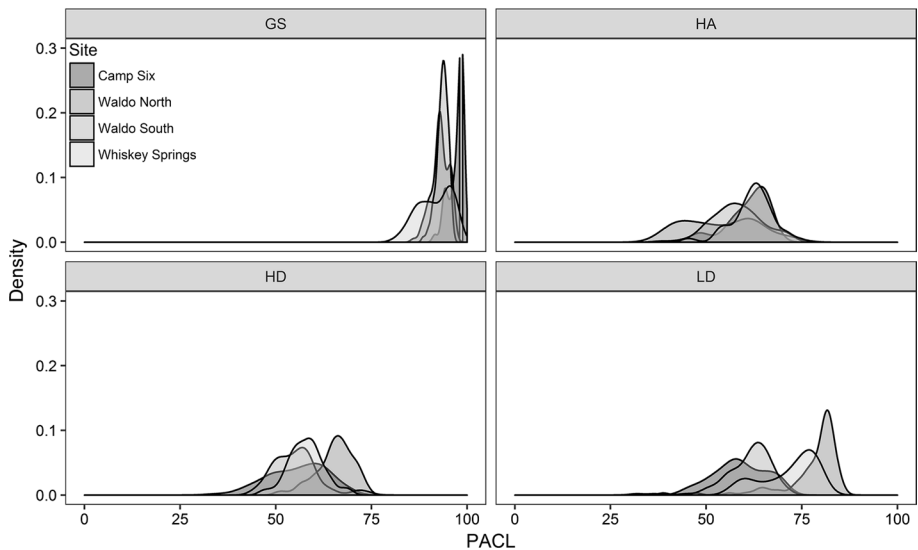

Fig. 1 Density plot of understory light (percent above canopy light; PACL) estimates for stump sprouts and planted seedlings in each multiaged treatment (*GS* group selection opening, n=426, *HA* high-density aggregated, n=416, *HD* high-density dispersed, n=506, *LD* low-density dispersed, n=411) at all four study sites

Table 1 Mean stand density index (SDI; metric), and mean percent above canopy light (PACL; %) (n = 17 plots) and range of PACL values at individual sample points (n = 1759), across all four sites (standard errors in parentheses)

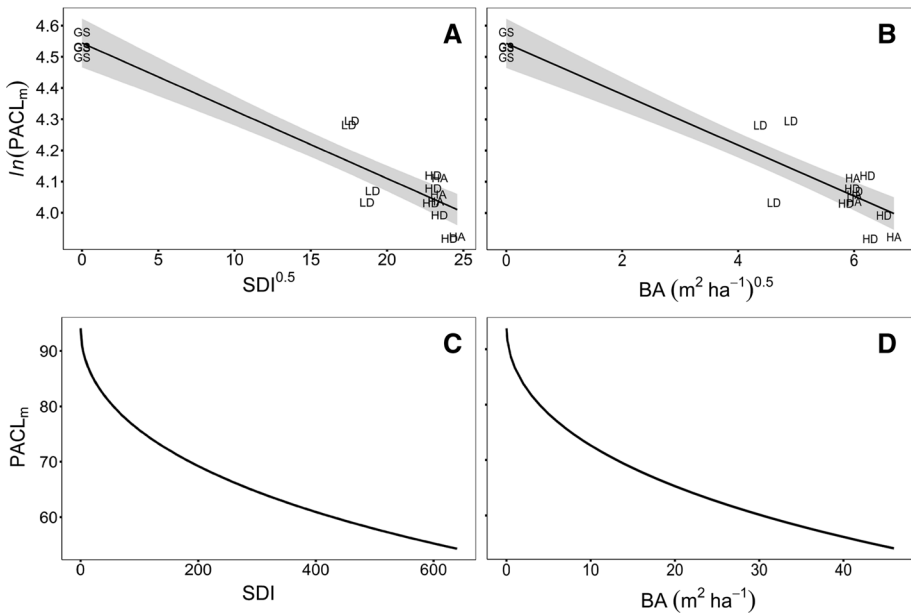| Treatment	No. plots	Mean SDI (SE)	Mean PACL (SE)	Min.–Max. PACL
Group selection	4	–	93.84 (0.17)	80.78–99.16
High density aggregated	4	537.31 (3.19)	59.10 (0.37)	37.74–75.15
High density dispersed	5	543.00 (0.92)	58.35 (0.30)	33.76–74.33
Low density dispersed	4	325.54 (1.17)	68.59 (0.62)	31.84–85.39

Fig. 2 The relationship of stand density index (SDI, metric) and basal area (BA) to mean percent above canopy light (PACLm, %) across all treatments: *GS* group selection, *LD* low-density dispersed, *HD* high-density dispersed, *HA* high-density aggregated single-tree selection. The area shaded gray represents the 95% confidence interval for each model: **a** $\ln(PACLm) = 4.5445 - 0.02173 * SDI^{0.5}$ (adj. $r^2 = 0.89$, n = 17 plots), **b** $\ln(PACL) = 4.54333 + -0.04657 * BA^{0.5}$ (adj. $r^2 = 0.89$, n = 17 plots). Predicted mean PACL values shown across a range of SDI (**c**) and BA (**d**). Coefficients taken from Table S2

Residual stand BA ranged from 0 to 40 m² ha⁻¹ and SDI ranged from 0 to 550 among all plots. PACL values ranged from 34 to 99%. Since most redwood trees had regenerated in clumps and Douglas-fir as single seedling-origin trees, the post-harvest spatial patterns of residual trees were not perfectly dispersed or aggregated. Mean PACL was almost equal in aggregated versus dispersed high density treatments with similar SDI (Table 1, Supplemental File, Table S1).

The high density aggregated and dispersed treatments had a similar range of PACL values across each plot, but the dispersed treatment had the lowest (minimum) values (Table 1). The relationship between stand density and PACL was most variable among LD plots at the four replicate sites (Figs. 1, 2; Supplemental File, Table S2).

Comparing height increment of redwood and tanoak

Two different models predicted mean height increment of redwood and tanoak stump sprouts (Supplemental File, Table S3). The treatment effects models included two categorical variables, species and treatment type, while the PACL model included log-transformed mean PACL and species as explanatory variables. An interaction with species (PACL×species, or treatment×species) improved the fit of both models, particularly in the second year sprout height increment models. A square root transformation on the dependent variable height increment was executed after observing Box–Cox results.

Generally, the mean height increment for each species was lower in year three than in year two, except for tanoak in GS which had more growth in year three (Fig. 3). Redwood sprouts grew faster than tanoak within all treatment blocks in both measurement years, with the greatest and most consistent growth rate advantage over tanoak sprouts in the LD treatment. Redwood height increment was similar between the HD and HA treatments in year two and year three. Tanoak grew slightly faster in HA than HD in year three. The treatment effects model fit the height increment data better than the PACL model in year two, while in year three the PACL model was the best fitting model (Supplemental File, Table S3). The difference in increment-PACL regression slopes between species (PACL×species interaction) was greater in year two than in year three for both types of models. Although the large standard error for the interaction term in both models indicated variability and uncertainty, this interaction did improve the model fit.

More variation in height increment was explained in year three than in year two by the models for both species, indicating that sprout growth had become more dependent on understory light (Supplemental File, Table S4). In particular, tanoak height increment was less affected by PACL in year two than in year three. While the relationship between PACL and height increment was stronger in year three, height increment generally decreased for both species. Model predictions across a range of PACL values, for both species in both years, depicted a diminishing benefit of extra light on growth (Fig. 4).
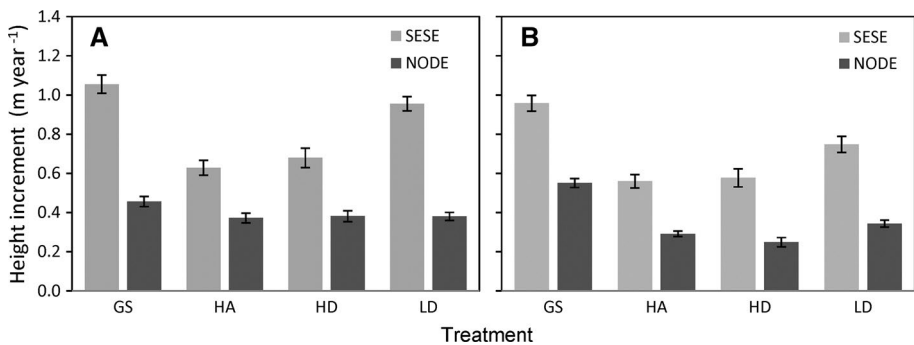

Fig. 3 Relationship of height increment for dominant redwood (SESE) and tanoak (NODE) stump sprouts in second year (**a**) and third year (**b**) to treatment type: *GS* group selection, *LD* low-density dispersed, *HD* high-density dispersed, *HA* high-density aggregated single-tree selection. Error bars depict standard error of the mean height increment among plots (n = 17). Coefficients taken from Table S3
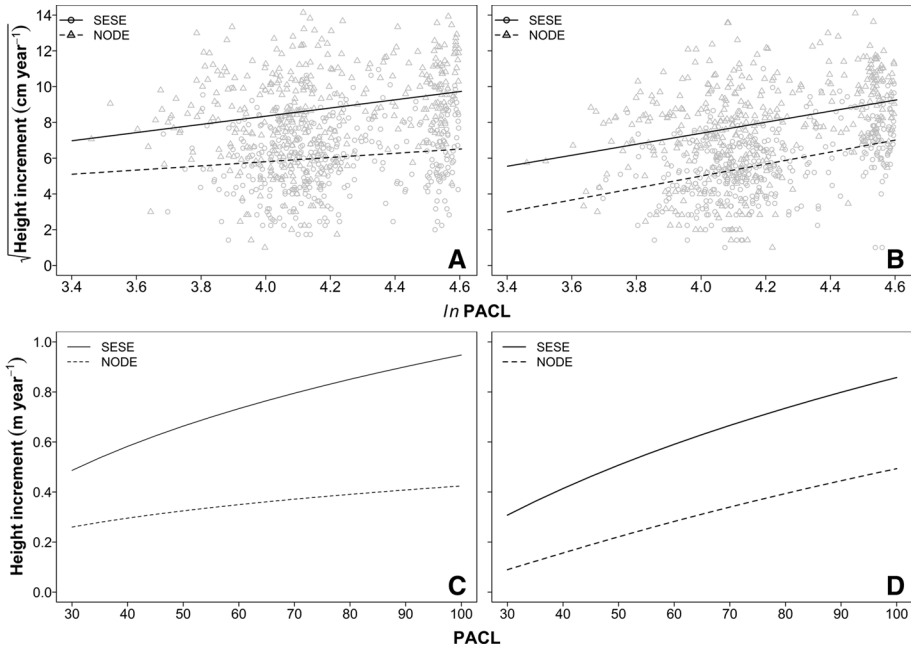
Fig. 4 Relationship between percent above canopy light (PACL, %) and height increment for individual dominant sprouts of redwood (SESE, n = 391) and tanoak (NODE, n = 394) in year two (**a**) and year three (**b**), and predicted height increment across a range of PACL values in year two (**c**) and year three (**d**). Coefficients taken from Table S4

Influence of stump size on redwood sprout growth

Likelihood ratio tests indicated that variation in redwood stump sprout height increment was significantly better explained when parent stump diameter was included in models for year two ($p < 0.0001$) and year three ($p < 0.0001$). The logarithmic transformation of both stump diameter and PACL resulted in the best model with lowest AICc and highest derived R^2 values. Sprouts on the smallest stumps grew more slowly than sprouts on medium- and large-sized stumps across the range of PACL values (Fig. 5a, b; Supplemental File, Table S4). In year two, after accounting for the influence of stump size in our model, the LD treatment was very close to producing the same height increment as the GS treatment. Also, HD and HA treatments shared nearly the same curve (Fig. 5c, d). This changed in year three, as height increment declined in low light. Height increment was more sensitive to differences in light and parent tree stump size in year three than in year two. Model predictions for redwood sprouts indicated that as stump diameters increased from 5 to 150 cm, an approximate doubling of redwood sprout height increment was expected (Fig. 5).
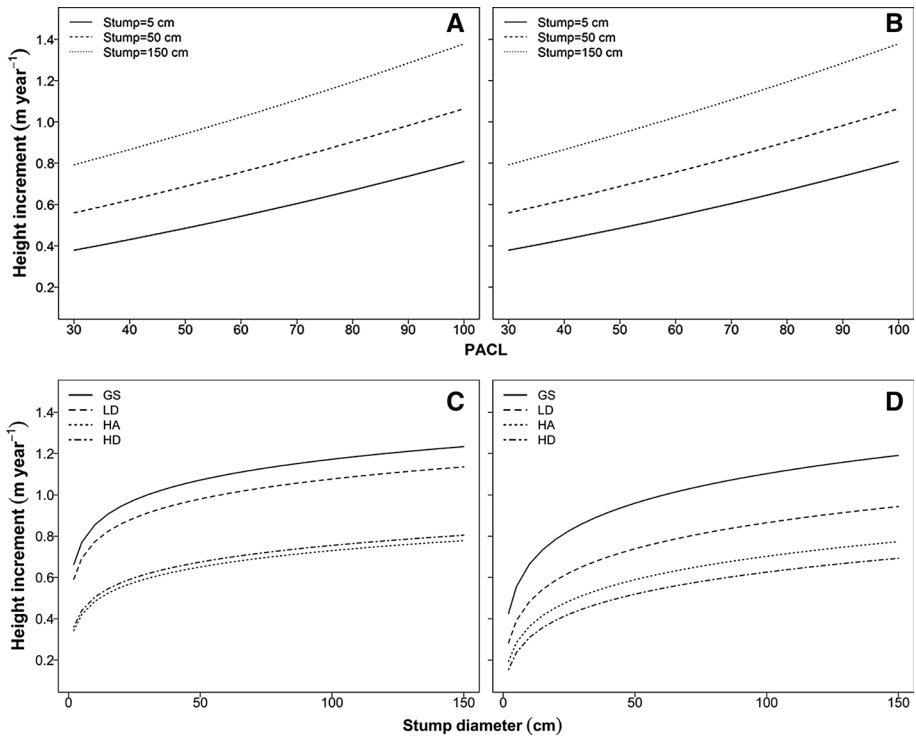
Fig. 5 Predicted dominant redwood stump sprout height increments across range of PACL values with stump diameter held constant at three levels in year two (**a**) and year three (**b**), and predicted height increment across a range of stump diameter values in year two (**c**) and year three (**d**) for treatments: *GS* group selection, *LD* low-density dispersed, *HD* high-density dispersed, *HA* high-density aggregated single-tree selection. Coefficients taken from Table S5

Discussion

Models that predict understory light and development of regeneration in multiaged stands can support forest management decision-making. Our models predicting mean PACL for different treatments depending on stand density allow model users to predict the average amount of understory light available given only an estimated SDI or BA. PACL was found to have a negative asymptotic relationship with stand density which is consistent with other research (Palik et al. 1997, 2002; O'Hara and Berrill 2010). Light availability was similar between aggregated and dispersed treatments which was consistent with a similar study in longleaf pine (Palik et al. 1997, 2002). Coast redwood naturally regenerates in clumps and therefore it was hard to achieve a completely dispersed spatial pattern in the residual stand while maintaining the same stand density and species composition as the aggregated treatments. Conversely, it was difficult to retain Douglas-fir in the aggregated treatments because these trees rarely formed tight clusters with conifer neighbors. Therefore in the redwood forest type, we may have inadvertently only achieved minor differences in structure between aggregated and dispersed retention which may have resulted in only minor, undetectable differences in understory light.

Height increment of the dominant redwood or tanoak stump sprout in each clump was well predicted by PACL. This is consistent with Rydberg (2000) who measured slower sprout growth in shade than full sun for European aspen (*Populus tremula*) and birch (*Betula* spp.) sprouts in Sweden, Rong et al. (2013) studying Liaodong oak (*Quercus liaotungensis*) in China, Keyser and Zarnoch (2014) who studied nine sprouting hardwood species in the Appalachian Mountains of North Carolina, and Forrester et al. (2014) who studied sprout development in different opening sizes in Wisconsin. We did not study light or sprout growth at the edge of GS openings. Our models predicted growth rates to be highest at/near the center of GS openings where there was more available light because the overstory was nonexistent. Here, we assumed light availability was not limiting the growth of sprouts. This is consistent with findings of Berrill and O'Hara (2007) that redwood trees in multiaged stands have higher growth efficiency in the overstory (full sun) than in shade.

Tanoak sprout growth is known to be limited under a conifer canopy (Tappeiner et al. 1990). In our high density treatments (HA and HD), redwood sprouts outgrew tanoak. However we cannot assume the redwood sprouts will continue to grow faster than tanoak while the residual overstory trees add leaf area and cast increasingly more shade until the next scheduled harvest when SDI reaches 1250 (50% of SDI upper limit for redwood; Reineke 1933). Within this DMZ, we expect the redwood sprouts to maintain a modest level of height growth and vigor throughout the cutting cycle (Berrill and O'Hara 2009). In the LD treatments redwood easily outgrew tanoak sprouts. This trend might be sustained throughout the cutting cycle until the next harvest when the stand reaches 750 SDI (30% of SDI upper limit for redwood); as a result, stand density will remain relatively low (Berrill and O'Hara 2009). Maximizing the growth advantage of redwood over tanoak is dependent on finding the optimal density and spatial pattern of overstory trees. In the short term, the LD treatment appeared to best meet this objective for stump sprouts, but this advantage will come at the expense of stand growth for this relatively low density management regime (Berrill and O'Hara 2009; O'Hara 2014).

Our data and models support earlier findings that sprout height increment of the dominant sprout in each clump was more dependent on light with advancing age (Boe 1975; Lindquist 1979; Barrett 1988). We doubt this was a result of changing light environment between measurement years because PACL remained high in these stands (all stands were < 25% relative density for redwood), and because the same results were obtained between redwood and tanoak in high light in GS openings. However, we recommend future studies assess understory light repeatedly to measure and model changes. In comparison to redwood, tanoak sprout growth became much more dependent on light in the third year. Redwood sprouts already exhibited dependence on light in year two, suggesting that the transition from using stored energy to producing photosynthates may have occurred earlier in redwood than tanoak. Ahrens and Newton (2008) reported that this transition occurred between the third and fourth growing season in tanoak re-sprouting after clearcutting and broadcast burning in southwest Oregon. Carbohydrate reserves are known to begin deteriorating immediately after cutting, and over time carbohydrates supplied by the roots of the parent tree begin to be replaced by those supplied by the sprout's growing photosynthetic system (Wiant and Powers 1967). Therefore the growth of new sprouts may be affected by carbohydrate reserves, but subsequent growth becomes progressively more of a function of light availability. It follows that growth would decline each year due to the declining energy reserves stored in the stump and root system while becoming more dependent on carbon production by the sprout clump itself (Bond and Midgley 2001).

Larger redwood stumps had faster growing sprouts. This is consistent with tanoak and Pacific madrone in SW Oregon and NW California (Harrington et al. 1984, 1992), and

sessile oak which had taller sprouts on larger stumps and in higher light but not hornbeam sprouts whose growth was associated with leaf area index but not stump size in the Czech Republic (Adamec et al. 2017). Redwood sprout growth was less sensitive to parent stump size in the second year than in the third year. Smaller stumps exhibited a decline in sprout height increment in their third year. This suggested that from the second to third year, carbohydrate reserves in these smaller stumps may have become depleted, and these smaller sprouts had to rely more on their photosynthetic system for resources, leading to reduced height increments. Another possibility is that the smaller root systems of these smaller redwood stumps failed to compete for belowground resources such as water which may become limiting throughout the dry summer season in this Mediterranean climate.

Redwood sprouts on large parent stumps maintained rapid height growth. This suggested that at larger stump sizes, more stored carbohydrates and roots were available to support and sustain sprout growth. Wiant and Powers (1967) described a "physiological equilibrium" for redwood stump sprouting where photosynthetic production equals carbohydrate requirements of the above- and belowground components of the sprouting organism. At smaller stump sizes, this "equilibrium" may not be reached quickly because smaller stumps do not provide the requirements for rapid early development of sprout clump leaf area and growth. This may leave sprouts too small to fulfill the necessary requirements via photosynthesis, constraining sprout height increments on small stumps. When stump sizes were larger, we suspected that the point of equilibrium had been surpassed sometime in year two, and the growth of sprouts was no longer limited by stump size and instead limited by light availability and competition for resources with other trees and sprouts (O'Hara et al. 2007). Additional variation in the relationship between PACL and height increment might be explained by factors such as deer browsing, and number of sprouts per clump because more sprouts may generate or need more resources. The decrease in height increment between year two and year three might also be age-related or could be attributed to soil moisture limitations. Leading up to the 2015–2016 growing season, these sites had received less rainfall than over the previous year.

Successful redwood natural regeneration resulting from seed fall is rare (Olson et al. 1990). Planting is a more reliable approach to restoring conifer dominance in areas where conifers have not regenerated naturally (O'Hara et al. 2017). Unfortunately, instances of animal browsing were recorded for most of our planted seedlings which negated most/all height growth and prevented meaningful comparison of height growth between sprouts and seedlings. The browsing damage may have masked another potential impact on growth of planted seedlings: belowground competition from established root systems of residual trees and sprouting conifer and hardwood stumps (Tappeiner et al. 2007). Future studies should consider protecting a subset of seedlings from browsing, to separate this impact on growth from other factors such as above- and belowground resource limitations. Another approach we recommend is trenching to isolate effects of above- and belowground competition in complex mixed multiaged stands (Harrington et al. 2003; Devine and Harrington 2008).

In conclusion, growth of redwood and tanoak stump sprouts exhibited more rapid growth in higher light, and became more affected by understory light availability with advancing age. The relationship between understory light and stand density can be used to make predictions of PACL from basic inventory data. Spatial pattern of retention had no discernible effect on mean PACL throughout our 0.2 ha plots, but the lowest light levels were measured in certain locations within LD and HD treatment plots. Light at the center of GS openings was most homogeneous. The HA treatment appeared to have the most spatially heterogeneous light environment. Across the range of understory light levels measured, redwood stump sprouts originating on larger stumps exhibited faster growth

than sprouts on smaller stumps. Among treatments tested, GS maximized height growth of both redwood and tanoak while LD treatments maximized the difference in height growth between the slower-growing tanoak and the faster-growing redwood sprouts.

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