UNDERSTORY LIGHT, REGENERATION, AND BROWSING EFFECTS IN IRREGULAR STRUCTURES CREATED BY PARTIAL HARVESTING IN COAST REDWOOD STANDS

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ABSTRACT

UNDERSTORY LIGHT, REGENERATION, AND BROWSING EFFECTS IN IRREGULAR STRUCTURES CREATED BY PARTIAL HARVESTING IN COAST REDWOOD STANDS

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Regeneration of commercial species is central to long-term success of multiaged management for wood production. We used a replicated uneven-aged silviculture experiment to study regeneration by stump sprouting (Chapter 1) and planted seedlings (Chapter 2). In Chapter 1, we present relationships between understory light, varying overstory tree retention, and growth of coast redwood (*Sequoia sempervirens*) and tanoak (*Notholithocarpus densiflorus*) stump sprouts initiated by group selection (GS) and single-tree selection harvesting. First, we quantified understory light throughout this 20 ha experiment comparing four different silvicultural treatments repeated at four sites. Then, we related understory light to post-treatment stand density and treatment type (i.e., complete harvest in 1 ha (2.5 acre) GS opening, low density dispersed retention (LD), and either aggregated (HA) or dispersed high-density retention (HD)). Finally, we quantified height increment of stump sprouts in response to understory light, treatment type, and other candidate variables influencing growth of stump sprout regeneration after partial harvesting. Mean and maximum understory light did not differ significantly between high density treatments. However, the HD treatment had lower minimum light

levels when compared to the HA treatment. 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 high density aggregated and dispersed treatments were minimal. In the LD treatments, redwood stump sprouts outperformed tanoak sprouts by the greatest margin. Regeneration of redwood and tanoak was most rapid in high light within GS openings.

In Chapter 2, we studied how incidences of animal browsing or mortality of planted seedlings related to multiaged treatment type, stand, and site variables. Deer browsing of planted seedlings was a pervasive problem. Incidence of browsing differed among seedling species, treatment type, and position on the landscape (elevation or distance to watercourse). Coast Douglas-fir (*Pseudotsuga menziesii* var *menziesii*) seedlings were preferred by browsers over redwood seedlings in this study. The most instances of browsing were recorded in GS treatments, followed by LD, HA, and HD treatments. In treatments with higher densities, browsing was less likely. As distance to watercourse and elevation increased, the probability of browsing diminished for both species.

Like browsing, survival of planted seedlings was largely dependent on their position on the landscape. Seedlings planted on a southwest aspect had the lowest survival rates, while seedlings planted on a northeast aspect had nearly complete survival, regardless of species. Overall, Douglas-fir seedlings had higher mortality rates than redwood. Mortality was highest in GS, followed by HA and HD treatments, and was lowest in LD treatments. Seedling survival exhibited a rise-peak-fall pattern with

increasing stand density. This pattern was the most distinct on southwest facing slopes. In general, dispersed treatments gave better results than aggregated and GS treatments when trying to maximize survival and minimize the occurrence of browsing.

These results inform forest managers implementing a conversion towards multiaged management in coast redwood stands receiving partial harvesting without site preparation or herbicide treatment of re-sprouting hardwoods. Presumably, a reduction in below ground competition from hardwood control would enhance survival of planted seedlings. However, any enhancement of seedling growth and vigor may result in elevated browsing activity. Specific recommendations for management include planting extra seedlings on southern slopes and in stands of lower densities such as group selection openings (in anticipation of elevated mortality), and implementing seedling protection measures (e.g., shelters, repellant, fencing) near watercourses where browsing occurs most often.

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CHAPTER 1

Modeling Understory Light and Stump Sprout Growth in Multiaged Coast Redwood Stands in Mendocino County, CA

INTRODUCTION

Multiaged forest management is becoming a common alternative to even-aged management for meeting multiple objectives in many forest types. Multiaged silviculture can create variable overstory tree arrangements which influence subsequent natural and artificial regeneration (O'Hara 2014). Spatial arrangement of the residual overstory can 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).

Available understory light is known to decline with increasing overstory stand density and vary with spatial arrangement (Palik et al. 1997). For example, when comparing dispersed vs. 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). This suggests that the 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 the influence of a conversion toward a multiaged stand on regeneration of different species may help us maximize benefits or preserve a mixture of species in mixed multiaged stands.

Multiaged silviculture is becoming a more common practice 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 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. In these forests, tanoak competes with and can outgrow redwood, especially within disturbed or harvested areas (Radosevich et al. 1976; Tappeiner et al. 1990, 1992, 2007; Berrill and O'Hara 2014, 2016). Stump sprouts often develop quickly to reoccupy growing space and comprise most of the 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 own 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).

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 can vary greatly over short distances in redwood forests (Berrill and O'Hara 2014, 2015, 2016; Berrill et al. 2017). For example, in stand structures with more available light, redwood sprouts grow rapidly with high survival and can be self-thinning within clumps, but in low light environments low survival and complete sprout clump mortality can occur (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 (GS), high density aggregated (HA), high density dispersed (HD), and low density dispersed (LD). 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 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 related 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 related to:

a. Understory light

b. Spatial pattern of retention

c. Size of parent tree at time of harvest (stump diameter)

MATERIALS AND METHODS

Site Description

Jackson Demonstration State Forest (JDSF) is located within Mendocino County in 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 (Figure 1). The forest extends east across the Coast Range, in the middle of redwood's natural range which extends north to 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 completely or partially cut during the early to mid 1900's. Subsequent harvest entries removed most but not all residual old-growth conifers. Many of the resulting 'second-growth' forests were treated by single-tree selection, along with some group selection, commercial thinning, and occasionally clearcutting, resulting in a mosaic of multiaged stands and some even-aged second and third-growth stands. The various disturbances released tanoak trees, seedlings, and stump sprouts to grow and occupy more growing space, and even dominate in 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*), giant chinquapin *(Chrysolepsis chrysophylla)*, and red alder (*Alnus rubra*).

Soils on the JDSF 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 hot, dry summers, with coastal fog moderating temperatures closer to the coast. Through deposition, coastal fog comprises up to 45% of annual requirements for transpiration of coast redwood trees (Dawson 1998). Precipitation near the coast averages 100 cm per year and 130 cm 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 (Figure 1). Prior to harvesting, four 2 ha silvicultural treatment blocks having similar stand conditions and position on the slope were identified (side-by-side or nearby) within each one of the four different 8 ha replicates, except the Whiskey Springs replicate which had five treatment blocks (Figures 2-5). Within each replicate, four (or five) 2 ha treatment blocks were randomly assigned one of four multiaged silvicultural treatments (Figure 6): low-density dispersed (LD), high-density dispersed (HD), high-density aggregated (HA), and group selection (GS). 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). 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. The residual SDI (metric) of each treatment plot was calculated using the summation method for uneven-aged stands (Shaw 2000) which is as follows:

$$SDI = \sum \left[\frac{D_i}{25}\right]^{1.605}$$

Aggregates (clumps) were created by retaining three to four 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 diameter, SDI 710-1640). Harvesting with a mix of ground-based and cable yarding systems began in autumn 2011 and continued into 2012 at some replicates. There were minor final density adjustments in 2013 at one replicate. Harvesting took place in the dry summer months.

Field Data Collection

Following harvest, slash and advanced regeneration was cut, lopped, and scattered. Well-formed trees were retained as part of the three single-tree selection prescriptions (i.e., HA, HD, LD). After harvest, one 0.2 ha measurement plot (45 × 45 m) was installed within each individual 2 ha treatment block. Residual trees in each plot were measured for diameter at breast height (DBH), height, and live crown base height.

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

Douglas-fir and redwood seedlings (20-35 of each species) were also planted within each plot (Chapter 2). Plot corners were used as survey points to map the location of stump sprouts 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 corners. A stem location map was created for stump sprouts and residual trees using ArcGIS.

Douglas-fir and redwood seedlings were also mapped in each plot for another study (Chapter 2).

GIS Component

In order to derive plot level variables to describe site conditions for each plot, ArcMap 10.1 (ESRI) was used to determine elevation and flow accumulation (upslope area contributing runoff to the plot) from a 10 meter Digital Elevation Model (DEM) (Table 1). A cosine transformation was performed on field-measured aspect (one measurement for each plot) to acquire a transformed aspect variable, ranging from zero for northeast facing aspects (45 degrees) to a maximum of 2 for southwest facing aspects (225 degrees), and values of 1 for northwest and southeast aspects (315 and 135 degrees) (Beers 1966).

One corners' coordinates of each 0.2 ha plot was collected with a Global Positioning System (GPS) unit and converted from degrees and decimal minutes to longitude and latitude in decimal degrees (for use in ArcMap) using Microsoft Excel. Distance and azimuth of each other corner was recorded and mapped from the single corner's coordinates (Figures 2-5). All stump sprouts and residual trees that were measured were mapped for analysis in ArcGIS. Distance and azimuth measured from nearest/most convenient corner to each tree and stump sprout were converted into longitude and latitude for the center of each tree or corresponding pin flag (for sprouts) by modifying equations from an ESRI forum:

Latitude of tree= (Latitude of Plot Corner)+((COS(RADIANS(Azimuth))(Distance to Tree (m)+(Tree DBH(m)/2))*(Degrees of Latitude/(m))* ` *(Eq.1)*

Longitude of tree= (Longitude of Plot Corner)+((SIN(RADIANS(Azimuth))(Distance to Tree (m)+(Tree DBH(m)/2))*(Degrees of Longitude/(m)) (Eq.2)*

Latitude of pinflag= (Latitude of Plot Corner)+((COS(RADIANS(Azimuth))(Distance to pinflag (m)*(Degrees of Latitude/(m))* ` *(Eq.3)*

Longitude of pinflag= (Longitude of Plot Corner)+((SIN(RADIANS(Azimuth))(Distance to pinflag (m)*(Degrees of Longitude/(m)) (Eq.4)*

Hemispherical Photography

Hemispherical photos were taken on each individual plot to quantify understory light above each stump sprout (Figure 7). These photos were taken using a Sigma SD15 camera with a 4.5mm 180° fisheye lens on a tripod. Hemispherical photos were taken at approximately 25% of stump sprouts and 25% of planted seedlings, for a total of 20 photo locations dispersed evenly across each plot.

ANALYSIS

Hemispherical Photography

All hemispherical photos were analyzed in Gap Light Analyzer 2.0 to quantify the amount of understory light (PACL) in a growing season (March 15th to September 15th, Bawcom et al. 1961) reaching each stump sprout and seedling. After photos were analyzed to obtain 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 was 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. In this process, interpolated values were attached to all stump sprout and seedling points and imported into Excel. For the subset of sampled point locations where photos were actually taken, this process replaced actual values derived from the hemispherical photos with interpolated estimates for those same locations so PACL could be used to create models predicting height increment of individual stump sprouts and seedlings. Linear models and Generalized Linear Mixed Models (GLMM's) were then used in R version 3.2.3 to model PACL as well as second and third year HI for both tanoak and redwood stump sprouts.

Regression Analysis

Several spatial variables were used in our analysis. Most were collected in the field, but some were derived from ArcGIS (Tables 1&2). All data were collected in the field except for distance to road, flow accumulation, elevation, and PACL values (Table 1). Regression analysis was used to examine the relationship between the response variables and multiple candidate explanatory variables. Variables were categorized as plot-level, tree/observation-level, and sprout/seedling-level).

1. Sprout and seedling level: species, height increment (HI), distance to road, elevation, and percent above canopy light (PACL).
2. Tree level: species, DBH, height, and live crown ratio (LCR).
3. Plot level: metric basal area (BA), metric stand density index (SDI), mean height increment (HI), mean PACL, mean stump diameter, mean flow accumulation, aspect, transformed aspect, and slope.

Regression analysis was completed using open-source statistical software package R version 3.2.3. In order to determine the best combination of variables within a model, two methods were used. These methods were Step AIC, and adjusted R^2. The models were then compared in terms of the sum of the absolute value of the residual error, AIC and AICc values. A derived R^2 was used for comparing GLMM's by using the r.squaredGLMM() function within the MuMln package in R. The best model was checked for errors and outliers using residual plots, Normal Q-Q plot 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 predictor variable was needed, and the Durbin-Watson test was used to identify autocorrelations among selected explanatory variables (Anderson 2007; Crawley 2012; Faraway 2016).

Several models were created. The first series of models predicted mean PACL for a given SDI, BA, or multiaged treatment. These models allow managers to use the growth models in this study by first obtaining PACL values from SDI or BA which can easily be collected with variable or fixed radius plots. Models were created predicting mean HI for each species, as well as HI of individual redwood and tanoak sprouts for each year to compare growth results for each species. A square root transformation of HI was done for all models after observing Box-Cox results. For all models, all candidate predictor variables were tested for inclusion in the best fitting linear and generalized linear mixed models. Models were also created for comparison of second and third year growth in redwood sprouts using different variables than the tanoak/redwood comparative models. These height growth models depended on parent stump diameter of sprout clump and PACL or treatment type.

HI:PACL ratio models were created for redwood sprouts to compare year two to year three. These models predicted HI:PACL with stump diameter and/or treatment type. The ratio HI:PACL is defined as height increment in mm for each unit of PACL.

RESULTS

PACL Models

Mean PACL ranged from 53.8 to 97.3% and SDI ranged from 0 to 605 across all plots (Table 2). There were stand structure differences among stands and heterogeneity within these mixed multiaged stands. Slope and aspect also changed from site to site, and although it was not significant in our height increment models, variation within each replicate may have contributed to differences in light environments within and among sites. In Camp Six and Waldo South replicates, the mean PACL in LD treatments was similar to the mean PACL in HA and HD treatments within the same replicate (Table 2). Mean live crown ratio (LCR) varied by as much as 25% among LD treatment plots and the Waldo North LD treatment had only 69 trees per hectare (TPHA). These were taller and larger in diameter than residual trees at other LD treatments. All other LD treatments had at least twice as many TPHA (Table 2).

The HA treatment had the most heterogeneous light environment when compared to the other treatments (Figure 8). Within the images of interpolated PACL for each treatment, the darker spots represent shaded areas in the understory adjacent to one or more points where a hemispherical image was taken and a low value of PACL was derived. Understory light was heterogeneous within all treatment blocks except for the GS (control) treatment, which was a very homogenous light environment (Figures 8&9). In the high density treatments, with density held constant, mean PACL did not change significantly when residual trees were aggregated vs. dispersed (Table 3). The range of light across sites for aggregated vs. dispersed high density treatments was also very similar ranging between 33 and 75% PACL, although HD had a lower minimum PACL (Table 3 and Figure 9). SDI explained variance of mean PACL the best out of the three candidate models, with the lowest AICc and highest R^2 of 0.889. The worst fit of the three models was the treatment model, which had an R^2 of 0.843 (Table 4). Mean PACL declined with increasing SDI and/or BA (Figure 10).

Mean Height Increment Models

Mean HI models were created using linear least squares regression. Two different types of models were created for predicting mean HI of the dominant stump sprout in each clump. The treatment effects models included species and treatment which were both categorical variables, while the PACL effects model included log transformed mean PACL, and species as variables. Models were created specifically for each growth year. It was found there was an interaction between species and treatment as well as between species and mean PACL, which improved the fit of both types of models, particularly in the second year models.

Generally, the mean HI for each species decreased from year two to year three, except for tanoak in GS treatments, which actually increased (Figure 11). Also, from year two to year three, the difference between tanoak and redwood HI decreased in the lower density treatments, where more light was available (LD and GS). The multiaged treatment which maximized HI difference between tanoak and redwood was the LD treatment. There was not a difference in redwood HI between the HD and HA treatments for both years. However, there was a difference in tanoak HI between HA and HD treatments in year three. The treatment effects model was a better fitting model in year two, while the PACL effects model was the better fitting model in year three (Table 5).

Individual Sprout Growth Models

Comparative growth models were made for each species in year two and three to compare the predicted difference in growth of individual sprouts. Generalized linear mixed models with random effects were used to account for the nesting of sprouts within each plot and within each site. The best model used PACL alone as an independent variable. For reasons of comparison, all models used the same predictor of PACL. Using a Box-Cox chart, it was found that a square root transformation of the dependent variable HI was needed. It was also found that a natural logarithmic transformation of PACL gave the best fit.

When looking at R^2 values of the models, it can be observed that in year two there was greater uncertainty associated with the coefficients (standard error) and less variance (R^2) was explained by the models for both species (Table 6 and Figure 12). In year three, more variance was explained by the models for both species, indicating that growth became more dependent on light. The relationship between PACL and HI became more pronounced from year two to year three, and HI was lower as PACL approached lower levels (30%) for both species (Figure 12). Notably, tanoak HI had very little relationship with PACL in year two. However, in year three this changed: the tanoak sprout growth regression had a similar slope to that of the redwood model (Figure 12).

Influence of Stump Size on Redwood Sprout Growth

There were two types of redwood HI models using parent stump diameter developed: treatment models and PACL models. When comparing these redwood models to the comparative models without parent stump diameter as a predictor variable (R^2=0.216 (year two), 0.250 (year three), Table 6), it can be seen that the variance is better explained when parent stump diameter is included in the model (R^2=0.270 (year two), 0.423 (year three), Table 7), especially in year three. In year two, the treatment model was a better fit for predicting redwood HI, indicating that growth was less dependent on PACL and stump size, and more dependent on treatment type (AICc=1766.20). However, this changed in year three, where it was evident that redwood sprout growth became more dependent on stump diameter and understory light than treatment type (AICc=1678.02). Although the PACL models had a lower AICc in year three, the treatment models explained more of the variance in the data with a derived conditional R^2 of 0.470 (Table 7).

Predictions of redwood sprout HI from the PACL models showed that at three levels of stump diameter (5 cm, 50 cm, 150 cm), HI increased as PACL increased (it should be noted that there were stumps measured which were less than 5 cm in diameter).

Height increment was lowest when stump diameter was at the lowest level of 5 cm (Figure 13). The absence of significant differences in regression slope resulted in models predicting that the growth of stump sprouts growing from smaller stumps was relatively more limited by light than the growth of stump sprouts growing from larger stumps. It was found that when PACL was held constant at three levels (33, 66, and 99%), predicted HI increased at a decreasing rate as parent stump diameter increased. When PACL and stump diameter were at their highest, HI was generally the same from year two to year three. However, sprouts on smaller stumps exhibited declining HI from year two to year three (Figure 14 A&B). It was found that in both years, HI increased as stump diameter increased for all treatment types (Figure 14 C&D). In year two, the LD treatment was very close to producing the same HI as the GS treatment. Also, HD and HA treatments shared nearly the same curve. This changed in year three, as HI curves were distinctly different. Also, when comparing year two to year three, lower stump sizes approached an HI of 0 in year 3, whereas in year two smaller stumps maintained a higher minimum HI.

Ratio of Redwood Height Increment to Understory Light

A model predicting the ratio of HI per unit of PACL (HI:PACL) was designed to determine which treatment maximized height growth increment (HI) per unit of understory light (PACL). It was found that the only significant variable that could be used to predict this ratio was either treatment type or parent stump diameter. Like the redwood growth models, it was found that a logarithmic transformation of stump diameter improved the fit of the model. Two separate models were created (and one for each year), one using only stump diameter, and the other using stump diameter and treatment type. Using AICc, the best model was the stump diameter model, which used only parent stump diameter to predict the ratio. However, the treatment models explained more of the variance in HI:PACL (R^2= 0.212 (year 2), 0.332 (year 3), Table 8). HI:PACL from lower to higher stump diameters was found to increase at a decreasing rate (Figure 15). From year two to year three there was an overall decrease in HI:PACL ratio, primarily at smaller stump diameters. Similar results were found with the redwood stump diameter models, where the decrease in HI from year two to year three was more distinct at lower stump diameters.

DISCUSSION

Models that predict understory light and development of regeneration in multiaged stands support forest management decision making in coast redwood stands. Our models predicting mean PACL using stand density allow model users to predict the average amount of understory light available for prescribed post-harvest SDI or BA values. PACL was found to have a negative exponential relationship with stand density, which is consistent with other research (Palik et al. 1997, 2002; O'Hara and Berrill 2010). Average understory light availability was similar between aggregated and dispersed treatments which is 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 an aggregated spatial pattern because these trees rarely had near 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. Another issue we encountered was unexpected inconsistencies in PACL data. The light environment was variable within and among stands. Presumably, differences in stand and tree attributes such as different canopy structure and light interception among species and differences in crown size led to more/less understory light being assessed for any level of SDI. For example, the LD treatment at Camp Six and

Waldo South had similar PACL levels to high density treatments. Some plots had more area with "concave" topography while others were on more "convex" sites upslope from a drainage. Additionally, some LD treatments had fewer residual trees which were taller with much higher average diameter, while other LD treatments had more trees that were shorter with a lower average diameter. It is likely that a combination of several variables caused these unexpected differences in PACL for LD treatments.

HI of the dominant 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 liotungensis*) in China, Keyser and Zarnoch (2014) who studied nine sprouting hardwood species in the Applachian 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 growth at the edge of GS openings. Our models predicted growth rates to be highest within GS openings where there was more available light because the overstory was nonexistent. In these openings, 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 have higher growth efficiency in the full sun than in shade. Tanoak sprout growth is known to be limited under a conifer canopy (Tappeiner et al. 1990). In the high density treatments, redwood sprouts outgrew tanoak. However, we cannot assume the redwood sprouts will continue to grow faster than the tanoak into the future as 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 sprouts 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 residual trees. In the short term, the LD treatment appeared to achieve this objective for stump sprouts (Figure 11), but this advantage comes 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 HI 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 GS openings. However, we recommend future studies assess understory light repeatedly to measure and model changes.

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 sprouting tanoak 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 progressively becomes more of a function of light and other factors defining growing space 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 southwest Oregon and northwest California (Harrington et al. 1984, 1992). This is also consistent with sessile oak (*Quercus petraea*), which had taller sprouts on larger stumps in higher light; but inconsistent with European hornbeam (*Carpinus betulus*) sprouts, whose growth was associated with leaf area index instead of stump size in the Czech Republic (Adamec et al. 2017). Smaller stumps exhibited a decline in sprout HI 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 smaller height increments. Another possibility is that the smaller root systems of these smaller stumps failed to compete for below ground resources (e.g., 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 below ground 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 growing from smaller stumps unable to fulfill the necessary requirements via photosynthesis, constraining sprout HI. 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 HI 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 HI 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.

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 discernable effect on mean PACL throughout our 0.2 ha plots, but the lowest light levels were measured in certain locations within HD and LD treatment plots. Light at the center of GS openings was the most homogenous. 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.

CHAPTER 2

Survival and Browsing of Planted Seedlings in Multiaged Systems

INTRODUCTION

Regeneration of trees is critical to sustainable forest management, but seedling mortality can be a pervasive problem in many forest types due to both biotic and abiotic factors (Paquette et al. 2006). Climate, herbivory, and pathogens can affect the survival of seedlings in many forest types (Comita et al. 2009; Yan et al. 2015; Frei et al. 2018). The interactions among herbivores, competing vegetation, topography, and type of silvicultural treatment are known to affect survival, growth, and future form of planted tree seedlings (Kern et al. 2011; Brousseau 2017). For example, in silvicultural treatments of lower densities or within group selection openings, there is more competition from other vegetation while protection from climatic stress and predation is diminished (Paquette et al. 2006). Early survival and growth of planted seedlings can be enhanced by retaining intermediate density levels (Brandeis et al. 2001; Palik et al. 2003; Dumais et al. 2018).

The rate of seedling and sapling height growth generally increases at a decreasing rate as more light is available (Gratzer et al. 2004; Paquette et al. 2006; Stancioiu and O’Hara 2006). Berrill et al. (2018) reported slightly diminished growth of redwood and Douglas-fir seedlings planted adjacent to sprouting hardwood stumps. Redwood stump sprouts exhibit faster early growth than planted seedlings, so rather than planting seedlings near sprouting stumps, it is common practice to interplant between distant stumps where less competition is expected (Lindquist and Palley 1967). Little is known about how the growth and survival of planted redwood and Douglas-fir seedlings competing with natural regeneration differs in group selection, dispersed, and aggregated retention regimes. For other forest types, the best combination of survival and growth of planted seedlings occurs under a managed uneven-aged overstory where an optimal compromise is reached between shelter, competition, and available resources, such as understory light (Lieffers and Stadt 1994; Lin et al. 2013; Santiago and Dawson 2014; Nuñez and Gouvenain 2015; Walters et al. 2016).

Seedling survival and growth can also be impacted by browsing. Over the past century, fire suppression and decreases in the size and number of timber sales on public lands and other contributing factors have created a decline of browsing habitats in northern coastal forests (Spies et al. 2007, Cook et al. 2016). Because of this, black-tailed deer (*Odocoileus hemionus columbianus*) often rely on recently harvested stands for forage (Geary et al. 2017). Browsing can have a direct effect on seedling survival rates and result in reduced seedling densities (Konig 1976; Healy 1997; Peebles-Spencer and Gorchov 2017). Seedling predation can also affect seedling growth and give less palatable nearby species (e.g., redwood) a competitive advantage (Molyneux and Ralphs 1992; Barbosa et al. 2009; Bee et al. 2009; Herfindal et al. 2015). The new shoots are the most actively growing and nutritious parts of seedlings and are preferentially selected by deer (Bryant and Kuropat 1980; Harper 1989). Continued browsing of this terminal leader can reduce height growth, and cause early mortality (Harper 1977; Gill 1992; Gerber and Schmidt 1996; Cermak 1998; Gill and Beardall 2001). For Douglas-fir, redwood, and other conifer species, the first few years is when seedlings are most exposed to wildlife damage, as they have not yet grown above browsing height. Damage to planted seedlings by herbivory of elk and deer in coastal forests is the most common and widespread form of damage to planted seedlings in the western US (Crouch et al. 1976; Taylor 2013).

Little is known about relationships among browsing of tree seedlings, topography, and disturbances from management activities. Deer can occupy the coastal regions year round, and the greatest impacts by deer herbivory take place in areas where deer are year round residents and can browse in any season (Dasmann 1953; Crouch 1968; Miller 1970). It is also known that deer respond to changes in forest cover (Lawrence 1969; Resler 1972; Hobbs et al. 1996; Dumais et al. 2018). Examining the relationships between multiaged silviculture treatments and browsing of seedlings may allow us to determine which treatments reduce the incidences of browsing on planted seedlings, while enhancing their survival. Successful redwood natural regeneration resulting from seed is rare, and because of this planting is often a more reliable approach to restoring conifer dominance in areas where conifers have not regenerated naturally (Olson et al. 1990; O’Hara et al. 2017).

In this study, we examined the effects of different multiaged treatments on first year survival of planted seedlings at four different sites in Mendocino County, California. We wanted to answer the following questions:

1) How does spatial arrangement and density of the residual overstory affect the survival of planted seedlings?

2) How does the location of planted seedlings on the landscape (aspect, elevation, etc.) influence the survival and herbivory of seedlings?

3) Which treatment results in low browsing occurrence while also providing high seedling survival rates?

To our knowledge, this is the first study to examine survival and browsing of seedlings planted in mixed multiaged coast redwood stands. Results will provide forest managers with useful information for underplanting coast redwood stands.

MATERIALS AND METHODS

Site Description

Jackson Demonstration State Forest (JDSF) is a 20,000 ha forest located on the northern coast of California, near the middle of redwood's natural range (39°21' N 123°36' W, Figure 1). Most of the old-growth redwood forests in this area had been cut over in the 1900's and many of the 'second-growth' forests were harvested using single-tree selection, group selection, commercial thinning, and clearcutting. This resulted in a mix of multiaged stands, and even-aged second-growth and third-growth stands. These disturbances released tanoak to occupy more growing space, and even dominate in some areas. Despite this, redwood is still dominant across the landscape, and commonly associates with Douglas-fir, tanoak, grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), Pacific madrone (*Arbutus menziesii*), giant chinquapin *(Chrysolepsis chrysophylla)*, and red alder (*Alnus rubra*).

On JDSF, the soils are well-drained, loamy moderately deep to deep, and derived from sandstone. Topography varies from steep slopes to valleys with ephemeral or permanent streams. Valley bottoms consist of soils with low to moderate permeability which are gravelly and deep. Elevation varies from 20 m near the coast up to 700 m further inland near the crest of the Coast Range. Precipitation is relatively high in this temperate rainforest, ranging annually from 100 cm near the coast to 130 cm further inland. This Mediterranean climate consists of cool, moist winters and hot, dry summers.

Near the coast, the climate is moderated with coastal fog, which also adds additional moisture by deposition and comprises up to 45% of annual requirements for transpiration of coast redwood trees (Dawson 1998).

Experimental Design

Before harvesting, four 2 ha experimental treatment blocks were laid out side-by-side. Each of these 2 ha treatment blocks were assigned a different multiaged silvicultural treatment, with individual trees marked for cutting prior to harvest (Figure 6). The same treatments were replicated at four sites in JDSF. Partial harvesting using cable yarder or ground-based systems began in autumn 2011 and was completed by autumn 2012 (Chapter 1). Harvesting only took place in the dry summer months to minimize impacts.

The density of different treatment types was held constant among replicate sites (Chapter 1, Table 2). Aggregates or “clumps” were created by leaving three to four residual trees in a clump. Clumps consisted of redwood or a mixture of redwood, Douglas-fir, and sometimes tanoak. In dispersed treatments, aggregates of residual trees were avoided as much as possible to introduce a less “clumpy” structure that was more uniform in spatial pattern. Each treatment had a managed relative density known as a Density Management Zone (DMZ). Prior to harvest, tree size ranged from 41-48 cm quadratic mean diameter and density ranged from 710-1640 SDI. The goal was to retain a species composition of residual trees at about 70-75% redwood, 20-25% Douglas-fir, and 0-5% tanoak consistently among treatments and across all four sites. The residual SDI (metric) of each treatment plot was calculated using the summation method suited to uneven-aged stands with non-normal diameter distributions (Shaw 2000). The goal for stand density after harvesting was 13% relative density post-harvest for low density treatments, and 21% for high density treatments. The expectation is to return to 30% relative density for low density and 50% for high density treatments before the next harvest entry (Chapter 1).

Field Data Collection

Following harvest, advanced regeneration and logging slash was lopped and scattered (Chapter 1). A 0.2 ha measurement plot (45 × 45 m) was then installed within each individual 2 ha treatment block after harvest. Trees within each plot were then measured for diameter at breast height (DBH), height, and live crown base height (Chapter 1). Next, 20-35 redwood and 20-35 Douglas-fir seedlings were planted throughout each plot as far away as possible from residual trees and stumps of sprouting species. Seedlings were planted in the winter of 2012/2013 at two sites and the winter of 2013/2014 at the remaining two sites. Upon planting, each seedling’s height was measured, and the placement location of the height pole marked with numbered pin flags (allowing for precise future re-measurements where the base of the height pole would be placed at same location). One year after planting (i.e., in the spring of 2014 or the spring of 2015), seedlings were measured again for height and assessed for browsing as well as survival.

GIS Component

One corner's location from each 0.2 ha plot was collected using a Global Positioning System (GPS) unit and converted from degrees and decimal minutes to longitude and latitude in decimal degrees (for use in ArcMap) using Microsoft Excel (Chapter 1). Distance and azimuth to each of the other three corners was recorded and coordinates were calculated in excel using a formula from an ESRI forum (Chapter 1). Locations of planted seedlings and residual trees were also recorded. This was done by collecting distance and azimuth to the nearest plot corner using a compass, Map Star compass module , impulse laser rangefinder and/or vertex hypsometer (Chapter 1). The distance and azimuth to seedling and tree locations were converted to latitude and longitude. ArcMap was then used to derive plot level and seedling level measurements from a 10 meter DEM. These variables included: distance to road, distance to watercourse, elevation, and flow accumulation. These were calculated individually for each seedling by using the interpolation toolset in ArcMap (Table 9).

ANALYSIS

Regression analysis was used to examine the relationship between the response variables and multiple candidate explanatory variables (Table 9). Variables were categorized as seedling level and plot level.

1. Seedling level: species, survival, browsing, distance to road, distance to watercourse, and elevation.
2. Plot level: metric stand density index (SDI), mean PACL, mean flow accumulation, aspect, transformed aspect, and slope.

Regression analysis was completed using open-source statistical software package R version 3.2.3 (R Core Team 2015). Generalized linear mixed-effects regression accounted for the random effects of each experimental replicate site. In order to determine the best combination of variables within a model, the Step AIC method of model selection was used. Models were then compared using Brier score, AIC and AICc values (Anderson 2007; Crawley 2012; Faraway 2016).

Several models were created. The first series of models predicted survival probability in the first year for planted seedlings for each multiaged treatment. The second set of models predicted survival probability using SDI instead of treatment type (a more universal model for managers). For all models, all candidate predictor variables were tested for inclusion in the best fitting linear and/or generalized linear mixed-effects models (Table 9). Models were also created for predicting browsing probability within the first year after planting seedlings. The first model tested for candidate independent variables including: distance to watercourse, aspect, elevation, and treatment type. The second model tested the same independent variables but substituted SDI for treatment type. PACL was also tested as a predictor of survival and browsing probability but was not found to improve the fit of these models when included.

RESULTS

Survival of Planted Seedlings

The data collected for seedling survival shows that there was a difference in survival (%) among sites and treatments (Figure 16 and Table 10). Underplanting of seedlings in the three single-tree selection treatments (i.e., HA, HD, LD) resulted in significantly higher survival than after planting in GS openings (p= (HA) 0.0028, (HD) 0.0001, (LD) <0.0001). Redwood seedlings had similar survival rates to Douglas-fir at north facing sites (Figure 16). Generally, on the south and west facing sites (Waldo North and Camp Six) there was a lower survival rate than on the north facing sites (Waldo South and Whiskey Springs). The lowest survival rate for redwood was at Waldo North, which had aspects facing almost directly southwest. The Camp Six replicate occupied an exposed ridgetop and had the lowest survival rates for Douglas-fir.

Several models were created to provide options for managers. The simpler "treatment model" had the same Brier score as the better fitting "aspect model" (Table 11), which suggested that the predictive power was about the same as the AIC-derived treatment model. The aspect model predicted that redwood seedlings had higher survival than Douglas-fir seedlings, except on northeast facing slopes where both species had high survival (Figure 17). Another set of models were created substituting SDI for treatment, which all had a poorer fit than the treatment models, except for the "quadratic SDI aspect model" which was the best fitting survival model (Table 12). Although SDI models had a poorer fit than the treatment models, they are more practical for managers because SDI is measurable, whereas treatment type represents a specific set of treatments in this study that may be difficult to replicate. The best fitting "quadratic SDI aspect model" included the coefficient of ln(Asp_trans+1) and two coefficents for the quadratic term $SDI^{0.5}$+ SDI. This model predicted a "rise-peak-fall" relationship between SDI and survival probability. With this model, the highest rates of survival were at densities of 100-300 SDI for both species. When aspect was held constant at 0 (northeast aspect), the model predicted very close to 100% survival for both species regardless of SDI. As aspect approached the southwest (transformed aspect of 20), the probability of survival decreased substantially. This effect was more pronounced at lower residual stand densities (approaching 0), where survival was as low as 40% for Douglas-fir seedlings and 60% for redwood seedlings (Figure 18 A&B). When SDI was held constant at 0, 300, and 600, the model predicted survival declining for both species at lower densities and on more southern or western facing slopes (Figure 18 C&D). Predicted survival was the highest for both species when SDI was at 300, and when seedlings were planted on northeast slopes (transformed aspect of 0). Redwood seedlings were predicted to have 60% survival at 0 SDI and 80% survival when SDI was 600 on southwest aspects. Douglas-fir seedlings were predicted to have less than 40% survival at 0 SDI and 60% survival when SDI was 600 on southwest aspects.

Browsing of Planted Seedlings

Browsing (%) was found to be most common in the GS and LD treatments. There was a difference in browsing occurrence among treatments and sites, but more notably, there was a difference between species (Figure 19 and Table 10). Underplanting of seedlings in high density treatments resulted in lower browsing probability than planting in GS openings ($p=$ (HA) 0.0164, (HD) <0.0001, Table 35). The highest browsing rates occurred for Douglas-fir in GS (54.5-75.0%) and LD (52.0-69.6%) treatments, where up to 75% of seedlings were browsed (Table 10). Similarly, redwood seedlings had a higher rate of browsing in the GS treatments than in any other treatment, except at Camp Six. The HD treatments appeared to minimize browsing occurrence in both species, while in the HA treatments on every site except Camp Six, browsing was near double what it was in the dispersed treatment of the same density. This result suggests that browsing rates were affected by spatial pattern of the overstory.

Models were created using elevation, species, treatment type, and distance to watercourse. Distance to watercourse and elevation could not be included in the same model because they were highly correlated. The best browsing model used elevation, treatment type, and species as predictor variables (Table 13). Species was the most significant variable, indicating a greater probability of browsing in Douglas-fir ($p= <0.0001$). Elevation was also highly significant, indicating a greater probability of browsing at lower elevations ($p= <0.0001$). Browsing probability of redwood was predicted to decrease to nearly 0% for all treatments at an elevation of 300 meters.

Browsing probability also decreased significantly for Douglas-fir as elevation increased, decreasing to 20% in the GS treatments at the highest elevations (Figure 20). As distance from a watercourse increased, probability of browsing decreased (Figure 21). This effect was the same for both species and all treatments. Like the other treatment models, browsing was predicted to be most common in GS openings, followed by LD, HA, and HD treatments. The difference between HD and HA treatments was pronounced for Douglas-fir, again indicating seedling browsing was higher in aggregated retention treatments than dispersed retention treatments of the same density.

Like the survival models, browsing models were also made using SDI instead of treatment as predictor variables to create models more practical for managers. The elevation model was the best model using SDI. Although AICc was 8 points higher than the treatment elevation model, the Brier score was similar, indicating it had similar predictive power (Tables 13&14). When SDI was held constant at three levels (0, 300, and 600), browsing was predicted to decrease as elevation increased, and was more likely at lower densities (Figure 22 A&B). When elevation was held constant at three levels (180, 250, and 320 m), browsing decreased as SDI increased. At a lower elevation of 180 meters, probability of browsing for redwood seedlings was the highest, and decreased from 60% at low densities (0 SDI) to 20% at high densities (600 SDI). For Douglas-fir seedlings, browsing probability remained relatively high (70%) as SDI approached 600 at the same elevation (180 m) (Figure 22 C&D). The watercourse models predicting browsing probability dependent on treatment or SDI and distance to watercourse had lower goodness-of-fit but predicted the same trends and have more general applicability than elevation models limited to a specific elevation range (Tables 13&14).

DISCUSSION

Aspect and treatment type were the most influential variables for predicting seedling survival. Aspect and shade are known to affect survival of planted seedlings (Hobbs 1980; Stage and Boyd 1987; Schneider et al. 1998; Germino et al. 2002; Jameson and Robards 2007; Yu et al. 2013). Seedlings planted on a southwest aspect were predicted to have the lowest survival rates, while seedlings planted on northeast aspects were predicted to have nearly complete survival. This is consistent with Yu et al. (2013) who studied several species of a pine-oak mixed forest in the mountains of China, and Germino et al. (2002) who studied Engellman spruce (*Picea engellmanii*) in the Snowy Range of Wyoming. Exposed sites with direct solar radiation can be stressful environments for planted seedlings. By planting seedlings in the shade, they can benefit from reduced evapotranspiration (Seidel 1986; Helgerson 1989). Redwood and Douglas-fir mortality rates were especially high in treatments where there was nearly full sunlight, suggesting that desiccation of the seedlings may have resulted in mortality. Survival model predictions indicated that GS treatments had the lowest survival rates for both species, while LD treatments had the highest rate of survival. Therefore, light shading of seedlings appeared to produce the most desirable results. This is consistent with a known characteristic of first year Douglas-fir seedlings, which survive best under light shade on south facing slopes (Hermann and Lavender 1990). Douglas-fir had lower survival rates than redwood seedlings, and there are many variables which may have contributed to this. Low precipitation, deer browsing, planting effects, and type/quality of seedling stock may all contribute to mortality within the first year after planting.

In many forests, grasses and shrubs quickly invade after a disturbance (Tappeiner 1992; Wagner and Radesovich 1998; Lauer and Glover 1999; Ward 2017), and these plants may interfere with a seedling's ability to survive. Even in multiaged stands, control of competing vegetation may be needed to ensure establishment and survival of first year seedlings as they may not grow as quickly as competing vegetation. In this study, shrubs and weeds were not controlled after partial harvesting, which may have impacted survival rates. Ward et al. (2017) found that removing competing vegetation improved survival rates of seedlings, and Walters et al. (2016) found that when not using weed control or deer fencing, single tree selection treatments had higher seedling survival than other treatment types. This was similar to our findings: the treatments which had the highest survival probability were dispersed single-tree selection treatments.

Deer browsing of planted seedlings was a pervasive problem near watercourses, at lower elevations, and among vigorous seedlings planted in high light environments. This is consistent with Campbell et al. (2006) who found browsing of several tree and shrub species in West Virginia was best predicted using elevation, and Walters et al. (2016) who found browsing of 18 northern hardwood species in Michigan was more common in high light environments where competing vegetation was not removed.

Black-tailed deer are known to migrate seasonally to winter ranges at lower elevations and summer ranges at higher elevations, while some can maintain year-round range at middle to lower elevations (Loft 1984; McCorquodale 1999; Forrester et al. 2015). This is consistent with observed behavior of mule deer (*Odocoileus hemionus*) in southern California (Nicholson et al.1997) and sika deer (*Cervus nippon*) in Japan (Igota et al. 2004). Black-tailed deer are also known to use watercourses for their migration routes. Consequently, it follows that deer would be more likely to browse seedlings at lower elevations and closer to streams. These habits of black-tailed deer were consistent with what was found in our study: there was a higher probability of browsing at lower elevations and closer to watercourses for both redwood and Douglas-fir seedlings.

Douglas-fir seedlings were preferred by browsing animals over redwood seedlings in this study. This was expected, as it is known that Douglas-fir is preferred winter and spring forage for black-tailed deer (Crouch 1966; Bunnell 1990). Redwood contains high levels of an allelochemical called tannin, which interferes with the digestion of deer. This makes plants high in tannin less desirable for foraging (Hanley 1997). Avoidance, or reduced preference for tannins during ungulate browsing has been observed in other research studies with other plant species (Schindler et al. 2003; Chapman et al. 2010; Bergvall and Leimer 2017).

Differences in browsing occurrence were evident among treatments, and GS treatments had the highest rates of browsing in this study. GS cuts and aggregated treatments increase the edge:area ratio. These locations with increased edge:area ratio are favored habitat for deer and can have increased occurrences of deer herbivory (Gill 1992; Kremsater and Bunnell 1999). In future studies, it would be beneficial to have dispersed and aggregated treatments at multiple levels of density with different sizes of aggregates and gaps. To compare browsing results, we only had aggregated treatments with high density, while there were dispersed treatments with both low and high density. It would be interesting to see if less browsing occurred in LD treatments than in an LA treatment where individual aggregates would be far apart, and planted seedlings would have received more light.

Unfortunately, instances of animal browsing were recorded for many of the planted seedlings which negated most/all height growth. The browsing damage may have masked or interacted with another potential impact on growth of planted seedlings: below ground competition from established root systems of residual trees and sprouting conifer and hardwood stumps (Tappeiner et al. 2007). Trenching would be an effective approach to isolate the effects of above and below ground competition in these multiaged stands (Harrington et al. 2003, Devine and Harrington 2008). Browsing may have contributed to the mortality of seedlings in this study as well. Young seedlings are vulnerable to browsing induced mortality, but after a certain age they are more able to withstand the damage from repeated browsing (Gill 1992). Deer fencing is an effective method for improving seedling survival and density by reducing likelihood of browsing occurrence (Ward et al. 2017). Protecting a subset of seedlings from browsing with fencing, shelters, or animal repellant to separate this impact on growth from other factors should be considered in future studies.

This seedling study coincided with a regional drought (2014-2015). The drought may have contributed to desiccation and lower survival rates of planted seedlings, as well as increased competition for soil moisture resulting in reduced above ground and below ground growth. In future studies, it may be useful to consider watering a subset of seedlings to control for the effects of drought stress on planted seedlings within the first year of planting.

California's stringent reforestation requirements motivate many forest managers to rely on nursery seedlings to ensure successful regeneration. Our research informs managers of forests in north coastal California interested in planting after partial harvesting in multiaged coast redwood stands. Another application of this research is restoration of conifer dominance through hardwood control and conifer planting (Berrill and Han 2017; Berrill and Boston 2019; Berrill and Howe 2019). On northeast facing slopes, managers can expect seedlings of both species to have high survival rates regardless of treatment and residual stand density (SDI). On south facing slopes, planting more seedlings to offset losses due to low survival may be the simplest mitigation approach, especially when harvesting using GS treatments. Another consideration is removing competing vegetation to minimize competition, especially in GS treatments on south facing slopes. We did not test this but expect that weed control in the immediate vicinity of planted seedlings would help enhance survival of seedlings planted in hot, dry, high light environments (Walters et al. 2016).

If the primary objective is survival of planted seedlings, a dispersed treatment with residual stand density of 100-300 SDI will provide the best results according to our models. However, it should also be considered that ideal conditions for survival are unlikely to also provide ideal conditions for seedling growth in these LD treatments. Due to rapid overstory tree growth in redwood forests after partial cutting, understory light declines rapidly (Dagley et al. 2018). LD treatments also had higher occurrences of browsing, especially near watercourses. To mitigate browsing impacts near watercourses where more browsing is expected, one could implement HD treatments. However, HD treatments did not have as favorable survival rates as LD treatments according to our models, and these higher mortality rates may have also masked browsing occurrence. When the objective is to improve survival and reduce browsing in areas or treatment types where browsing is more likely (i.e. LD and GS treatments), the survival and browsing models in this study can aid managers in determining how many additional seedlings need to be planted and/or where seedling protection measures should be implemented to maintain full stocking levels and successfully regenerate an understory of redwood and Douglas-fir in mixed multiaged coast redwood stands.

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APPENDIX A

Tables

Table 1. Candidate variables tested for inclusion in all understory light and height increment models.

Variables	Description	Source	Use in Model	Continuous	Categorical
HI (cm)	Height increment of tanoak and/or redwood stump sprouts.	Field	Response	**X**	
SDI	Stand density index	Field	Predictor	**X**	
PACL	Percentage of available above canopy light which is reaching the understory at a given point	Field/ ArcMap Kriging	Predictor and Response	**X**	
Slope	Percent slope within treatment block.	Field	Predictor	**X**	
Asp_trans	A transformed aspect, ranging from 0 for northeast facing aspects to a maximum of 2 for southwest facing aspects	Field	Predictor	**X**	
Road	Distance to a road in meters (used a 10 meter DEM).	ArcMap	Predictor	**X**	
Trtmt	Treatment blocks which include treatments of LD, HA, HD, and GS (control).	Field	Predictor		**X**
flow_accum	A measure of accumulated flow to each cell (used a 10 meter DEM).	ArcMap	Predictor	**X**	
Stump	Stump diameter of cut stumps associated with each measured redwood stump sprout.	Field	Predictor	**X**	
Year_2	Second year mean height increment of tanoak/redwood	Field	Predictor	**X**	
Year_3	Third year mean height increment of each of tanoak/redwood	Field	Predictor	**X**	
Mean.PACL	Average percent above canopy light for a given plot.	Field	Predictor/ Response	**X**	
mean_stump	Mean stump diameter of entire treatment plot.	Field	Predictor	**X**	
Elevation	Elevation in meters (used 10 meter DEM).	ArcMap	Predictor	**X**	

Table 2. Location and attributes of each multiaged silviculture treatment. 'Mean LCR' is mean live crown ratio and 'Trees Per Ha' is a measure of residual stand density in trees per hectare.

Plot No.	Latitude (ºN)	Longitude (ºW)	Slope (%)	Aspect (º)	Elevation (m)	Treatment	Mean PACL (%)	SDI	Mean DBH (cm)	Trees Per Ha	Mean LCR (%)	Mean Stump Diameter (cm)	Stump Diameter Min-Max (cm)
Whiskey Springs													
1	39.3620	123.6719	22	11	199	LD	71.8	306	31.9	177	34.3	34.3	6-56
2A	39.3606	123.6707	19	36	199	HD	58.8	530	41.8	207	36.8	36.8	5-70
2B	39.3607	123.6716	17	49	227	HD	57.0	523	41.3	198	31.3	31.3	5-79
3	39.3605	123.6678	26	357	187	GS	91.5	0	0	0	0	0	1-80
4	39.3605	123.6659	30	51	154	HA	62.2	550	41.2	227	37.3	37.3	1-68
Waldo North													
1	39.3780	123.6322	20	212	206	HA	53.8	605	45.7	197	67.9	67.9	15-120
2	39.3810	123.6350	10	185	195	GS	92.9	0	0	0	0	0	5-97
3	39.3806	123.6362	16	179	195	HD	65.4	530	58.0	128	46.0	46.0	2-80
4	39.3812	123.6390	24	171	194	LD	77.9	313	60.1	69	52.6	52.6	14-136
Waldo South													
1	39.3754	123.6391	22	25	222	HA	58.1	538	48.0	172	50.6	50.6	1-81
2	39.3756	123.6403	23	343	204	HD	55.3	549	58.7	123	61.8	61.8	6-151
3	39.3762	123.6427	24	17	183	LD	59.7	363	39.2	158	63.0	63.0	11-93
4	39.3765	123.6427	28	11	165	GS	93.5	0	0	0	0	0	6-98
Camp Six													
1	39.4143	123.6550	5	273	298	GS	97.3	0	0	0	0	0	2-145
2	39.4149	123.6570	14	256	271	LD	58.9	349	35.5	182	54.9	54.9	1-62
3	39.4158	123.6580	6	280	261	HA	61.0	546	39.3	237	48.8	48.8	8-95
4	39.4163	123.6590	13	290	251	HD	55.7	580	42.8	217	59.9	59.9	5-65

Table 3. Mean stand density index (SDI; metric), and mean percent above canopy light (PACL; %) and range of PACL values at individual points, across all four sites for JDSF in Mendocino County, California, USA (standard errors in parentheses, n=17).

Treatment	**No. plots**	**Mean SDI (SE)**	**Mean PACL (SE)**	**Min.-Max. PACL**
GS	4	0	93.84 (0.17)	80.78-99.16
HA	4	559.75 (3.19)	59.10 (0.37)	37.74-75.15
HD	5	542.40 (0.92)	58.35 (0.30)	33.76-74.33
LD	4	332.75 (1.17)	68.59 (0.62)	38.83-85.39

Table 4. Mean PACL model coefficients (s.e. as percent of coefficient in parentheses) for JDSF in Mendocino County, California, USA (n=17). Mean PACL ($PACL_m$)= the average PACL on a plot. Response=$ln PACL_m$.

	SDI Model	**BA Model**	**Treatment Model**
Model selection method	AICc	AICc	AICc
Intercept	4.54445 (1%)	4.54333 (1%)	4.53478 (1%)
$BA^{0.5}$	—	-0.04657 (9%)	—
$SDI^{0.5}$	-0.02173 (9%)	—	—
Treatment (HA)	—	—	-0.50229 (13%)
Treatment (HD)	—	—	-0.50719 (12%)
Treatment (LD)	—	—	-0.36494 (17%)
Adj. R^2	0.889	0.888	0.843
AICc	-35.167	-34.922	-32.580
AIC	-36.024	-35.779	-23.040
ΔAIC	0.000	0.245	7.530
AIC Weights	0.524	0.464	0.012
Log Likelihood	21.012	20.890	19.247

Table 5. Mean height increment model coefficients (s.e. as percent of coefficient in parentheses) for JDSF in Mendocino County, California, USA (n=17). Response = Mean HI (meters $year^{-1}$).

	Treatment Effects Model	**PACL Effects Model**	**Treatment Effects Model**	**PACL Effects Model**
Increment year	2	3	2	3
Model selection method	AICc	AICc	AICc	AICc
Intercept	0.45630 (16%)	-0.40710 (198%)	0.55070 (13%)	-2.15290 (30%)
Species (SESE)	0.59895 (18%)	-1.62740 (67%)	0.40730 (25%)	-0.41740 (210%)
Treatment (HA)	-0.08417 (125%)	—	-0.25903 (40%)	—
Treatment (HD)	-0.07452 (134%)	—	-0.30212 (33%)	—
Treatment (LD)	-0.07602 (139%)	—	-0.20725 (50%)	—
Species (SESE)x trtmt (HA)	-0.34208 (44%)	—	-0.13910 (106%)	—
Species (SESE)x trtmt (HD)	-0.30165 (47%)	—	-0.07868 (100%)	—
Species (SESE)x trtmt (LD)	-0.02380 (627%)	—	-0.00290 (500%)	—
*ln*Mean.PACL	—	0.19080 (100%)	—	0.59450 (26%)
*ln*Mean.PACLx Species (SESE)	—	0.49210 (53%)	—	0.18820 (111%)
Adjusted R^2	0.7241	0.6963	0.6859	0.7657
AICc	-25.5393	-21.6644	-19.3898	-36.1079
AIC	-29.3990	-23.8073	-25.1498	-38.2507
Log Likelihood	20.9640	16.9037	20.7736	24.1254

Table 6. Height increment (cm) coefficients (s.e. as percent of coefficient in parentheses) for JDSF in Mendocino County, California, USA (SESE (redwood) n=391, NODE (tanoak) n=394). Response = sqrt (HI (cm $year^{-1}$)).

	Stump Diameter PACL Model	**Stump Diameter PACL Model**	**Stump Diameter Treatment Model**	**Stump Diameter Treatment Model**
Increment year	2	3	2	3
Modeling Method	GLMM	GLMM	GLMM	GLMM
Model selection method	AICc	AICc	AICc	AICc
Intercept	-0.82147 (405%)	-4.94026 (65%)	1.10628 (269%)	-8.39132 (27%)
***ln*PACL**	2.29228 (35%)	3.08402 (25%)	1.17428 (60%)	3.34762 (16%)
Marginal R^2	0.049	0.092	0.017	0.164
Conditional R^2	0.216	0.250	0.163	0.221
AICc	1800.14	1778.54	1631.86	1529.90
AIC	1799.93	1772.38	1631.64	1529.69
Log Likelihood	-893.96	-880.19	-809.82	-758.84

Table 7. Redwood sprout height increment-stump diameter model coefficients (s.e. as percent of coefficient in parentheses) for JDSF in Mendocino County, California, USA (n=391). Response = sqrt (HI (cm year^{-1})).

	Stump Diameter PACL Model	Stump Diameter PACL Model	Stump Diameter Treatment Model	Stump Diameter Treatment Model
Increment year	2	3	2	3
Modeling Method	GLMM	GLMM	GLMM	GLMM
Model selection method	AICc	AICc	AICc	AICc
Intercept	-3.79681 (81%)	-9.31648 (29%)	7.66471 (7%)	5.81410 (27%)
***ln*PACL**	2.43752 (30%)	3.25008 (22%)	__	__
***ln*Stump**	0.69910 (16%)	1.08733 (9%)	0.68718 (16%)	1.07109 (10%)
Treatment (HA)	__	__	-2.28549 (25%)	-2.12076 (33%)
Treatment (HD)	__	__	-2.13937 (26%)	-2.59150 (27%)
Treatment (LD)	__	__	-0.45121 (127%)	-1.20127 (59%)
Marginal R^2	0.155	0.340	0.244	0.359
Conditional R^2	0.270	0.423	0.305	0.470
AICc	1769.74	1678.02	1766.20	1685.80
AIC	1769.45	1677.73	1765.73	1685.33
Log Likelihood	-877.73	-831.87	-873.86	-833.66

Table 8. Height Increment:PACL ratio (mm yr^{-1} $PACL^{-1}$) model coefficients (s.e. as percent of coefficient in parentheses) for Jackson Demonstration State Forest in Mendocino County, California, USA (n=391). Response = sqrt (HI:PACL (mm yr^{-1} $PACL^{-1}$)).

	SESE Light Use Efficiency Model	**SESE Light Use Efficiency Model**	**SESE Light Use Efficiency Treatment Model**	**SESE Light Use Efficiency Treatment Model**
Increment year	2	3	2	3
Modeling Method	GLMM	GLMM	GLMM	GLMM
Model selection method	AICc	AICc	AICc	AICc
Intercept	2.49097 (7%)	1.63195 (10%)	2.32845 (10%)	1.62478 (17%)
***ln*Stump**	0.27203 (17%)	0.42741 (10%)	0.27446 (17%)	0.42836 (10%)
Treatment (HA)	—	—	0.00723 (3463%)	0.01980 (1176%)
Treatment (HD)	—	—	0.09998 (249%)	-0.15123 (153%)
Treatment (LD)	—	—	0.52072 (12%)	0.15542 (150%)
Marginal R^2	0.090	0.242	0.125	0.248
Conditional R^2	0.202	0.316	0.212	0.332
AICc	1070.43	975.18	1074.68	983.69
AIC	1070.21	974.96	1074.21	983.21
Log Likelihood	-529.10	-481.48	-528.11	-482.61

Table 9. Candidate variables tested for inclusion in all browsing and survival models.

Variables	**Description**	**Source**	**Use in Model**	**continuous**	**categorical**
survival	Survival of seedlings recorded as 1 for survival and 0 for mortality	Field	Response		**X**
browse	Browsing of seedlings recorded as 1 for browsed and 0 for not browsed	Field	Response		**X**
SDI	Stand density index- a measurement of tree density within a plot.	Field	Predictor	**X**	
Slope	Slope (%) within treatment block one for each treatment at each site	Field	Predictor	**X**	
Asp_trans	A transformed aspect, ranging from 0 for northeast facing aspects to a maximum of 2 for southwest facing aspects, and values of 1 for northwest and southeast aspects	Field	Predictor	**X**	
Road	Distance to road in meters (used a 10 meter DEM).	ArcMap	Predictor	**X**	
planted height	Height of seedlings when planted in centimeters.	Field	Predictor	**X**	
Dist_stream	Distance to nearest watercourse in meters, 10 meter resolution.	ArcMap	Predictor	**X**	
trtmt	Treatment blocks which include treatments of LD, HA, HD, and GS (control).	Field	Predictor		**X**
flow_accum	A measure of accumulated flow to each cell (used a 10 meter DEM).	ArcMap	Predictor	**X**	
Elevation	Elevation in meters (used 10 meter DEM).	ArcMap	Predictor	**X**	

Table 10. Summary data for residual stand and seedlings planted in each treatment plot (n=17 plots). Seedling sample size (n) is during time of planting (i.e., prior to browse/mortality). Elevation and distance to watercourse for each seedling was derived from a DEM in group selection (GS; n=115, n=115), low density dispersed (LD; n=112, n=113), high density dispersed (HD; n=132, 132), and high density aggregated treatments (HA; n=108, 107) for redwood and Douglas-fir seedlings, respectively. Browsing and survival percentage was calculated for every plot and 'Mean' is average of those plots (n).

	Treatment	n	Mean	s.d.	Min.	Max.
Residual tree DBH (cm)	All	17	44.9	8.6	31.9	60.1
Residual tree density (stems ha^{-1})	LD	4	146.5	45.6	69.0	182.0
	HD	5	174.6	40.6	123.0	217.0
	HA	4	208.3	25.6	172.0	237.0
Stand density index (metric)	LD	4	332.8	23.9	306.0	363.0
	HD	5	542.4	20.7	523.0	580.0
	HA	4	559.8	26.5	538.0	605.0
Planted density (seedlings ha^{-1})	All	17	271.1	29.2	232.1	325.9
Elevation of seedling (m)	All	934	236.2	39.4	176.0	326.0
Distance from watercourse (m)	All	934	218.5	70.8	78.0	354.0
Redwood seedlings						
Planted height (cm)	All	467	21.0	5.1	9.0	49.0
Height After 1 year (cm)	All	427	23.9	6.3	4.0	49.0
Not Browsed (cm)	All	383	24.2	6.1	7.0	49.0
Browsed (cm)	All	44	22.0	7.7	4.0	40.0
Browsed (%)	GS	4	25.9	17.7	4.3	53.6
	LD	4	6.9	4.0	0.0	10.0
	HD	5	3.7	4.2	0.0	10.3
	HA	4	8.5	3.0	5.6	13.3
Survival (%)	GS	4	78.7	19.3	48.0	96.7
	LD	4	96.0	6.9	84.0	100.0
	HD	5	97.7	1.5	96.0	100.0
	HA	4	93.6	9.0	78.3	100.0
Douglas-fir seedlings						
Planted height (cm)	All	467	45.0	24.1	15.0	104.0
Height After 1 year (cm)	All	383	42.4	23.9	8.0	103.0
Not Browsed (cm)	All	208	40.7	23.0	8.0	103.0
Browsed (cm)	All	175	44.4	24.8	13.0	93.5
Browsed (%)	GS	4	65.4	7.3	54.5	75.0
	LD	4	60.9	7.0	52.0	69.6
	HD	5	24.7	16.6	3.4	50.0
	HA	4	42.5	11.2	24.1	52.9
Survival (%)	GS	4	68.7	26.7	36.7	96.7
	LD	4	94.2	4.5	88.2	100.0
	HD	5	82.5	17.3	57.1	100.0
	HA	4	82.2	17.3	57.1	100.0

Table 11. Survival treatment model coefficients (s.e. as percent of coefficient in parentheses) for JDSF in Mendocino County, California, USA (SESE (redwood) n=467, PSME (Douglas-fir) n=467). Response = Browsing Probability (0-1).

	Aspect Model	**Treatment Model**
Modeling Method	GLMM	GLMM
Model selection method	AICc	AICc
Intercept	3.47440 (13%)	1.0781 (76%)
Treatment (HA)	1.18220 (26%)	1.2486 (24%)
Treatment (HD)	1.36540 (22%)	1.4063 (21%)
Treatment (LD)	2.36630 (16%)	2.3417 (16%)
Species (SESE)	1.11870 (22%)	1.1221 (22%)
*ln***(Asp_trans+1)**	-1.36930 (12%)	__
Brier Score (MSE)	0.082	0.082
Prediction Error	12.1%	12.1%
AICc	506.81	519.09
AIC	506.70	519.00
Log Likelihood	-250.10	-253.50

Table 12. Survival SDI model coefficients (s.e. as percent of coefficient in parentheses) for JDSF in Mendocino County, California, USA (SESE (redwood) n=467, PSME (Douglas-fir) n=467). Response= Browsing Probability (0-1).

	Quadratic SDI Aspect Model	**SDI Model**	**PACLModel**
Modeling Method	GLMM	GLMM	GLMM
Model selection method	AICc	AICc	AICc
Intercept	3.53313 (43%)	1.34830 (58%)	4.71737 (19%)
Species (SESE)	1.12387 (24%)	1.04710 (22%)	1.04647 (22%)
SDI	-0.01476 (0%)	0.00247 (19%)	__
$SDI^{0.5}$	0.04015 (8%)	__	__
***ln*(Asp_trans+1)**	-1.35206 (165%)	__	-0.03537 (19%)
Brier Score (MSE)	0.080	0.088	0.089
Prediction Error	__	12.1%	26.3%
AICc	502.12	543.48	544.42
AIC	502.00	543.40	544.00
Log Likelihood	-245.00	-267.70	-268.00

Table 13. Browsing model coefficients (s.e. as percent of coefficient in parentheses) for JDSF in Mendocino County, California, USA (SESE (redwood) n=467, PSME (Douglas-fir) n=467). Response = Browsing Probability (0-1).

	Watercourse Model	**Elevation Model**	**Treatment Model**
Modeling Method	GLMM	GLMM	GLMM
Selection method	AICc	AICc	AICc
Intercept	1.53878 (20%)	7.1962 (21%)	0.9433 (22%)
Treatment (HA)	-1.18367 (22%)	-1.4034 (19%)	-1.2606 (21%)
Treatment (HD)	-2.05548 (13%)	-2.2581 (13%)	-2.1691 (13%)
Treatment (LD)	-0.20480 (33%)	-0.8682 (29%)	-0.8733 (28%)
Species (SESE)	-2.14636 (9%)	-2.1952 (29%)	-2.1359 (9%)
SDI	—	—	—
Elevation	—	-0.0264 (23%)	—
Dist_stream$^{0.5}$	-0.00321	—	0.9433 (22%)
Brier Score (MSE)	0.152	0.149	0.321
Prediction Error	22.5%	22.8%	21.9%
AICc	763.01	753.44	767.81
AIC	752.90	753.30	767.70
Log Likelihood	-374.40	-369.70	-377.90

Table 14. SDI Browsing model coefficients (s.e. as percent of coefficient in parentheses) for JDSF in Mendocino County, California, USA (SESE (redwood) n=467, PSME (Douglas-fir) n=467). Response = Browsing Probability (0-1).

	Watercourse Model	Elevation Model	SDI Model
Modeling Method	GLMM	GLMM	GLMM
Model selection method	AICc	AICc	AICc
Intercept	2.80718 (24%)	7.03573 (20%)	0.96135 (20%)
Species (SESE)	-2.16879 (9%)	-1.95506 (9%)	-2.11262 (9%)
SDI	-0.00262 (17%)	-0.00253 (13%)	-0.00306 (14%)
Elevation	—	-0.02838 (18%)	—
Dist_stream$^{0.5}$	-0.00896 (31%)	—	—
Brier Score (MSE)	0.154	0.150	0.155
Prediction Error	27.5%	23.8%	26.3%
Marginal R^2	0.370	0.399	0.321
Conditional R^2	0.416	0.547	0.321
AICc	769.70	761.50	778.21
AIC	769.76	761.40	778.20
Log Likelihood	-379.80	-375.70	-385.10

Figures

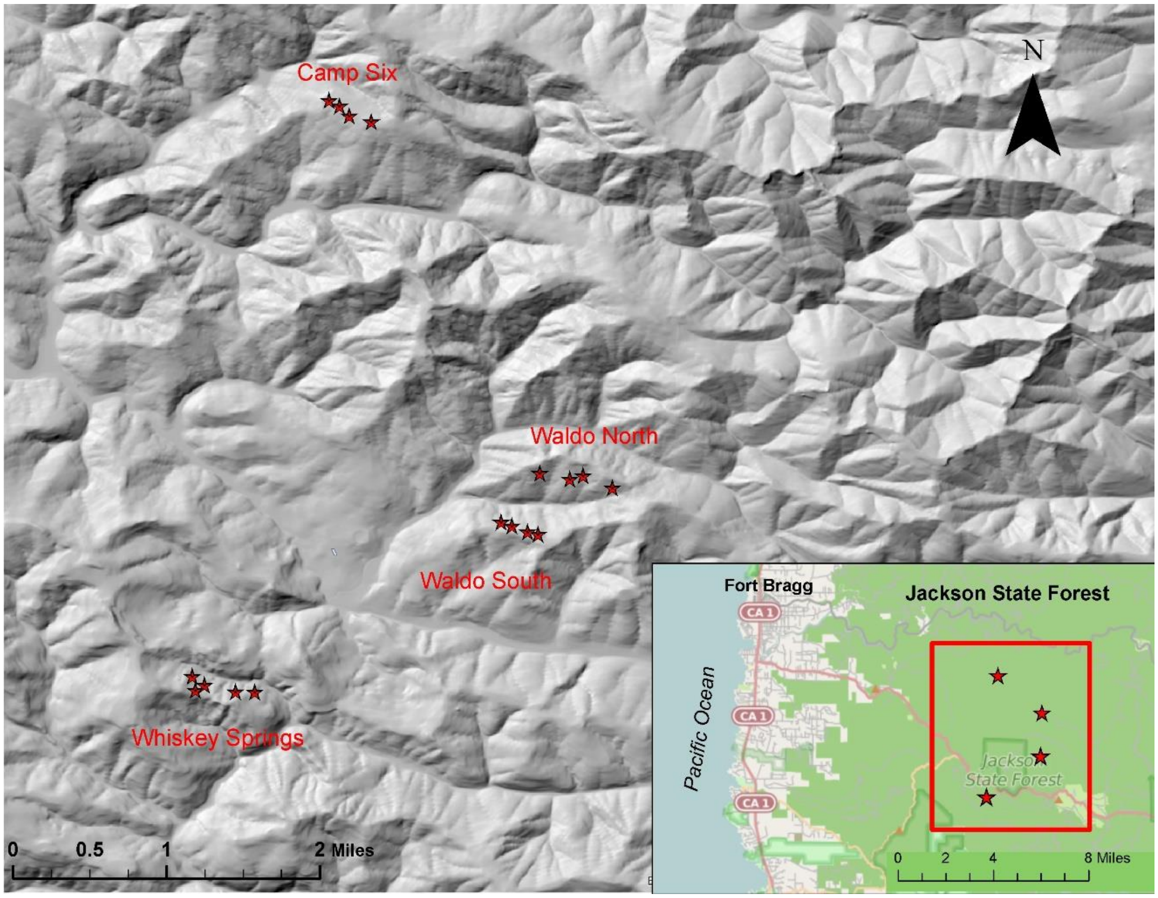

Figure 1. Location of four study sites with treatment blocks in Jackson State Demonstration Forest, Mendocino County, California.

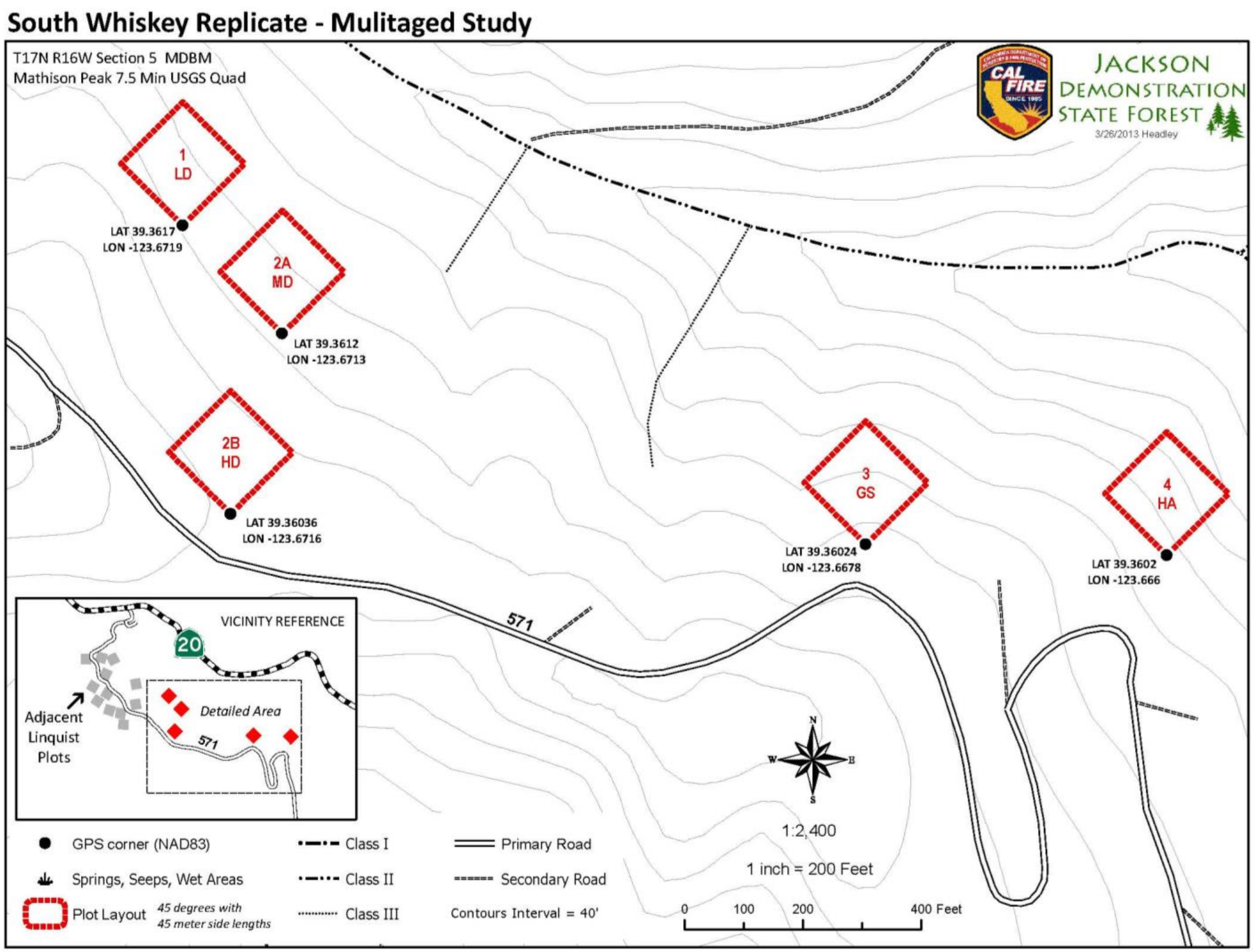

Figure 2. South Whiskey (Whiskey Springs) replicate with five treatment blocks.

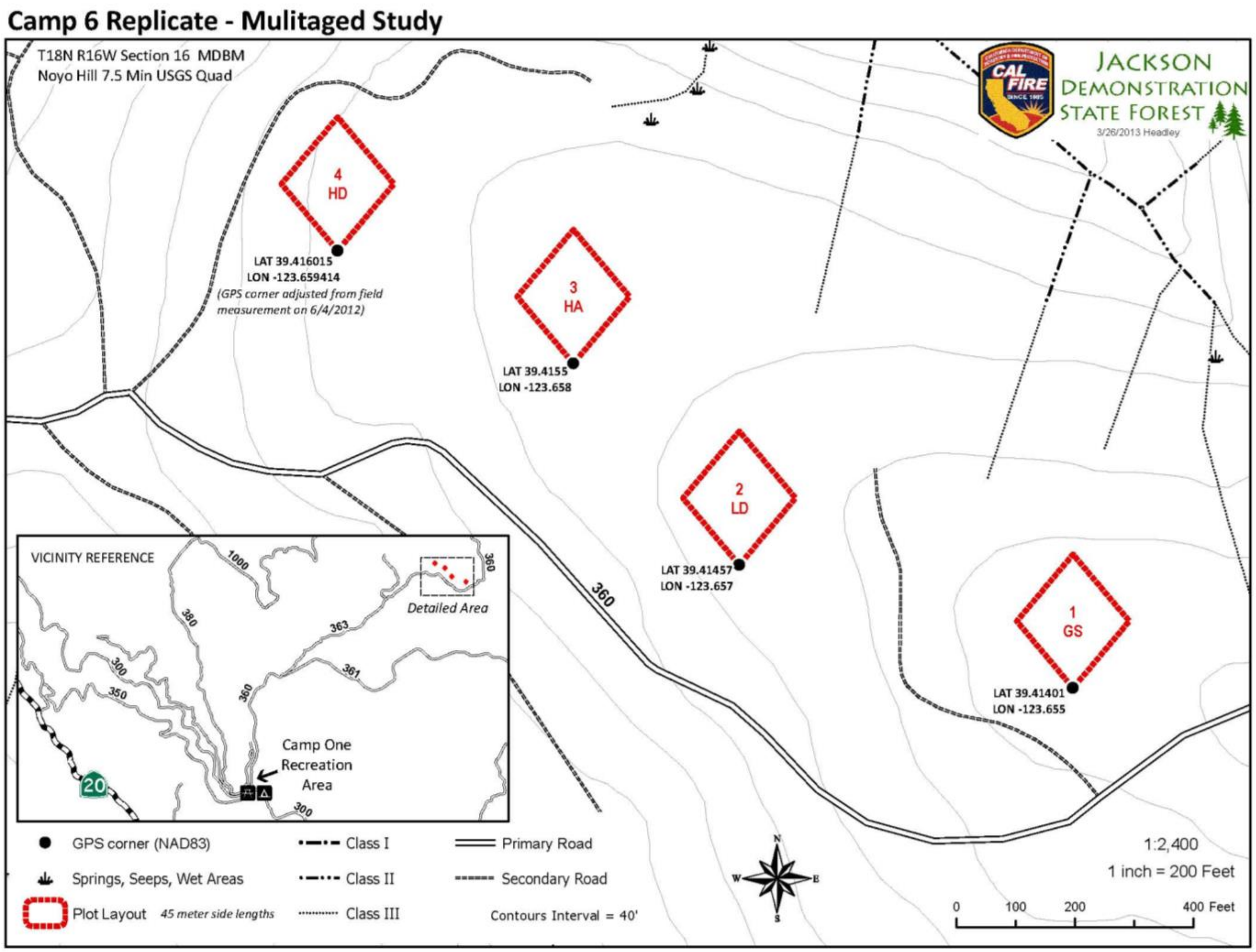

Figure 3. Camp 6 replicate.

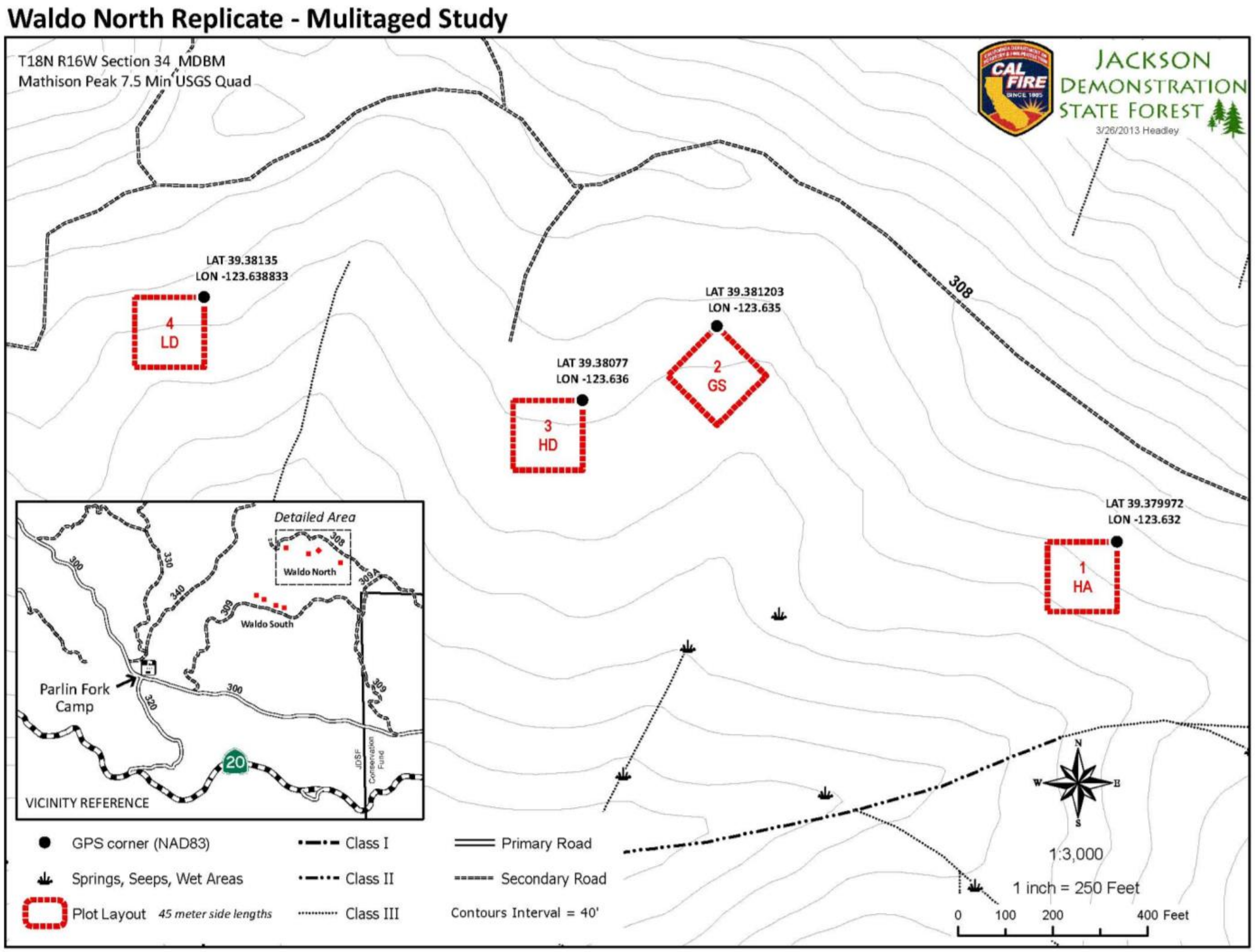

Figure 4. Waldo North replicate.

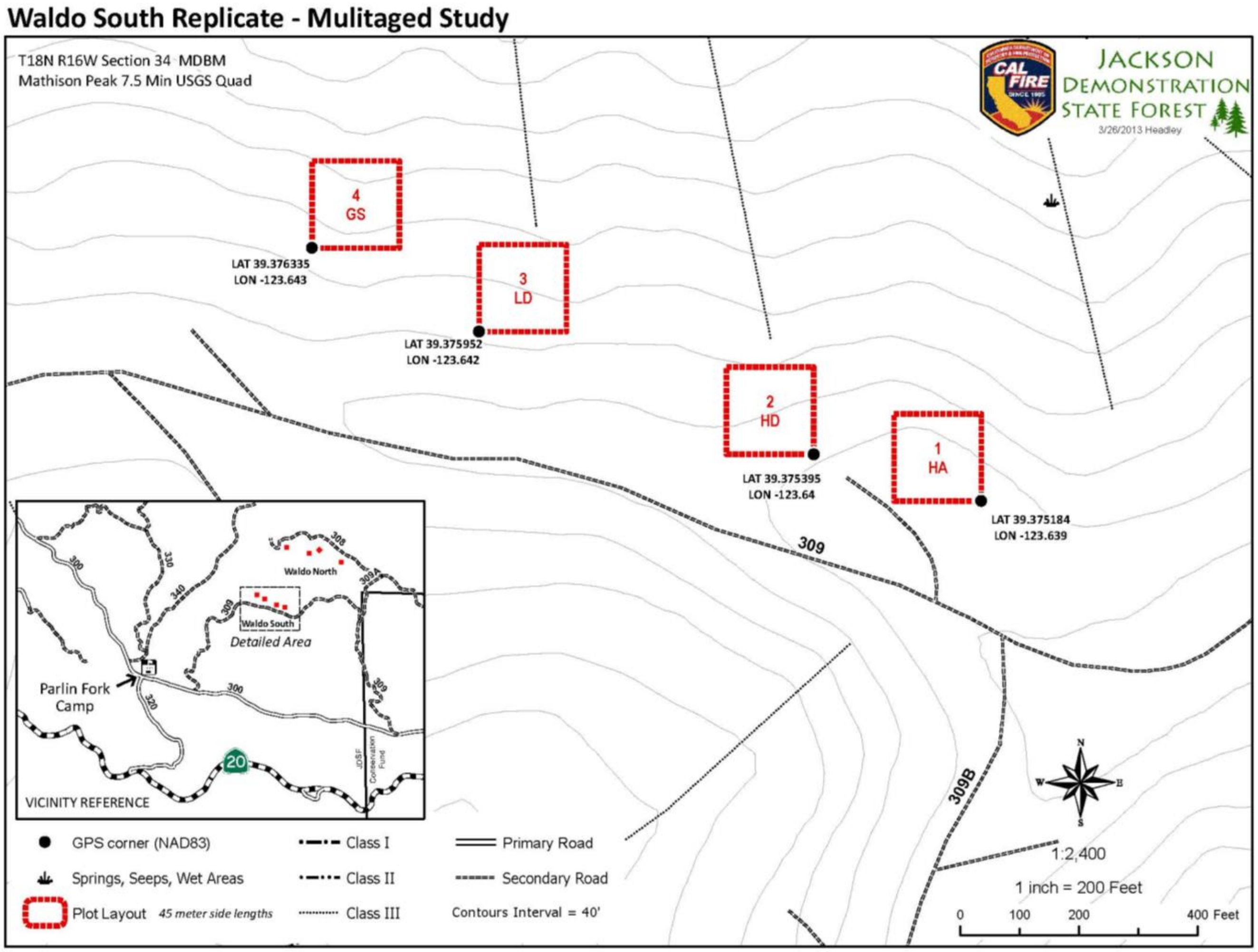

Figure 5. Waldo South replicate.

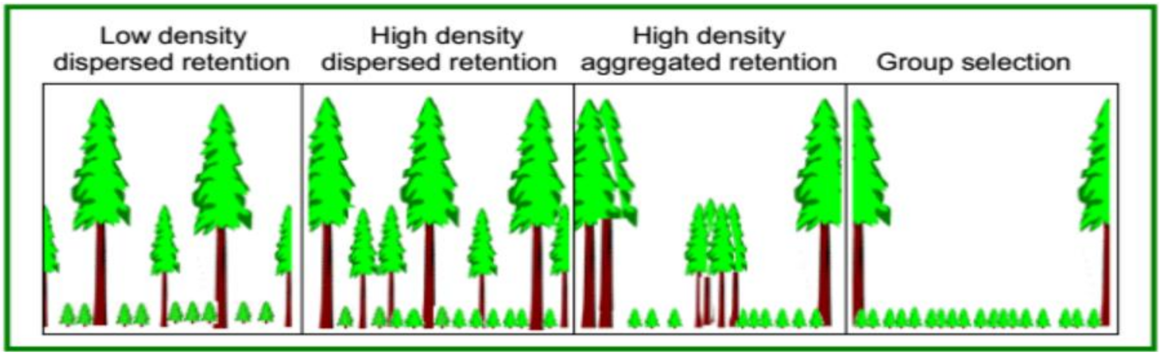

Figure 6. Schematic diagram of one multiaged replicate on the Jackson Demonstration State Forest.

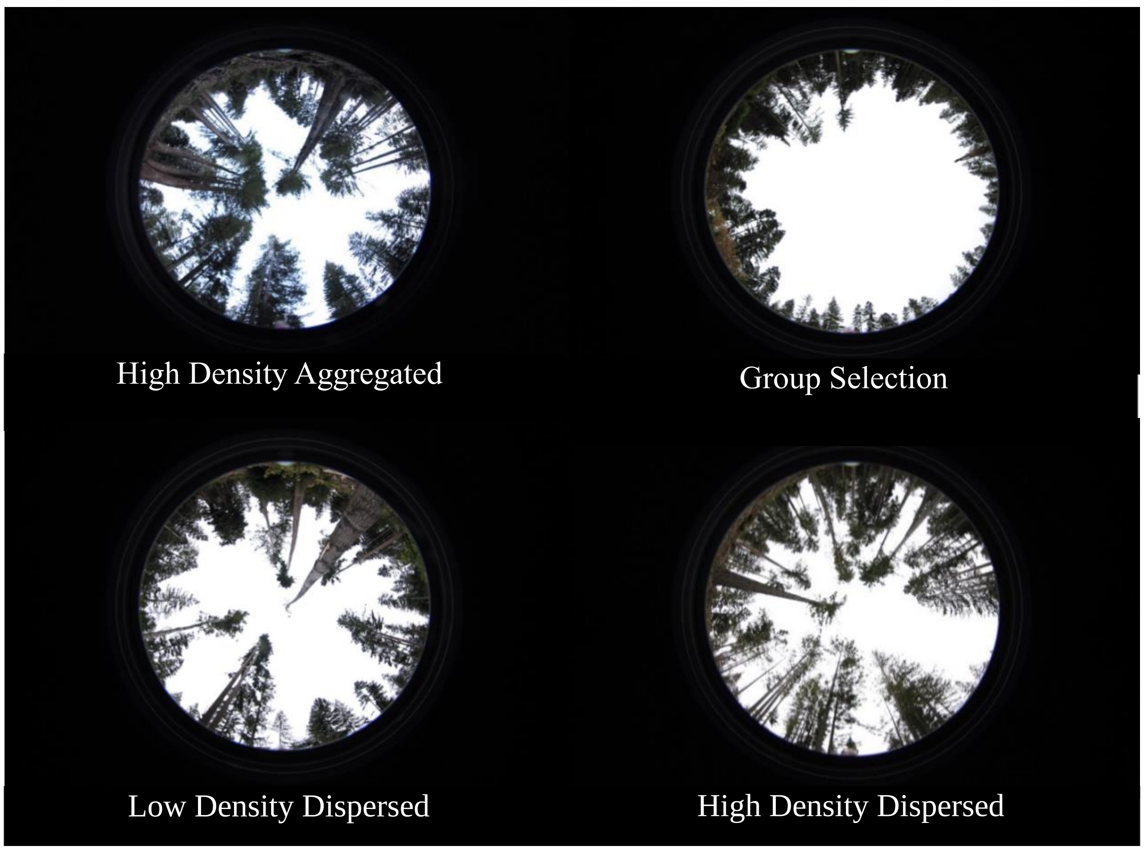

Figure 7. Hemispherical photos taken at each treatment type.

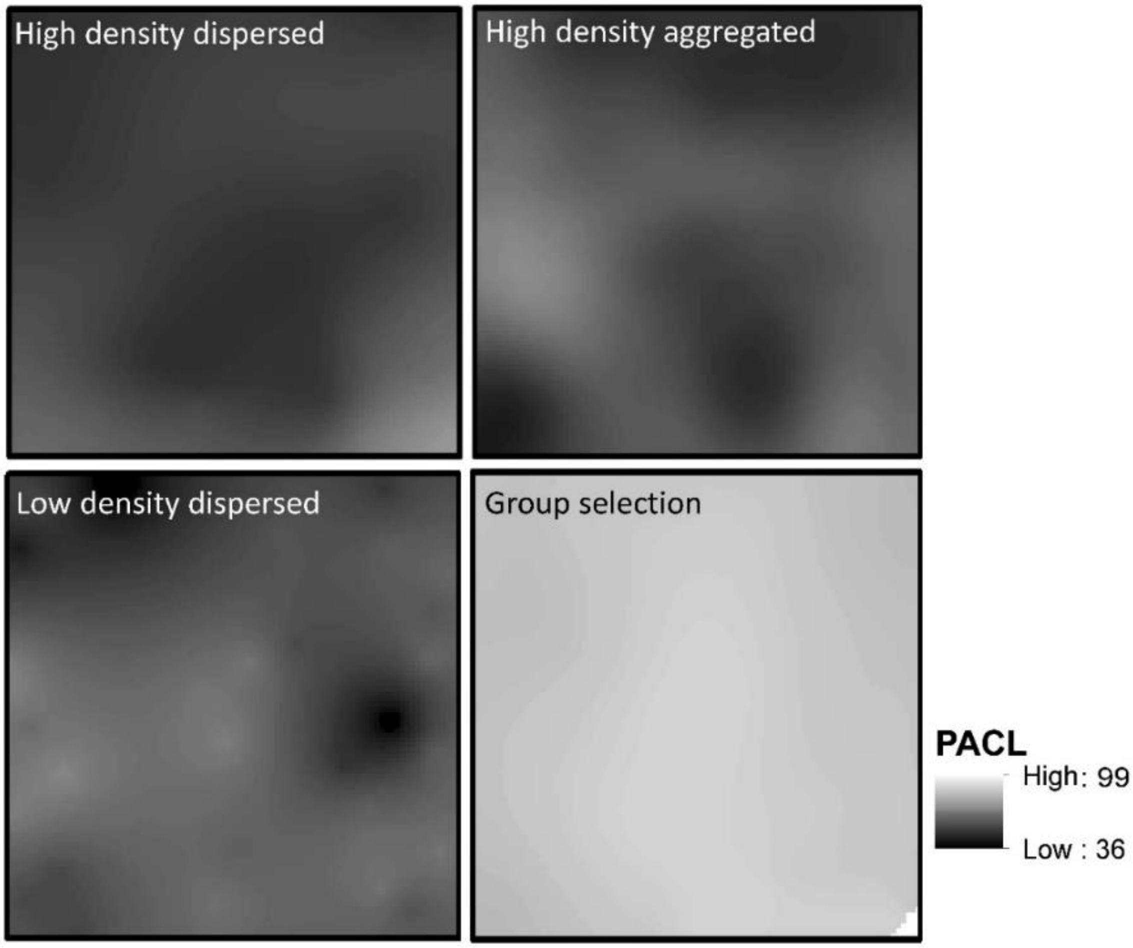

Figure 8. Kriging interpolation of percent above canopy light (PACL) in four treatment blocks at one site.

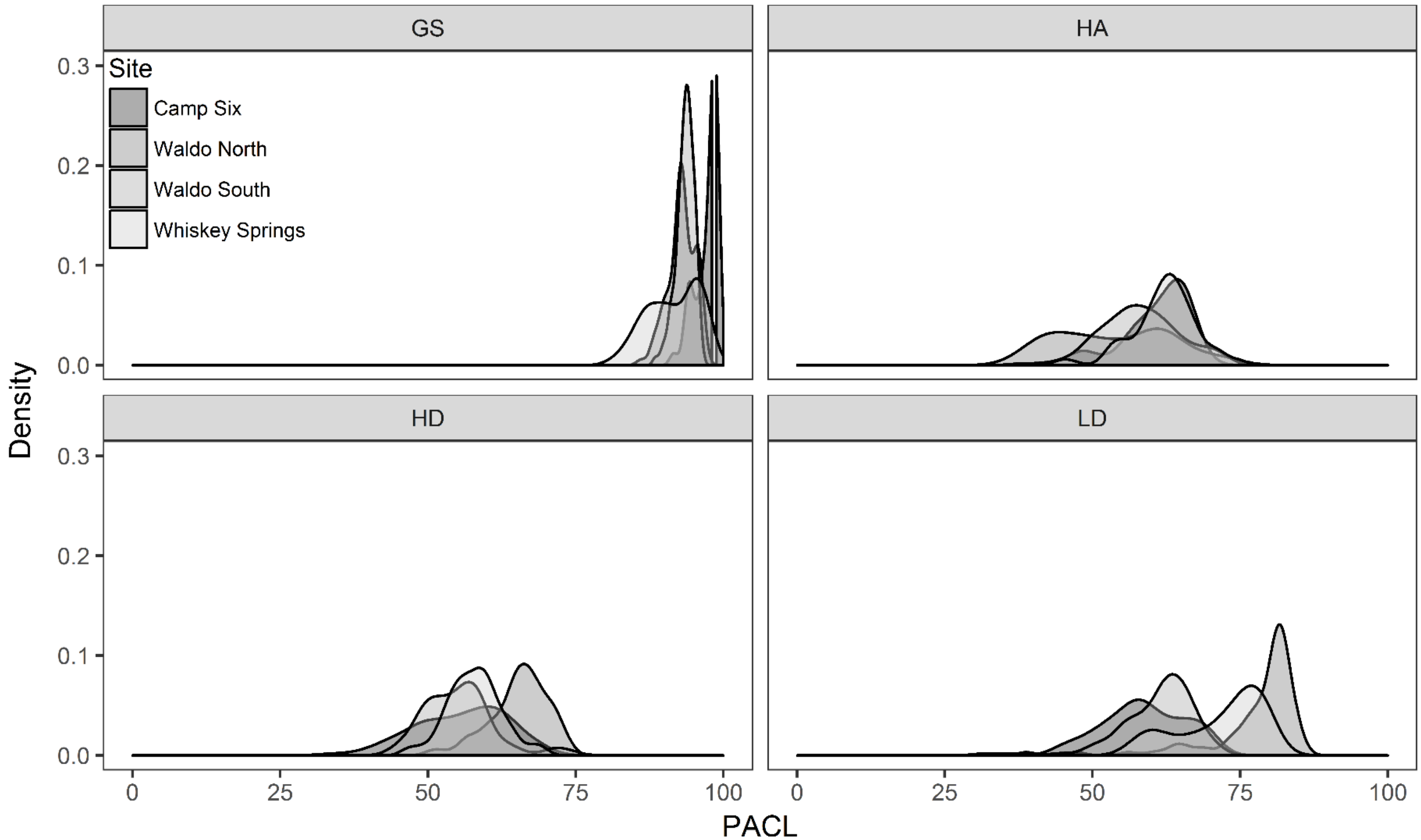

Figure 9. Density plot of understory light (percent above canopy light; PACL) estimates for stump sprouts and planted seedlings in each multiaged treatment (GS opening, n=426, HA, n=416, HD, n=506, LD, n=411) at all four study sites.

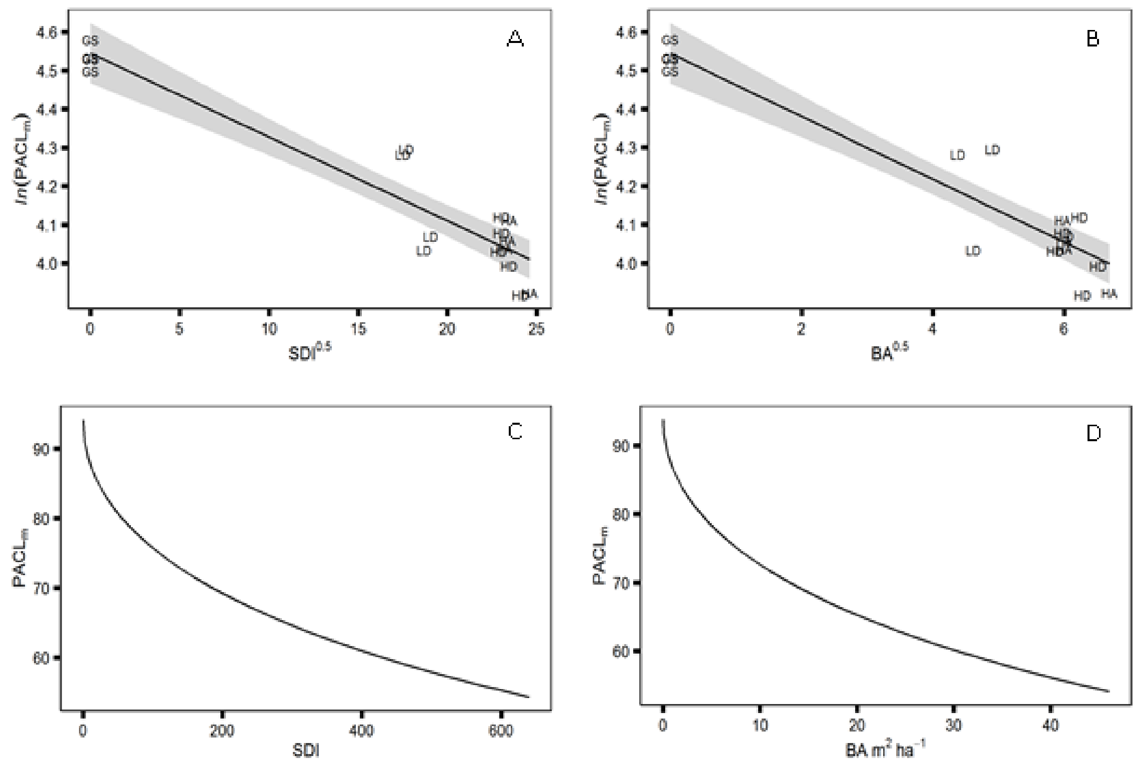

Figure 10. The relationship of SDI (metric) and BA (metric) to mean PACL (%) across all treatments. The area shaded gray represents the 95% confidence interval for each model. Models were as follows: (A) $\log(\text{PACL}) = 4.5445 - 0.02173 * SDI^{0.5}$ (adj. r^2 =0.89, n=17), (B) $\log(\text{PACL}) = 4.54333 - 0.04657 * BA^{0.5}$ (R^2=0.89, n=17). C and D represent relationship of predicted mean PACL (derived from models in figures A and B) values across a range of SDI and BA.

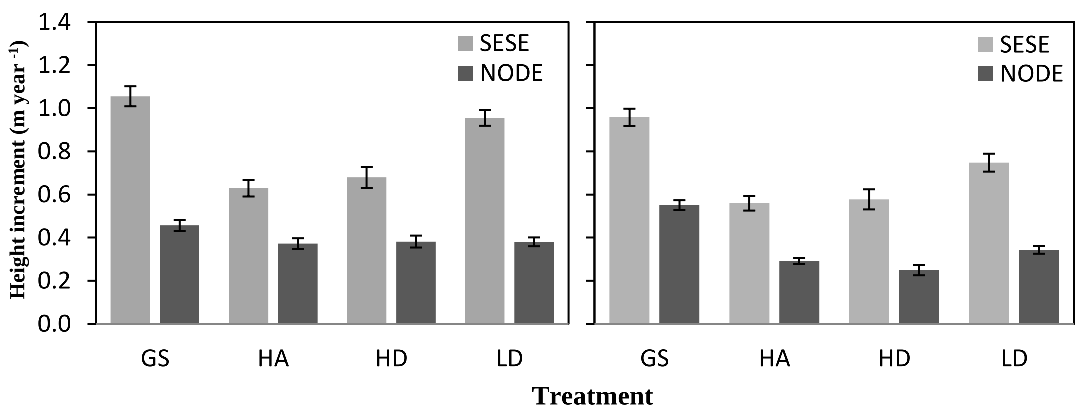

Figure 11. Relationship of treatment type to second year (A) and third year (B) height increment (n=17 plots).

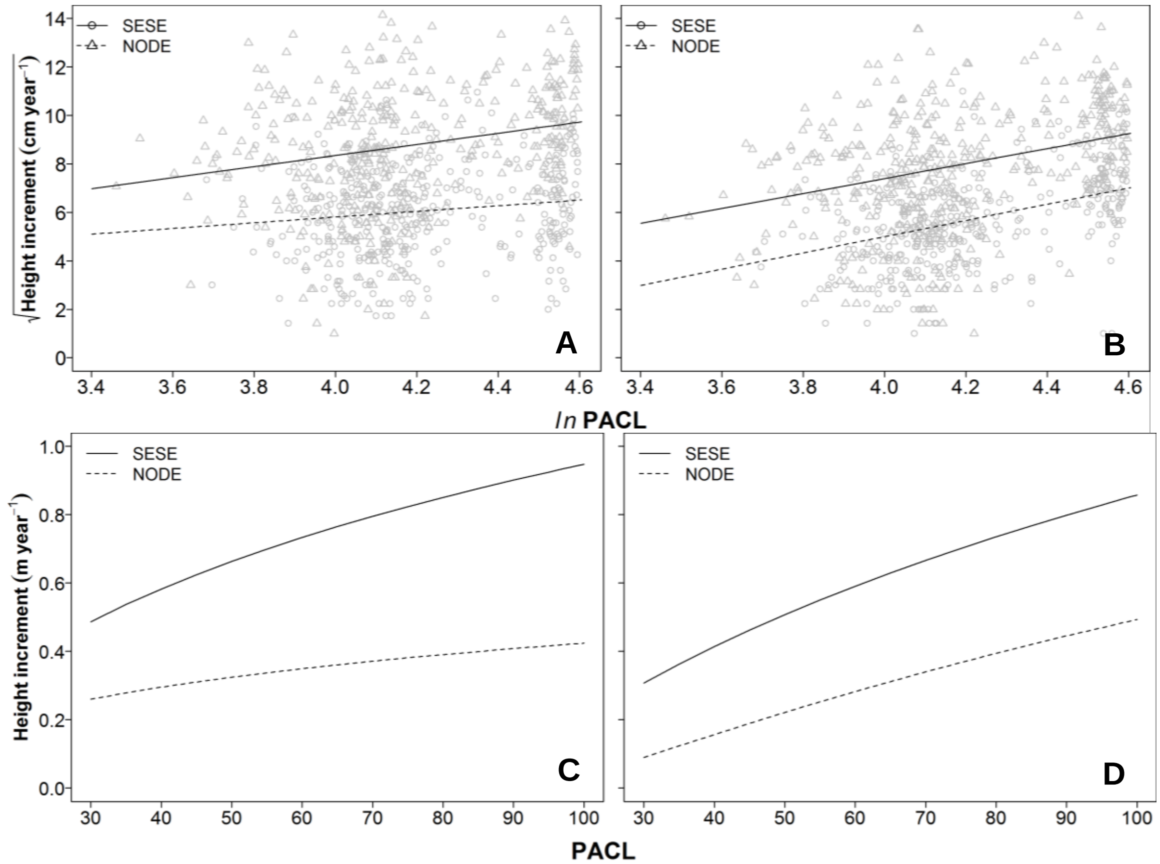

Figure 12. Relationship between understory light (PACL) and height increment for tanoak (NODE, n=394) and redwood (SESE, n=391) in year two (A) and year three (B). Transformed model plotted on transformed data to show variance explained by models. C and D represent relationship of predicted height increment (m) (derived from models in figures A and B) values across a range of PACL values.

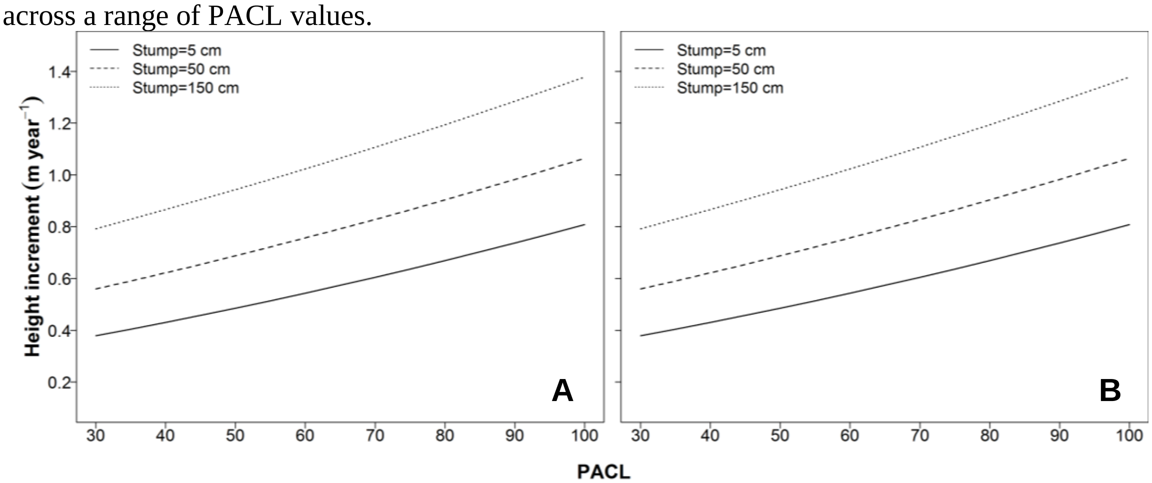

Figure 13. Predicted height increments across a range of PACL values when stump diameter is held constant at three levels in year two (A, n=391) and year three (B, n=391).

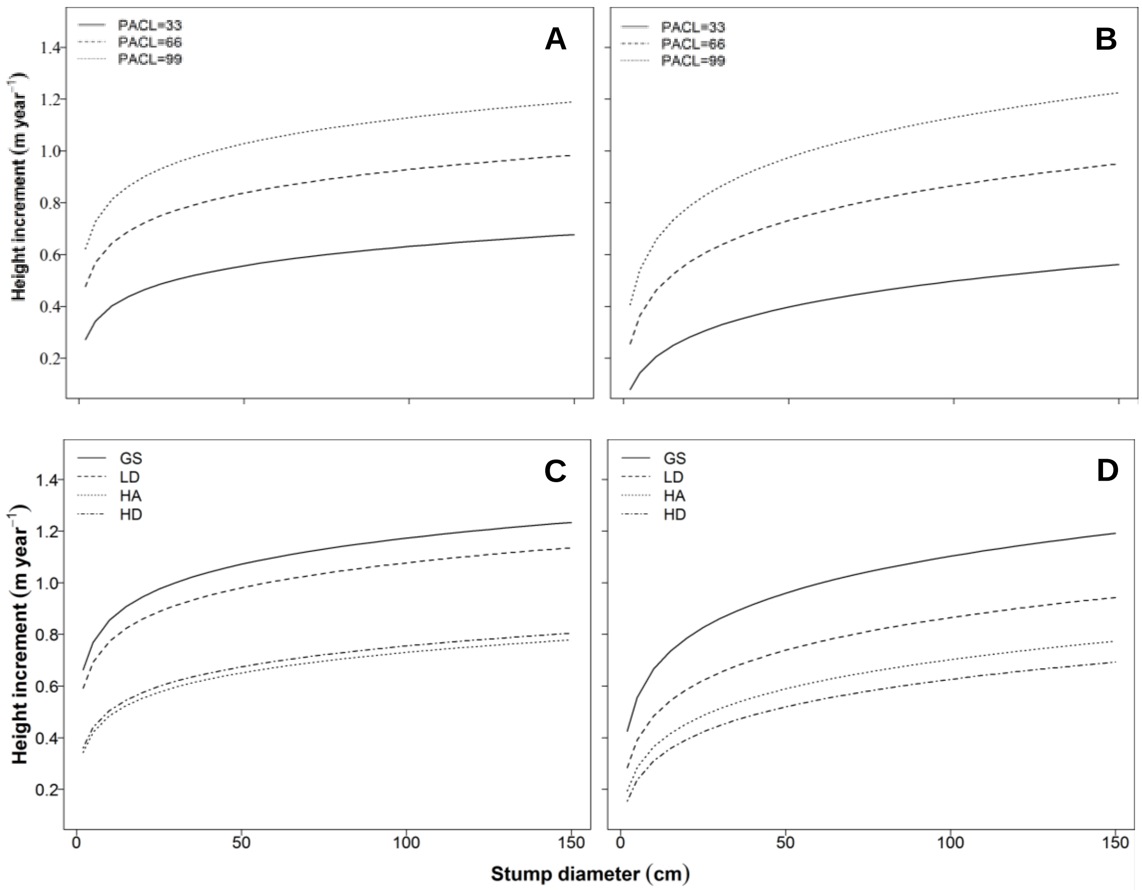

Figure 14. Predicted dominant redwood stump sprout height increments across range of stump diameter with PACL held constant at three levels in year two (A) and year three (B), and predicted height increment across a range of stump diameter values in year two (C) and year three (D) for treatments: GS = group selection; LD = low density dispersed; HD = high density dispersed; HA = high density aggregated.

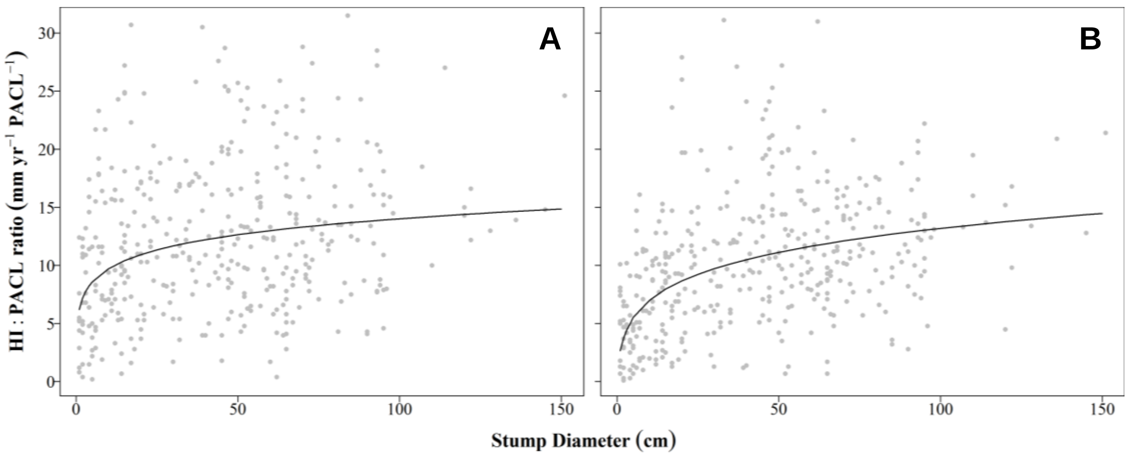

Figure 15. Predicted HI:PACL ratios (mm yr^{-1} $PACL^{-1}$) across a range of parent stump diameters (cm) using light-use efficiency models fitted to actual data for year two (A) and year three (B).

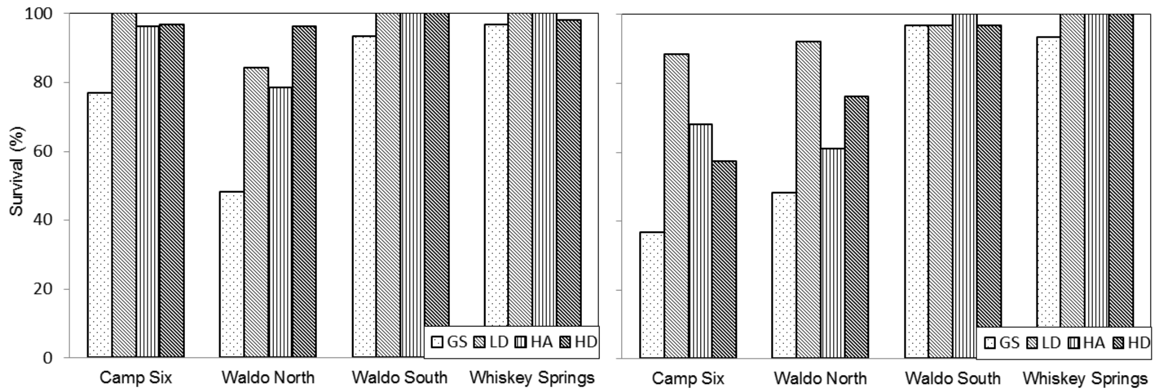

Figure 16. Survival percentage for both species redwood (left, n=467) and Douglas-fir (right, n=467)

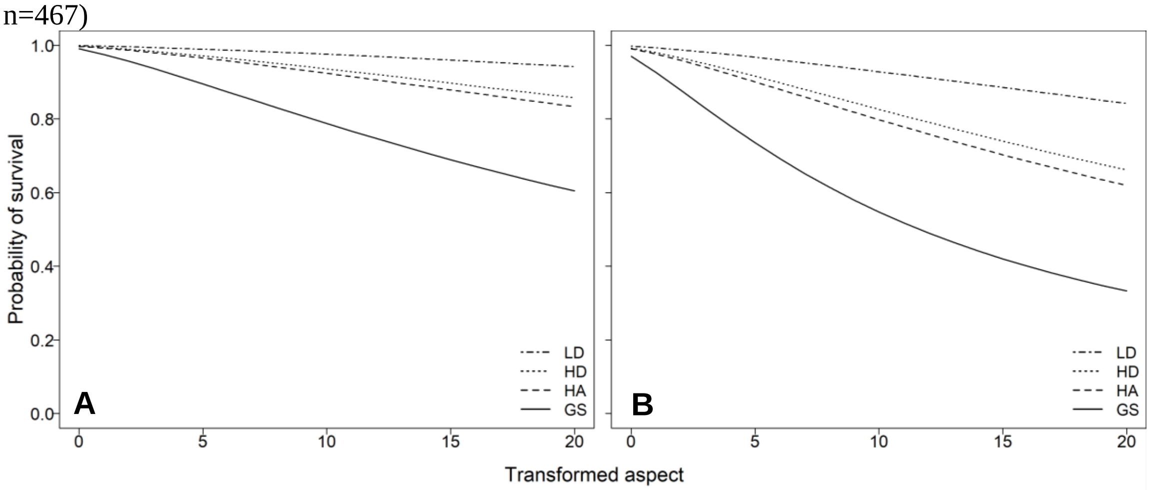

Figure 17. Predicted survival probability for redwood (A) and Douglas-fir (B) seedlings.

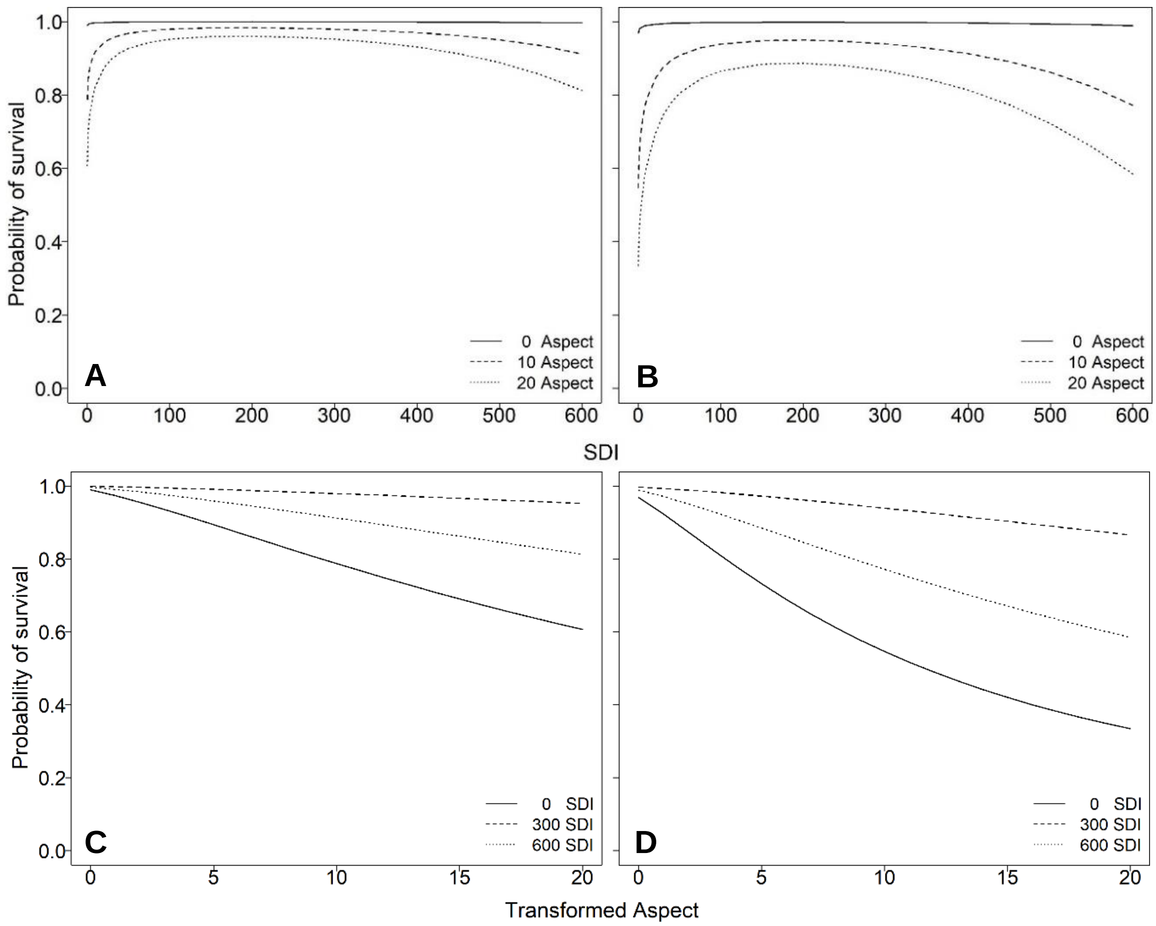

Figure 18. Predicted probability of survival for redwood (A&C) and Douglas-fir (B&D) when Aspect is held constant at three levels (A&B) and when SDI is held constant at three levels (C&D). Model formula is: $survival\ probability = 1/(1 + EXP(-1 *$ (3.42765 - (0.014673 * SDI)+ (0.40158 * $SDI^{0.5}$)+ 1.12387(SESE)-(1.352062*(*ln*(Asp_trans+1)))).

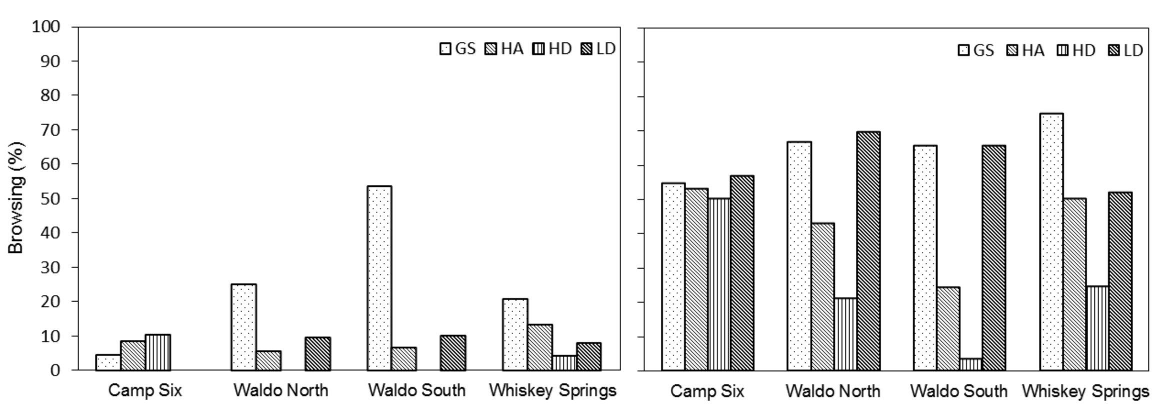

Figure 19. Browsing percentage for both species redwood (left, n=467) and Douglas-fir (right, n=467).

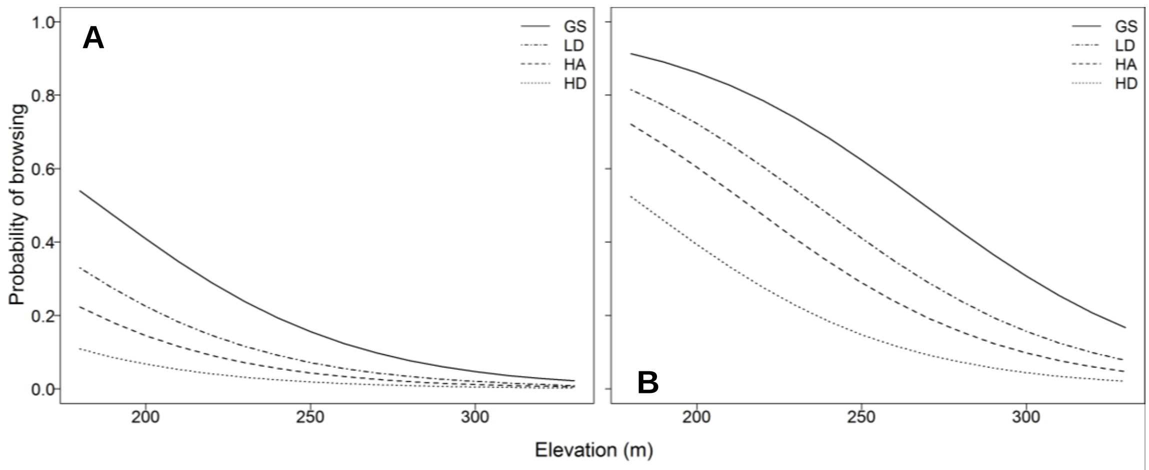

Figure 20. Predicted probability of browsing for redwood (A) and Douglas-fir (B) across a range of elevations.

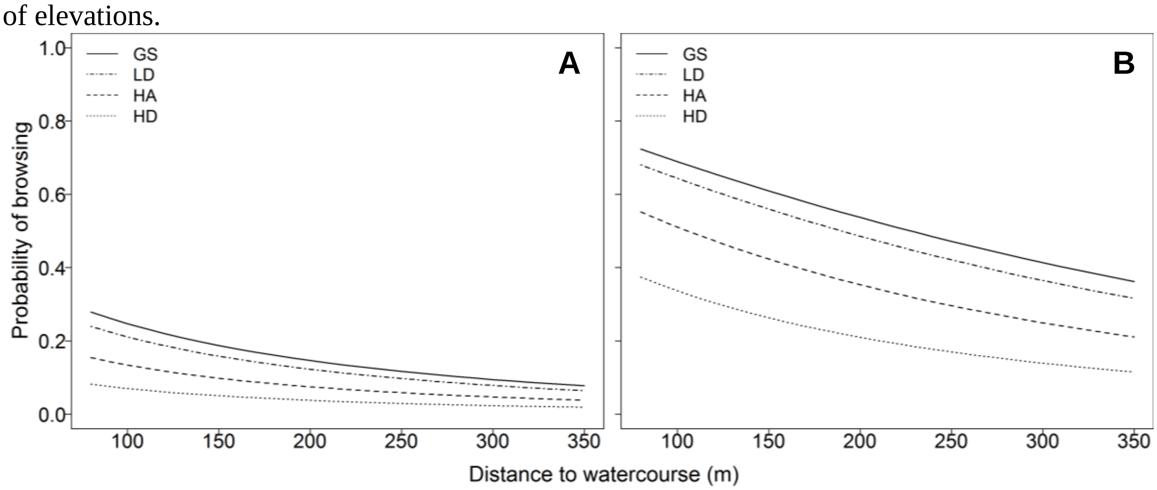

Figure 21. Predicted probability of browsing across a range of distances from a watercourse (m) for (A) redwood and (B) Douglas-fir seedlings.

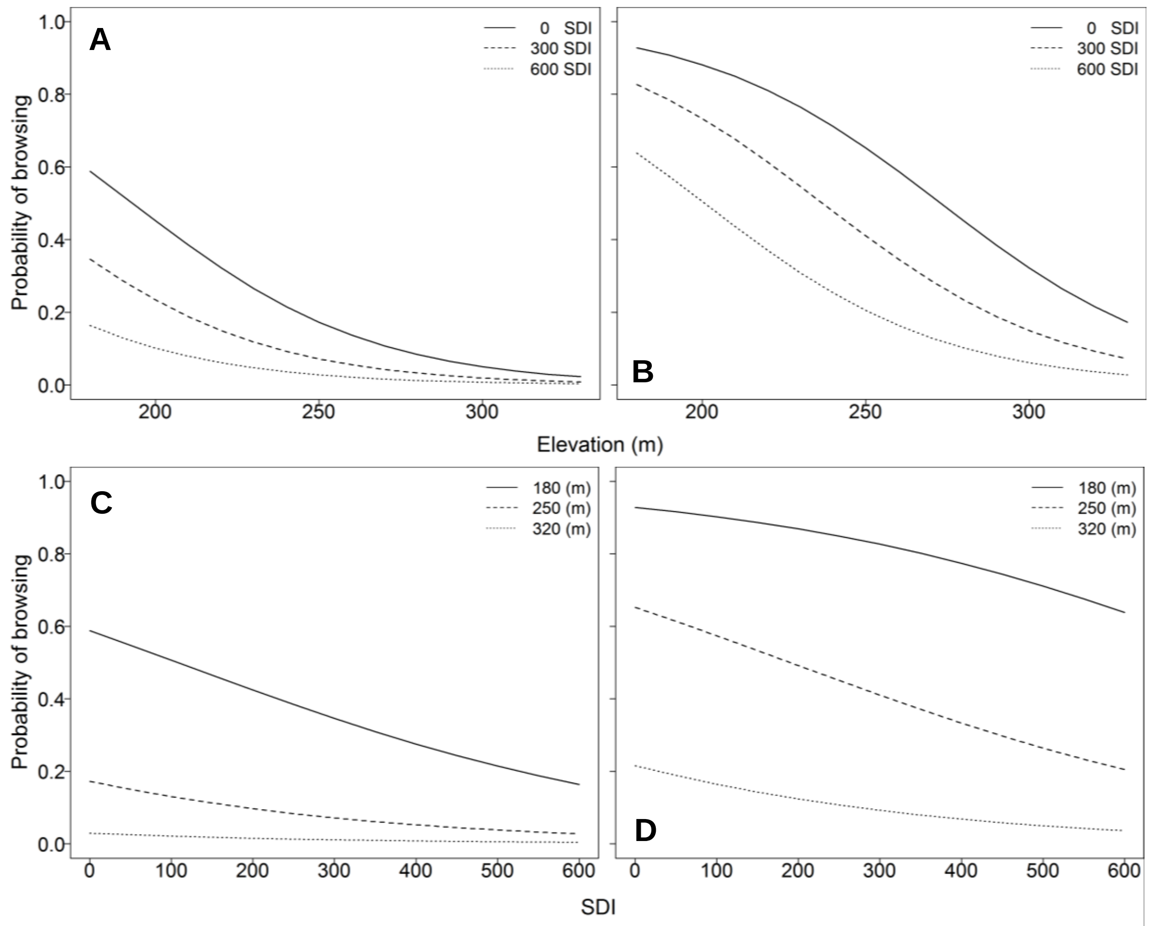

Figure 22. Predicted probability of browsing across a range of elevation for redwood (A) and Douglas-fir (B) when SDI is held constant at three levels. Predicted probability of browsing for redwood (C) and Douglas-fir (D) across a range of SDI when elevation is held constant at three levels.

APPENDIX B

R Model Printout Tables

Table 15. Treatment PACL Model at JDSF Mendocino County, California.

```
lm(formula = log(mean.PACL) ~ trtmt)
```

```
Residuals:
      Min        1Q    Median        3Q       Max 
-0.136665 -0.036531  0.003273  0.050278  0.125126 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  4.53478    0.04459 101.689  < 2e-16 ***
trtmtHA     -0.50229    0.06307  -7.964 2.35e-06 ***
trtmtHD     -0.50719    0.05983  -8.477 1.18e-06 ***
trtmtLD     -0.36494    0.06307  -5.787 6.31e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 

Residual standard error: 0.08919 on 13 degrees of freedom
Multiple R-squared:  0.8724,     Adjusted R-squared:  0.843 
F-statistic: 29.63 on 3 and 13 DF,  p-value: 4.419e-06
```

Table 16. Basal Area PACL Model at JDSF Mendocino County, California.

```
lm(formula = (log(mean.PACL)) * 10 ~ sqrt(BA))
```

```
Residuals:
     Min       1Q   Median       3Q      Max 
-0.13391 -0.03501 -0.01138  0.03590  0.15185 

Coefficients:
             Estimate Std. Error t value Pr(>|t|)    
(Intercept)  4.543332   0.036876   123.2  < 2e-16 ***
sqrt(BA)    -0.081523   0.007217   -11.3 9.82e-09 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 

Residual standard error: 0.07538 on 15 degrees of freedom
Multiple R-squared:  0.8948,     Adjusted R-squared:  0.8878 
F-statistic: 127.6 on 1 and 15 DF,  p-value: 9.824e-09
```

Table 17. Stand Density Index PACL Model at JDSF Mendocino County, California.

```
lm(formula = log(mean.PACL) ~ sqrt(SDI))
```

```
Residuals:
     Min       1Q   Median       3Q      Max 
-0.10540 -0.04619 -0.01249  0.03479  0.13489 

Coefficients:
             Estimate Std. Error t value Pr(>|t|)    
(Intercept)  4.544445   0.036674  123.92  < 2e-16 ***
sqrt(SDI)   -0.021726   0.001908  -11.39 8.81e-09 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 

Residual standard error: 0.07484 on 15 degrees of freedom
Multiple R-squared:  0.8963,     Adjusted R-squared:  0.8894 
F-statistic: 129.7 on 1 and 15 DF,  p-value: 8.812e-09
```

Table 18. Second year PACL Effects Mean Height Increment Model at JDSF Mendocino County, California.

```
lm(formula = year_2 ~ log(mean.PACL) * Species)
```

```
Residuals:
     Min       1Q   Median       3Q      Max 
-0.25197 -0.09024 -0.03588  0.12568  0.28402 

Coefficients:
                           Estimate Std. Error t value Pr(>|t|)  
(Intercept)                 -0.4071     0.8074  -0.504   0.6178  
log(mean.PACL)               0.1908     0.1914   0.997   0.3269  
SpeciesSESE                 -1.6274     1.0876  -1.496   0.1450  
log(mean.PACL):SpeciesSESE   0.4921     0.2587   1.902   0.0668 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 

Residual standard error: 0.1567 on 30 degrees of freedom
Multiple R-squared:  0.7239,     Adjusted R-squared:  0.6963 
F-statistic: 26.22 on 3 and 30 DF,  p-value: 1.589e-08
```

Table 19. Third year PACL Effects Mean Height Increment Model at JDSF Mendocino County, California.

```
lm(formula = year_3 ~ Species * log(mean.PACL))
```

```
Residuals:
     Min       1Q   Median       3Q      Max 
-0.27432 -0.07413 -0.00064  0.05523  0.32585 

Coefficients:
                           Estimate Std. Error t value Pr(>|t|)    
(Intercept)                 -2.1529     0.6529  -3.298  0.00252 ** 
SpeciesSESE                 -0.4174     0.8795  -0.475  0.63854    
log(mean.PACL)               0.5945     0.1548   3.841  0.00059 ***
SpeciesSESE:log(mean.PACL)   0.1882     0.2092   0.900  0.37536    
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 

Residual standard error: 0.1267 on 30 degrees of freedom
Multiple R-squared:  0.787,      Adjusted R-squared:  0.7657 
F-statistic: 36.94 on 3 and 30 DF,p-value: 3.383e-10
```

Table 20. Second year Treatment Effects Mean Height Increment Model at JDSF Mendocino County, California.

```
lm(formula = year_2 ~ Species * trtmt)
```

```
Residuals:
     Min       1Q   Median       3Q      Max 
-0.25945 -0.10132 -0.01940  0.06998  0.32115 

Coefficients:
                    Estimate Std. Error t value Pr(>|t|)    
(Intercept)          0.45630    0.07468   6.110 1.85e-06 ***
SpeciesSESE          0.59895    0.10561   5.671 5.77e-06 ***
trtmtHA             -0.08417    0.10561  -0.797   0.4327    
trtmtHD             -0.07452    0.10019  -0.744   0.4637    
trtmtLD             -0.07602    0.10561  -0.720   0.4780    
SpeciesSESE:trtmtHA -0.34208    0.14936  -2.290   0.0304 *  
SpeciesSESE:trtmtHD -0.30165    0.14170  -2.129   0.0429 *  
SpeciesSESE:trtmtLD -0.02380    0.14936  -0.159   0.8746    
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 

Residual standard error: 0.1494 on 26 degrees of freedom
Multiple R-squared:  0.7826,     Adjusted R-squared:  0.7241 
F-statistic: 13.37 on 7 and 26 DF,  p-value: 3.462e-07
```

Table 21. Third year Treatment Effects Mean Height Increment Model at JDSF Mendocino County, California.

```
lm(formula = year_3 ~ Species * trtmt)
```

```
Residuals:
     Min       1Q   Median       3Q      Max 
-0.32325 -0.07236  0.01157  0.06428  0.36965 

Coefficients:
                    Estimate Std. Error t value Pr(>|t|)    
(Intercept)          0.55070    0.07335   7.508  5.7e-08 ***
SpeciesSESE          0.40730    0.10373   3.926 0.000566 ***
trtmtHA             -0.25903    0.10373  -2.497 0.019186 *  
trtmtHD             -0.30212    0.09841  -3.070 0.004962 ** 
trtmtLD             -0.20725    0.10373  -1.998 0.056287 .  
SpeciesSESE:trtmtHA -0.13910    0.14670  -0.948 0.351763    
SpeciesSESE:trtmtHD -0.07868    0.13917  -0.565 0.576687    
SpeciesSESE:trtmtLD -0.00290    0.14670  -0.020 0.984379    
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 

Residual standard error: 0.1467 on 26 degrees of freedom
Multiple R-squared:  0.7525,     Adjusted R-squared:  0.6859 
F-statistic: 11.29 on 7 and 26 DF,  p-value: 1.709e-06
```

Table 22. Second year Individual SESE Sprout Growth Model at JDSF Mendocino County, California.

```
lm(formula = sqrt_yr2_incr ~ log(PACL),random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC      BIC    logLik
  1799.925 1823.706 -893.9625

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev   Corr
(Intercept)     1.026839 (Intr)
1 | SITE.IDTRUE 1.026839 -0.463
Residual        2.302322

Fixed effects: sqrt_yr2_incr ~ log(PACL)
                 Value Std.Error  DF    t-value p-value
(Intercept) -0.8214713  3.329845 374 -0.2466995  0.8053
log(PACL)    2.2922798  0.793255 374  2.8897145  0.0041
 Correlation:
          (Intr)
log(PACL) -0.996
Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.0646997 -0.5842142  0.0192649  0.6608894  2.6421242

Number of Observations: 391
Number of Groups: 16
> r.squaredGLMM(mod)
       R2m        R2c
0.04955156 0.21689132
> AICc(mod)
[1] 1800.144
```

Table 23. Third year Individual SESE Sprout Growth Model at JDSF Mendocino County, California.

```
lm(formula = sqrt_yr3._incr ~ log(PACL), random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC     BIC    logLik
  1772.378 1796.16 -880.1892

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr
(Intercept)     0.9851702 (Intr)
1 | SITE.IDTRUE 0.9851702 -0.483
Residual        2.2240259

Fixed effects: sqrt_.yr3_incr ~ log(PACL)
                Value Std.Error  DF   t-value p-value
(Intercept) -4.940257  3.189478 374 -1.548923  0.1222
log(PACL)    3.084019  0.759899 374  4.058461  0.0001
 Correlation:
          (Intr)
log(PACL) -0.996

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.77921462 -0.65185053  0.08703011  0.61115421  3.22945530

Number of Observations: 391
Number of Groups: 16
> r.squaredGLMM(mod)
      R2m       R2c
0.1291650 0.2600034
> AICc(mod)
[1] 1778.54
```

Table 24. Second year Individual NODE Sprout Growth Model at JDSF Mendocino County, California.

```
lm(formula = sqrt_yr2_incr ~ log(PACL), random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC      BIC    logLik
  1631.638 1655.451 -809.8192

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr
(Intercept)     0.8167169 (Intr)
1 | SITE.IDTRUE 0.8167169 -0.559
Residual        1.8388876

Fixed effects: sqrt_yr2incr ~ log(PACL)
               Value Std.Error  DF   t-value p-value
(Intercept) 1.106276  2.979398 375 0.3713085  0.7106
log(PACL)   1.174277  0.706103 375 1.6630397  0.0971
 Correlation:
          (Intr)
log(PACL) -0.998

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.35502567 -0.68551079  0.03147966  0.62262379  2.79355884

Number of Observations: 393
Number of Groups: 17
> r.squaredGLMM(mod)
       R2m        R2c
0.01716391 0.16270138
> AICc(mod)
[1] 1631.856
```

Table 25. Third year Individual NODE Sprout Growth Model at JDSF Mendocino County, California.

```
lm(formula = sqrt_.yr3_incr ~ log(PACL), random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC    BIC    logLik
  1529.688 1553.5 -758.8439

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr
(Intercept)     0.6775777 (Intr)
1 | SITE.IDTRUE 0.6779466 -0.786
Residual        1.6339972

Fixed effects: sqrt_.yr3_incr ~ log(PACL)
                Value Std.Error  DF   t-value p-value
(Intercept) -8.391315 2.2346549 375 -3.755083   2e-04
log(PACL)    3.347622 0.5298786 375  6.317716   0e+00
 Correlation:
          (Intr)
log(PACL) -0.998

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-3.72850478 -0.55834838 -0.03438597  0.60886130  3.57021588

Number of Observations: 393
Number of Groups: 17
> r.squaredGLMM(mod)
      R2m       R2c
0.1642634 0.2214872
> AICc(mod)
[1] 1529.905
```

Table 26. Second year Individual SESE Sprout Growth Model with Parent Stump Diameter (cm) at JDSF Mendocino County, California.

```
lme(sqrt_yr2_incr~log(stumps)+log(PACL),random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC      BIC    logLik
  1769.451 1797.178 -877.7257

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr  
(Intercept)     0.9522474 (Intr)
1 | SITE.IDTRUE 0.9522474 -0.573
Residual        2.2141568       

Fixed effects: sqrt_yr2_incr ~ log(stumps) + log(PACL)
                Value Std.Error  DF   t-value p-value
(Intercept) -3.796809 3.0664669 373 -1.238170  0.2164
log(stumps)  0.699103 0.1150139 373  6.078421  0.0000
log(PACL)    2.437522 0.7251249 373  3.361520  0.0009
 Correlation: 
            (Intr) lg(st)
log(stumps) -0.126       
log(PACL)   -0.989 -0.001

Standardized Within-Group Residuals:
         Min           Q1          Med           Q3          Max 
-3.653801552 -0.587784907 -0.001049603  0.670330326  2.773867878 

Number of Observations: 391
Number of Groups: 16 
> AICc(mod)
[1] 1769.744
> r.squaredGLMM(mod)
      R2m       R2c
0.1545277 0.2698006
```

Table 27. Third year Individual SESE Sprout Growth Model with Parent Stump Diameter (cm) at JDSF Mendocino County, California

```
lm(formula = sqrt_.yr3_incr~log(PACL)+sqrt_stump,random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC      BIC    logLik
  1677.731 1705.458 -831.8654

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr
(Intercept)     0.8436544 (Intr)
1 | SITE.IDTRUE 0.8436544 -0.584
Residual        1.9682411

Fixed effects: sqrt_.yr3_incr ~ log(stumps) + log(PACL)
                Value Std.Error  DF   t-value p-value
(Intercept) -9.316471 2.7105944 373 -3.437058   7e-04
log(stumps)  1.087331 0.1021329 373 10.646235   0e+00
log(PACL)    3.250075 0.6410087 373  5.070251   0e+00
 Correlation:
            (Intr) lg(st)
log(stumps) -0.126
log(PACL)   -0.989 -0.002

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.83121969 -0.59162850  0.05441829  0.62075336  3.12564147

Number of Observations: 391
Number of Groups: 16
> AICc(mod)
[1] 1678.023
> r.squaredGLMM(mod)
      R2m       R2c
0.3348542 0.4230792
```

Table 28. Second year Individual SESE Sprout Light-use Efficiency Model (mm yr^{-1}/PACL) at JDSF Mendocino County, California

```
lme(sqrt(mm.PACL_yr_2)~log(stumps),random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC     BIC    logLik
  1070.208 1093.99 -529.1041

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr
(Intercept)     0.3835012 (Intr)
1 | SITE.IDTRUE 0.3835012 -0.612
Residual        0.9027094

Fixed effects: sqrt(mm.PACL_yr_2) ~ log(stumps)
               Value  Std.Error  DF   t-value p-value
(Intercept) 2.490968 0.18510456 374 13.457088       0
log(stumps) 0.272026 0.04670127 374  5.824809       0
 Correlation:
            (Intr)
log(stumps) -0.854

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-3.78504385 -0.59712571 -0.01610868  0.62556096  2.79766363

Number of Observations: 391
Number of Groups: 16
> AICc(mod)
[1] 1070.427
> r.squaredGLMM(mod)
       R2m        R2c
0.08990081 0.20163271
```

Table 29. Third year Individual SESE Sprout Light-use Efficiency Model (mm yr^{-1}/PACL) at JDSF Mendocino County, California

```
lme(sqrt(mm.PACL_yr_3)~log(stumps),random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC     BIC    logLik
  974.9605 998.742 -481.4802

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr
(Intercept)     0.3332231 (Intr)
1 | SITE.IDTRUE 0.3332231 -0.684
Residual        0.8014980

Fixed effects: sqrt(mm.PACL_yr_3) ~ log(stumps)
                Value  Std.Error  DF  t-value p-value
(Intercept) 1.6319457 0.15942520 374 10.23644       0
log(stumps) 0.4274142 0.04109429 374 10.40082       0
 Correlation:
            (Intr)
log(stumps) -0.872

Standardized Within-Group Residuals:
         Min           Q1          Med           Q3          Max
-2.970284326 -0.528557735  0.006960989  0.590257126  3.172682216

Number of Observations: 391
Number of Groups: 16
> AICc(mod)
[1] 975.1792
> r.squaredGLMM(mod)
      R2m       R2c
0.2411945 0.3160278
```

Table 30. Second year Individual SESE Sprout Light-use Efficiency Treatment Model (mm yr^{-1}/PACL) at JDSF Mendocino County, California

```
lme(sqrt(mm.PACL_yr_2)~Treatment+log(stumps),random=~1|SITE.ID|Plot.ID
)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
      AIC      BIC   logLik
  1074.21 1109.813 -528.105

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr
(Intercept)     0.3758028 (Intr)
1 | SITE.IDTRUE 0.3758028 -0.679
Residual        0.9027974

Fixed effects: sqrt(mm.PACL_yr_2) ~ Treatment + log(stumps)
                Value  Std.Error  DF  t-value p-value
(Intercept) 2.3284518 0.24239140 374 9.606165  0.0000
TreatmentHA 0.0072363 0.25055864  12 0.028881  0.9774
TreatmentHD 0.0999821 0.24878453  12 0.401882  0.6948
TreatmentLD 0.5207221 0.25224922  12 2.064316  0.0613
log(stumps) 0.2744559 0.04639979 374 5.915025  0.0000
 Correlation:
            (Intr) TrtmHA TrtmHD TrtmLD
TreatmentHA -0.556
TreatmentHD -0.546  0.505
TreatmentLD -0.541  0.498  0.501
log(stumps) -0.683  0.058  0.039  0.042

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-3.87217808 -0.61387109  0.00734324  0.63547756  2.71370712

Number of Observations: 391
Number of Groups: 16
> r.squaredGLMM(mod)
      R2m       R2c
0.1253538 0.2128262
> AICc(mod)
[1] 1074.682
```

Table 31. Third year Individual SESE Sprout Light-use Efficiency Treatment Model (mm yr^{-1}/PACL) at JDSF Mendocino County, California

```
lme(sqrt(mm.PACL_yr_3)~Treatment+log(stumps),random=~1|SITE.ID|Plot.ID
)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC      BIC    logLik
  983.2132 1018.816 -482.6066

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr
(Intercept)     0.3371391 (Intr)
1 | SITE.IDTRUE 0.3371360 -0.644
Residual        0.8012600

Fixed effects: sqrt(mm.PACL_yr_3) ~ Treatment + log(stumps)
                 Value  Std.Error  DF   t-value p-value
(Intercept)  1.6247780 0.22111028 374  7.348270  0.0000
TreatmentHA  0.0197962 0.23299976  12  0.084962  0.9337
TreatmentHD -0.1512287 0.23152464  12 -0.653186  0.5260
TreatmentLD  0.1554171 0.23443960  12  0.662930  0.5199
log(stumps)  0.4283559 0.04136948 374 10.354393  0.0000
 Correlation:
            (Intr) TrtmHA TrtmHD TrtmLD
TreatmentHA -0.563
TreatmentHD -0.554  0.504
TreatmentLD -0.549  0.498  0.501
log(stumps) -0.668  0.056  0.037  0.039

Standardized Within-Group Residuals:
         Min           Q1          Med           Q3          Max
-3.014767576 -0.550705778  0.002563556  0.591279683  3.130106606

Number of Observations: 391
Number of Groups: 16
> AICc(mod)
[1] 983.6856
> r.squaredGLMM(mod)
      R2m       R2c
0.2478397 0.3321163
```

Table 32. Second year Individual SESE Sprout Growth Treatment/Stump Diameter Model at JDSF Mendocino County, California

```
lme(sqrt_yr2_incr~Treatment+log(stumps),random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC     BIC    logLik
  1765.727 1801.33 -873.8636

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                 StdDev    Corr
(Intercept)      0.9071237 (Intr)
1 | SITE.IDTRUE 0.9071237 -0.738
Residual         2.2166936

Fixed effects: sqrt_yr2_incr ~ Treatment + log(stumps)
                 Value Std.Error  DF   t-value p-value
(Intercept)   7.664712 0.5681669 374 13.490249  0.0000
TreatmentHA -2.285485 0.5668697  12 -4.031764  0.0017
TreatmentHD -2.139374 0.5619621  12 -3.806973  0.0025
TreatmentLD -0.451206 0.5713269  12 -0.789752  0.4450
log(stumps)  0.687175 0.1129117 374  6.085946  0.0000
 Correlation:
            (Intr) TrtmHA TrtmHD TrtmLD
TreatmentHA -0.542
TreatmentHD -0.532  0.506
TreatmentLD -0.526  0.498  0.501
log(stumps) -0.710  0.063  0.042  0.046

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-3.83863358 -0.63929146  0.02539033  0.66492328  2.85977170

Number of Observations: 391
Number of Groups: 16
> r.squaredGLMM(mod)
      R2m       R2c
0.2436423 0.3047371
> AICc(mod)
[1] 1766.2
```

Table 33. Third year Individual SESE Sprout Growth Treatment/Stump Diameter Model at JDSF Mendocino County, California

```
lme(sqrt_.yr3_incr~Treatment+log(stumps),random=~1|SITE.ID|Plot.ID)
```

```
Linear mixed-effects model fit by REML
 Data: NULL
       AIC      BIC    logLik
  1685.326 1720.929 -833.6631

Random effects:
 Formula: ~1 | SITE.ID | Plot.ID
 Structure: General positive-definite, Log-Cholesky parametrization
                StdDev    Corr
(Intercept)     0.8797812 (Intr)
1 | SITE.IDTRUE 0.8797812 -0.47
Residual        1.9771963

Fixed effects: sqrt_.yr3_incr ~ Treatment + log(stumps)
                Value Std.Error  DF   t-value p-value
(Intercept)  5.814098 0.6194552 374  9.385825  0.0000
TreatmentHA -2.120764 0.7031440  12 -3.016116  0.0107
TreatmentHD -2.591496 0.7003474  12 -3.700301  0.0030
TreatmentLD -1.201269 0.7061045  12 -1.701262  0.1146
log(stumps)  1.071087 0.1037120 374 10.327517  0.0000
 Correlation:
            (Intr) TrtmHA TrtmHD TrtmLD
TreatmentHA -0.594
TreatmentHD -0.587  0.503
TreatmentLD -0.583  0.499  0.500
log(stumps) -0.597  0.046  0.030  0.031

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.95557553 -0.61783858  0.06152735  0.59960266  3.15414484

Number of Observations: 391
Number of Groups: 16
> r.squaredGLMM(mod)
      R2m       R2c
0.3588653 0.4701315
> AICc(mod)
[1] 1685.799
```

Table 34. Distance to Watercourse Browsing Model at JDSF Mendocino County, California

```
glmer(browse~trtmt+species+dist_stream+(1|SITE.ID),family=binomial)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: browse ~ trtmt + species + dist_stream + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   762.9    795.8   -374.4    748.9      814

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.8861 -0.5161 -0.2940  0.5645  5.6278

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0        0
Number of obs: 821, groups:  SITE.ID, 4

Fixed effects:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)  1.538782   0.308537   4.987 6.12e-07 ***
trtmtHA     -1.183695   0.262038  -4.517 6.26e-06 ***
trtmtHD     -2.055478   0.280793  -7.320 2.48e-13 ***
trtmtLD     -0.743249   0.249352  -2.981  0.00288 **
speciesSESE -2.146362   0.201832 -10.634  < 2e-16 ***
dist_stream -0.003212   0.001232  -2.606  0.00915 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Correlation of Fixed Effects:
            (Intr) trtmHA trtmHD trtmLD spSESE
trtmtHA     -0.379
trtmtHD     -0.336  0.480
trtmtLD     -0.320  0.525  0.509
speciesSESE -0.374  0.185  0.229  0.159
dist_stream -0.752 -0.091 -0.134 -0.187  0.060
> r.squaredGLMM(mod)
      R2m       R2c
0.3597855 0.3597855
> AICc(mod)
[1] 763.0067
> mean(output)
[1] 0.1521547
```

Table 35. Elevation Effect Browsing Model at JDSF Mendocino County, California

```
glmer(browse~trtmt+species+Elevation+(1|SITE.ID),family=binomial)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: browse ~ trtmt + species + Elevation + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   753.3    786.3   -369.7    739.3      814

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.2197 -0.4602 -0.2999  0.5500  5.6597

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0.9641   0.9819
Number of obs: 821, groups:  SITE.ID, 4

Fixed effects:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)  7.192627   1.516535   4.743 2.11e-06 ***
trtmtHA     -1.403411   0.271370  -5.172 2.32e-07 ***
trtmtHD     -2.258112   0.288696  -7.822 5.21e-15 ***
trtmtLD     -0.868159   0.251015  -3.459 0.000543 ***
speciesSESE -2.195175   0.204788 -10.719  < 2e-16 ***
Elevation   -0.026444   0.005993  -4.412 1.02e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Correlation of Fixed Effects:
            (Intr) trtmHA trtmHD trtmLD spSESE
trtmtHA     -0.234
trtmtHD     -0.217  0.484
trtmtLD     -0.103  0.513  0.500
speciesSESE -0.190  0.195  0.232  0.178
Elevation   -0.936  0.152  0.134  0.002  0.131> AICc(mod)
> AICc(mod)
[1] 753.4432
> r.squaredGLMM(mod)
      R2m       R2c
0.4115930 0.5456789
> mean(output)
[1] 0.15007
```

Table 36. Treatment Browsing Model at JDSF Mendocino County, California

```
glmer(browse~trtmt+species+(1|SITE.ID),family=binomial)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: browse ~ trtmt + species + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   767.7    796.0   -377.9    755.7      815

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.6027 -0.5418 -0.2933  0.6240  5.3699

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0        0
Number of obs: 821, groups:  SITE.ID, 4

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   0.9433     0.2024   4.661 3.14e-06 ***
trtmtHA      -1.2606     0.2594  -4.860 1.17e-06 ***
trtmtHD      -2.1691     0.2769  -7.833 4.75e-15 ***
trtmtLD      -0.8733     0.2438  -3.583  0.00034 ***
speciesSESE  -2.1359     0.2007 -10.643  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) trtmHA trtmHD trtmLD
trtmtHA     -0.682
trtmtHD     -0.667  0.474
trtmtLD     -0.711  0.520  0.497
speciesSESE -0.500  0.194  0.239  0.177
> r.squaredGLMM(mod)
     R2m       R2c
0.3483399 0.3483399
> AICc(mod)
[1] 767.8175
> mean(output)
[1] 0.1532547

> emmeans(mod3,list(pairwise~trtmt+species),adjust="tukey")
$`emmeans of trtmt, species`
 trtmt species emmean    SE  df asymp.LCL asymp.UCL
 GS    PSME     0.158 0.197 Inf    -0.228     0.545
 HA    PSME    -0.636 0.213 Inf    -1.052    -0.219
 HD    PSME    -1.493 0.233 Inf    -1.950    -1.037
 LD    PSME    -0.154 0.200 Inf    -0.547     0.238
 GS    SESE    -1.717 0.224 Inf    -2.156    -1.277
 HA    SESE    -2.511 0.254 Inf    -3.008    -2.013
 HD    SESE    -3.368 0.280 Inf    -3.918    -2.819
 LD    SESE    -2.029 0.235 Inf    -2.489    -1.569
```

```
Results are given on the logit (not the response) scale.
Confidence level used: 0.95

$`pairwise differences of trtmt, species`
 contrast          estimate    SE  df z.ratio p.value
 GS,PSME - HA,PSME    0.794 0.235 Inf  3.384  0.0164
 GS,PSME - HD,PSME    1.652 0.256 Inf  6.449  <.0001
 GS,PSME - LD,PSME    0.313 0.221 Inf  1.416  0.8500
 GS,PSME - GS,SESE    1.875 0.191 Inf  9.804  <.0001
 GS,PSME - HA,SESE    2.669 0.316 Inf  8.457  <.0001
 GS,PSME - HD,SESE    3.526 0.339 Inf 10.394  <.0001
 GS,PSME - LD,SESE    2.188 0.298 Inf  7.333  <.0001
 HA,PSME - HD,PSME    0.858 0.269 Inf  3.189  0.0309
 HA,PSME - LD,PSME   -0.481 0.239 Inf -2.010  0.4746
 HA,PSME - GS,SESE    1.081 0.289 Inf  3.737  0.0046
 HA,PSME - HA,SESE    1.875 0.191 Inf  9.804  <.0001
 HA,PSME - HD,SESE    2.732 0.337 Inf  8.097  <.0001
 HA,PSME - LD,SESE    1.394 0.299 Inf  4.655  0.0001
 HD,PSME - LD,PSME   -1.339 0.261 Inf -5.138  <.0001
 HD,PSME - GS,SESE    0.223 0.299 Inf  0.748  0.9955
 HD,PSME - HA,SESE    1.017 0.322 Inf  3.157  0.0342
 HD,PSME - HD,SESE    1.875 0.191 Inf  9.804  <.0001
 HD,PSME - LD,SESE    0.536 0.309 Inf  1.737  0.6627
 LD,PSME - GS,SESE    1.562 0.286 Inf  5.468  <.0001
 LD,PSME - HA,SESE    2.356 0.313 Inf  7.521  <.0001
 LD,PSME - HD,SESE    3.214 0.337 Inf  9.529  <.0001
 LD,PSME - LD,SESE    1.875 0.191 Inf  9.804  <.0001
 GS,SESE - HA,SESE    0.794 0.235 Inf  3.384  0.0164
 GS,SESE - HD,SESE    1.652 0.256 Inf  6.449  <.0001
 GS,SESE - LD,SESE    0.313 0.221 Inf  1.416  0.8500
 HA,SESE - HD,SESE    0.858 0.269 Inf  3.189  0.0309
 HA,SESE - LD,SESE   -0.481 0.239 Inf -2.010  0.4746
 HD,SESE - LD,SESE   -1.339 0.261 Inf -5.138  <.0001

Results are given on the log odds ratio (not the response) scale.
P value adjustment: tukey method for comparing a family of 8 estimates
```

Table 37. SDI Watercourse Browsing Model at JDSF Mendocino County, California

```
glmer(browse~trtmt+species+dist_stream+(1|SITE.ID),family=binomial)
```

```
eneralized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: binomial  ( logit )
Formula: browse ~ SDI + species + dist_stream + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   769.7    793.2   -379.8    759.7      816

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.9830 -0.5505 -0.2838  0.5550  5.5934

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0.263    0.5128
Number of obs: 821, groups:  SITE.ID, 4

Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  2.8071755  0.6657770   4.216 2.48e-05 ***
SDI         -0.0026233  0.0004347  -6.035 1.59e-09 ***
speciesSESE -2.1687900  0.2032166 -10.672  < 2e-16 ***
dist_stream -0.0089613  0.0027817  -3.222  0.00128 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) SDI    spSESE
SDI         -0.004
speciesSESE -0.256  0.214
dist_stream -0.875 -0.264  0.121
> AICc(mod)
[1] 769.7631
> r.squaredGLMM(mod)
R2m       R2c
0.3696741 0.4163403
> mean(output)
[1] 0.1538374
```

Table 38. SDI Elevation Effect Browsing Model at JDSF Mendocino County, California

```
glmer(browse~trtmt+species+Elevation+(1|SITE.ID),family=binomial)
```

```
eneralized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: binomial  ( logit )
Formula: browse ~ SDI + species + dist_stream + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   769.7    793.2   -379.8    759.7      816

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.8618 -0.5474 -0.2881 -0.1634  6.1203

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0.9276   0.9631
Number of obs: 934, groups:  SITE.ID, 4

Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  7.0357366  1.3622514   5.165 2.41e-07 ***
SDI         -0.0025306  0.0003879  -6.523 6.88e-11 ***
speciesSESE -1.9550602  0.1979365  -9.877  < 2e-16 ***
Elevation   -0.0283808  0.0052582  -5.397 6.76e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) SDI    spSESE
SDI         -0.004
speciesSESE -0.256  0.214
dist_stream -0.875 -0.264  0.121
> AICc(mod)
[1] 761.5006
> r.squaredGLMM(mod)
      R2m       R2c
0.3989614 0.5472326
> mean(output)
[1] 0.1499531
```

Table 39. SDI Browsing Model at JDSF Mendocino County, California

```
glmer(browse~trtmt+species+(1|SITE.ID),family=binomial)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: browse ~ SDI + species + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   778.2    797.0   -385.1    770.2      817

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.6172 -0.6401 -0.2497  0.6184  4.4923

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0        0
Number of obs: 821, groups:  SITE.ID, 4

Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  0.9613541  0.1907449   5.040 4.66e-07 ***
SDI         -0.0030636  0.0004136  -7.407 1.29e-13 ***
speciesSESE -2.1126249  0.1996739 -10.580  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) SDI
SDI         -0.828
speciesSESE -0.515  0.258>
AICc(mod)
[1] 778.2096
> r.squaredGLMM(mod)
      R2m       R2c
0.3212228 0.3212228
> mean(output)
[1] 0.1548855
```

Table 40. PACL Browsing Model at JDSF Mendocino County, California

```
glmer(browse~PACL+species+(1|SITE.ID),family=binomial)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: browse ~ PACL + species + (1 | SITE.ID)

     AIC      BIC   logLik deviance df.resid
   888.9    908.3   -440.5    880.9      930

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.2363 -0.6281 -0.2969 -0.2111  5.1848

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0.0368   0.1918
Number of obs: 934, groups:  SITE.ID, 4

Fixed effects:
             Estimate Std. Error z value Pr(>|z|)
(Intercept) -2.525157   0.401889  -6.283 3.32e-10 ***
PACL         0.028501   0.005268   5.410 6.30e-08 ***
speciesSESE -1.835467   0.189321  -9.695  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) PACL
PACL        -0.939
speciesSESE -0.006 -0.127>
> AICc(mod3)
[1] 888.9835> r.squaredGLMM(mod)
      R2m       R2c
0.2609427 0.3799181
```

Table 41.Treatment Survival Model at JDSF Mendocino County, California

```
glmer(survival~trtmt+species+(1|SITE.ID),family=binomial)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: survival ~ trtmt + species + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   519.0    548.0   -253.5    507.0      929

Scaled residuals:
     Min       1Q   Median       3Q      Max
-13.7989   0.0806   0.1504   0.3583   1.3519

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 2.478    1.574
Number of obs: 935, groups:  SITE.ID, 4

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   1.0781     0.8211   1.313    0.189
trtmtHA       1.2486     0.3019   4.136 3.54e-05 ***
trtmtHD       1.4603     0.3016   4.841 1.29e-06 ***
trtmtLD       2.3417     0.3708   6.315 2.70e-10 ***
speciesSESE   1.1221     0.2412   4.653 3.27e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) trtmHA trtmHD trtmLD
trtmtHA     -0.129
trtmtHD     -0.131  0.374
trtmtLD     -0.104  0.312  0.312
speciesSESE -0.116  0.098  0.105  0.124
> AICc(mod)
[1] 519.0865
> r.squaredGLMM(mod)
      R2m       R2c
0.1475479 0.5137379
> mean(output)
[1] 0.08236455
```

Table 42. Aspect Treatment Survival Model at JDSF Mendocino County, California

```
glmer(survival~trtmt+species+log(Asp_trans20+1)+(1|SITE.ID),family=binomial)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: survival ~ trtmt + species + log(Asp_trans20 + 1) + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   506.7    540.6   -246.3    492.7      928

Scaled residuals:
     Min       1Q   Median       3Q      Max
-16.0075   0.0625   0.1418   0.3428   1.3739

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0        0
Number of obs: 935, groups:  SITE.ID, 4

Fixed effects:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)            3.4744     0.4406   7.886 3.13e-15 ***
trtmtHA                1.1822     0.3056   3.869 0.000109 ***
trtmtHD                1.3654     0.3002   4.548 5.41e-06 ***
trtmtLD                2.3663     0.3740   6.328 2.49e-10 ***
speciesSESE            1.1187     0.2422   4.619 3.86e-06 ***
log(Asp_trans20 + 1)  -1.3693     0.1618  -8.461  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> r.squaredGLMM(mod)
      R2m       R2c
0.3212228 0.3212228
> mean(output)
[1] 0.08243193
> AICc(mod)
[1] 506.8179

> mod3<-
glmer(survival~trtmt+species+log(Asp_trans20+1)+(1|SITE.ID),family=binomial)
> emmeans(mod3,list(pairwise~trtmt+species),adjust="tukey")
$`emmeans of trtmt, species`
 trtmt species emmean    SE  df asymp.LCL asymp.UCL
 GS    PSME     0.473 0.212 Inf    0.0575     0.888
 HA    PSME     1.655 0.266 Inf    1.1327     2.177
 HD    PSME     1.838 0.254 Inf    1.3393     2.337
 LD    PSME     2.839 0.340 Inf    2.1733     3.505
 GS    SESE     1.591 0.232 Inf    1.1363     2.046
 HA    SESE     2.773 0.306 Inf    2.1733     3.373
 HD    SESE     2.956 0.298 Inf    2.3733     3.540
 LD    SESE     3.957 0.384 Inf    3.2054     4.710

Results are given on the logit (not the response) scale.
Confidence level used: 0.95
```

```
$`pairwise differences of trtmt, species`
 contrast          estimate    SE  df z.ratio p.value
 GS,PSME - HA,PSME  -1.1821 0.306 Inf -3.868  0.0028
 GS,PSME - HD,PSME  -1.3652 0.300 Inf -4.548  0.0001
 GS,PSME - LD,PSME  -2.3662 0.374 Inf -6.327  <.0001
 GS,PSME - GS,SESE  -1.1186 0.242 Inf -4.618  0.0001
 GS,PSME - HA,SESE  -2.3007 0.407 Inf -5.650  <.0001
 GS,PSME - HD,SESE  -2.4838 0.404 Inf -6.141  <.0001
 GS,PSME - LD,SESE  -3.4848 0.471 Inf -7.406  <.0001
 HA,PSME - HD,PSME  -0.1831 0.341 Inf -0.537  0.9995
 HA,PSME - LD,PSME  -1.1841 0.402 Inf -2.945  0.0640
 HA,PSME - GS,SESE   0.0636 0.372 Inf  0.171  1.0000
 HA,PSME - HA,SESE  -1.1186 0.242 Inf -4.618  0.0001
 HA,PSME - HD,SESE  -1.3016 0.420 Inf -3.102  0.0405
 HA,PSME - LD,SESE  -2.3026 0.479 Inf -4.807  <.0001
 HD,PSME - LD,PSME  -1.0010 0.402 Inf -2.492  0.1988
 HD,PSME - GS,SESE   0.2466 0.366 Inf  0.674  0.9977
 HD,PSME - HA,SESE  -0.9355 0.417 Inf -2.242  0.3263
 HD,PSME - HD,SESE  -1.1186 0.242 Inf -4.618  0.0001
 HD,PSME - LD,SESE  -2.1196 0.478 Inf -4.437  0.0002
 LD,PSME - GS,SESE   1.2476 0.419 Inf  2.977  0.0584
 LD,PSME - HA,SESE   0.0655 0.460 Inf  0.143  1.0000
 LD,PSME - HD,SESE  -0.1176 0.460 Inf -0.255  1.0000
 LD,PSME - LD,SESE  -1.1186 0.242 Inf -4.618  0.0001
 GS,SESE - HA,SESE  -1.1821 0.306 Inf -3.868  0.0028
 GS,SESE - HD,SESE  -1.3652 0.300 Inf -4.548  0.0001
 GS,SESE - LD,SESE  -2.3662 0.374 Inf -6.327  <.0001
 HA,SESE - HD,SESE  -0.1831 0.341 Inf -0.537  0.9995
 HA,SESE - LD,SESE  -1.1841 0.402 Inf -2.945  0.0640
 HD,SESE - LD,SESE  -1.0010 0.402 Inf -2.492  0.1988

Results are given on the log odds ratio (not the response) scale.
P value adjustment: tukey method for comparing a family of 8 estimates
```

Table 43. SDI Survival Model at JDSF Mendocino County, California

```
glmer(survival~SDI+species+(1|SITE.ID),family=binomial)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: survival ~ SDI + species + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   543.4    562.8   -267.7    535.4      931

Scaled residuals:
     Min       1Q   Median       3Q      Max
-13.5078   0.0832   0.1410   0.3513   1.1400

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 2.271    1.507
Number of obs: 935, groups:  SITE.ID, 4

Fixed effects:
             Estimate Std. Error z value Pr(>|z|)
(Intercept) 1.3483009  0.7880483   1.711   0.0871 .
SDI         0.0024647  0.0004655   5.295 1.19e-07 ***
speciesSESE 1.0479963  0.2327063   4.504 6.68e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) SDI
SDI         -0.168
speciesSESE -0.111  0.097
> AICc(mod)
[1] 543.4804
> mean(output)
[1] 0.08760429
```

Table 44. SDI Aspect Survival Model at JDSF Mendocino County, California

glmer(survival~SDI+species+log(Asp_trans20+1)+(1|SITE.ID),family=binomial)

```
eneralized linear mixed model fit by maximum likelihood (Laplace
  Approximation) [glmerMod]
 Family: binomial  ( logit )
Formula:
survival ~ SDI + species + log(Asp_trans20 + 1) + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   533.2    557.4   -261.6    523.2      930

Scaled residuals:
     Min       1Q   Median       3Q      Max
-13.6452   0.0761   0.1318   0.3587   1.1374

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0        0
Number of obs: 935, groups:  SITE.ID, 4

Fixed effects:
                       Estimate Std. Error z value Pr(>|z|)
(Intercept)           3.5331384  0.4274187   8.266  < 2e-16 ***
SDI                   0.0023393  0.0004663   5.016 5.27e-07 ***
speciesSESE           1.0399226  0.2331996   4.459 8.22e-06 ***
log(Asp_trans20 + 1) -1.2630433  0.1525733  -8.278  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) SDI    spSESE
SDI         -0.261
speciesSESE -0.153  0.092
lg(As_20+1) -0.884 -0.080 -0.082
> AICc(mod)
[1] 533.2223
> mean(output)
[1] 0.08814141
```

Table 45. Quadratic SDI Aspect Survival Model at JDSF Mendocino County, California

```
glmer(survival~SDI+SDI^0.5+Species+log(Asp_trans20+1)+(1|SITE.ID),family=binomi
al)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation
) [
glmerMod]
 Family: binomial  ( logit )
Formula: survival ~ SDI + SDI_root + species + log(Asp_trans20 + 1) +
    (1 | SITE.ID)

     AIC      BIC   logLik deviance df.resid
   502.0    531.1   -245.0    490.0      928

Scaled residuals:
     Min       1Q   Median       3Q      Max
-15.3465   0.0652   0.1357   0.3366   1.3704

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 0        0
Number of obs: 934, groups:  SITE.ID, 4

Fixed effects:
                      Estimate Std. Error z value Pr(>|z|)
(Intercept)           3.427647   0.439290   7.803 6.06e-15 ***
SDI                  -0.014673   0.003399  -4.317 1.58e-05 ***
SDI_root              0.401586   0.080151   5.010 5.43e-07 ***
speciesSESE           1.123872   0.242662   4.631 3.63e-06 ***
log(Asp_trans20 + 1) -1.352062   0.161909  -8.351  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) SDI    SDI_rt spSESE
SDI          0.013
SDI_root    -0.040 -0.992
speciesSESE -0.141 -0.077  0.093
lg(As_20+1) -0.880  0.061 -0.078 -0.114
convergence code: 0
boundary (singular) fit: see ?isSingular

> r.squaredGLMM(mod)
                  R2m       R2c
theoretical 0.5430998 0.5430998
delta       0.3063735 0.3063735

> AICc(mod)
[1] 502.1218
> mean(output)
[1] 0.07997712
```

Table 46. PACL Survival Model at JDSF Mendocino County, California.

```
glmer(survival~PACL+species+(1|SITE.ID),family=binomial)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: survival ~ PACL + species + (1 | SITE.ID)
   Data: Seed1

     AIC      BIC   logLik deviance df.resid
   544.0    563.4   -268.0    536.0      931

Scaled residuals:
     Min       1Q   Median       3Q      Max
-14.3618   0.0865   0.1522   0.3588   1.0944

Random effects:
 Groups  Name        Variance Std.Dev.
 SITE.ID (Intercept) 2.116    1.455
Number of obs: 935, groups:  SITE.ID, 4

Fixed effects:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)  4.717371   0.909977   5.184 2.17e-07 ***
PACL        -0.035368   0.006801  -5.200 1.99e-07 ***
speciesSESE  1.046474   0.232301   4.505 6.64e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) PACL
PACL        -0.564
speciesSESE -0.029 -0.093
> AICc(mod)
[1] 544.4153
```

Stem Maps

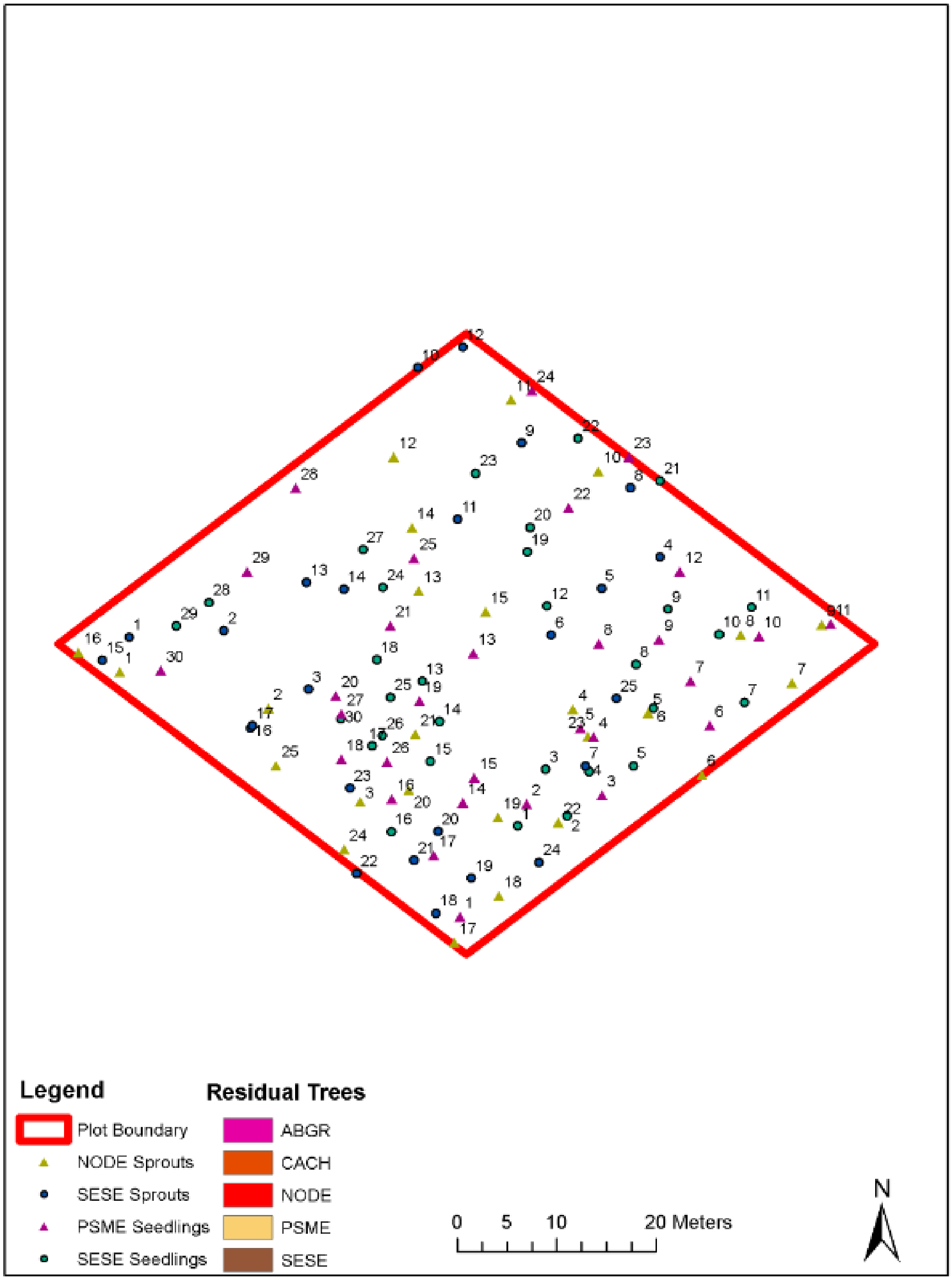

Figure 23. Stem map of group selection treatment at Camp Six in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

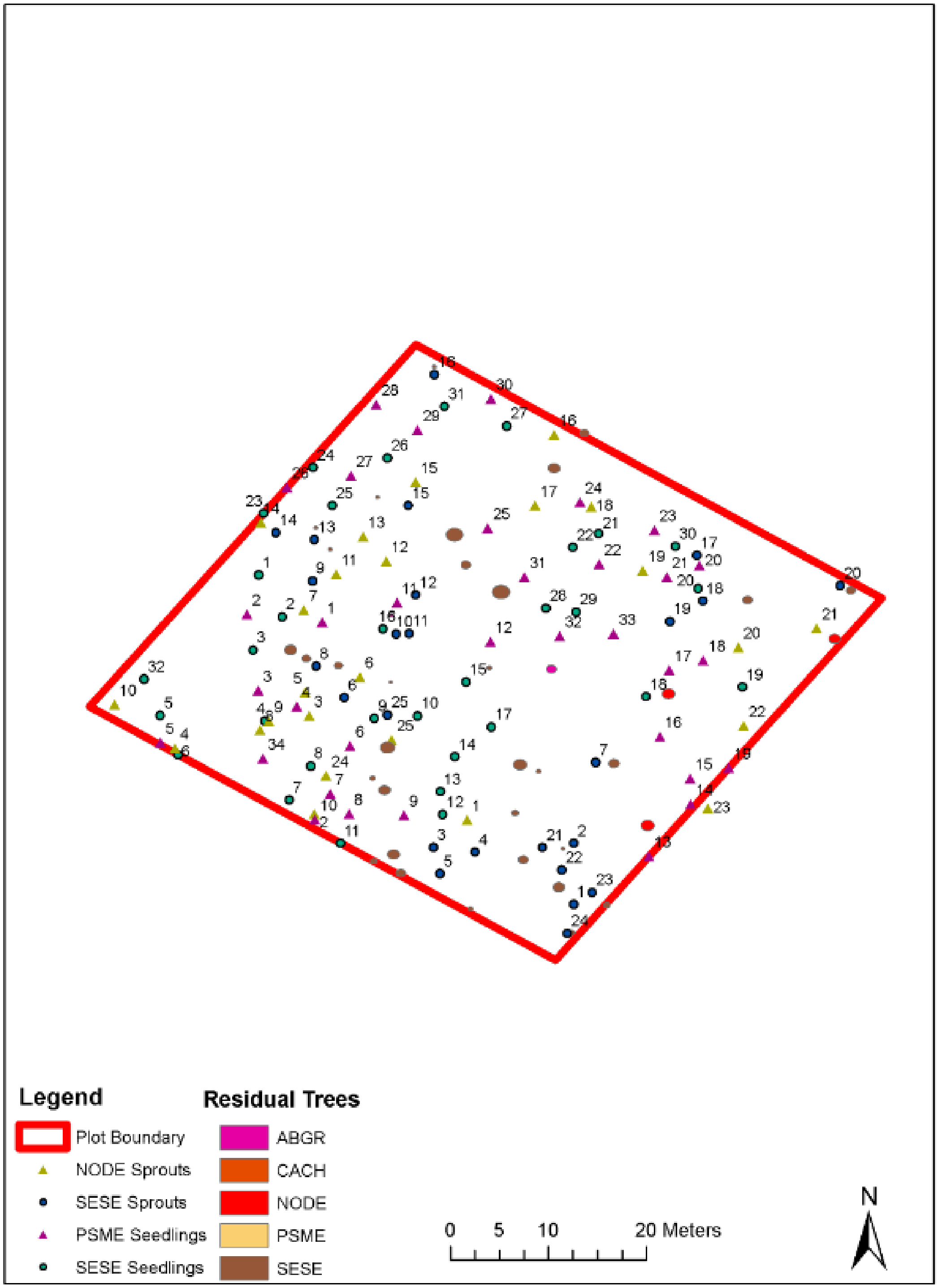

Figure 24. Stem map of low density dispersed treatment at Camp Six in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

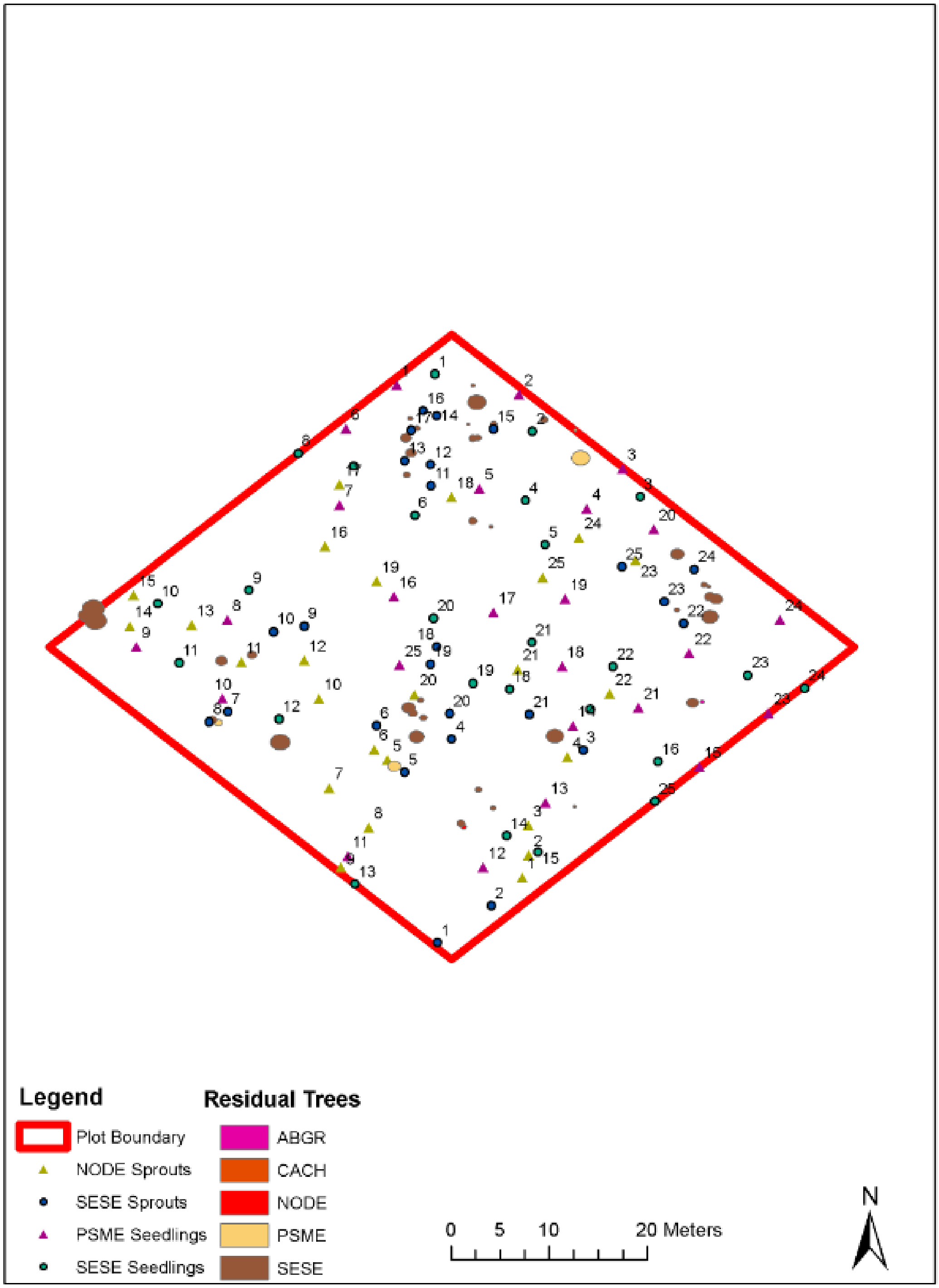

Figure 25. Stem map of high density aggregated treatment at Camp Six in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

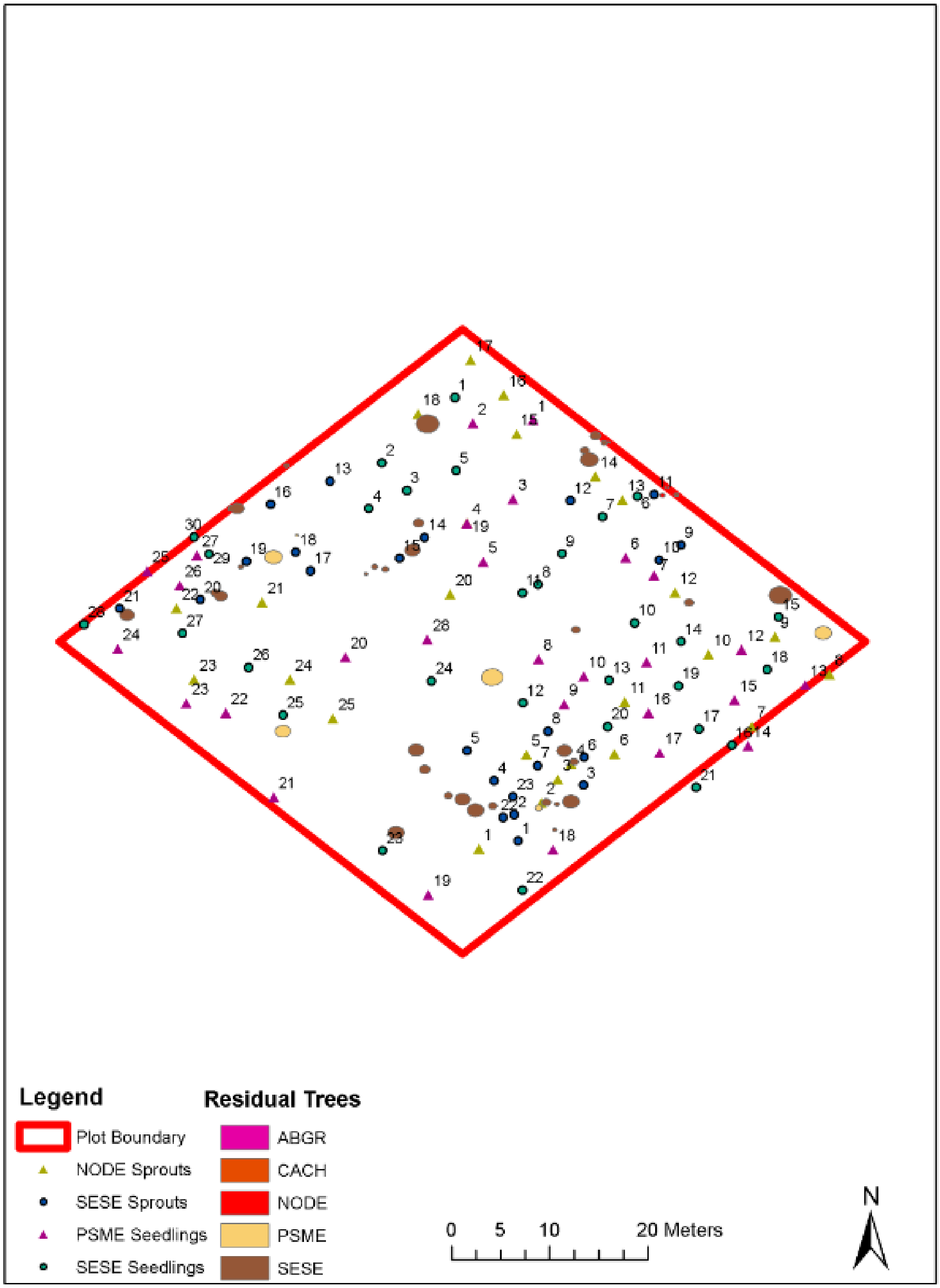

Figure 26. Stem map of high density dispersed treatment at Camp Six in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

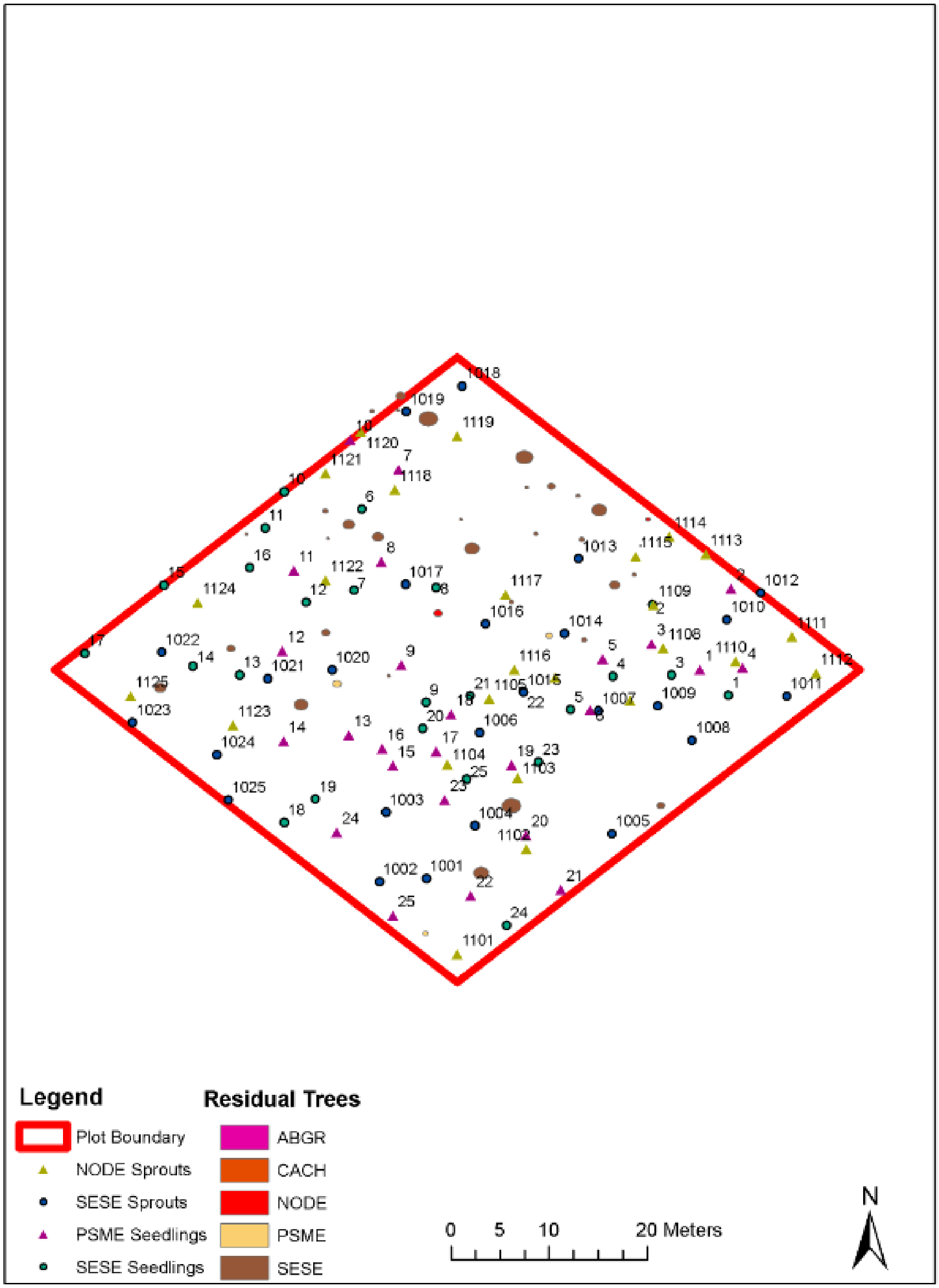

Figure 27. Stem map of low density dispersed treatment at Whiskey Springs in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

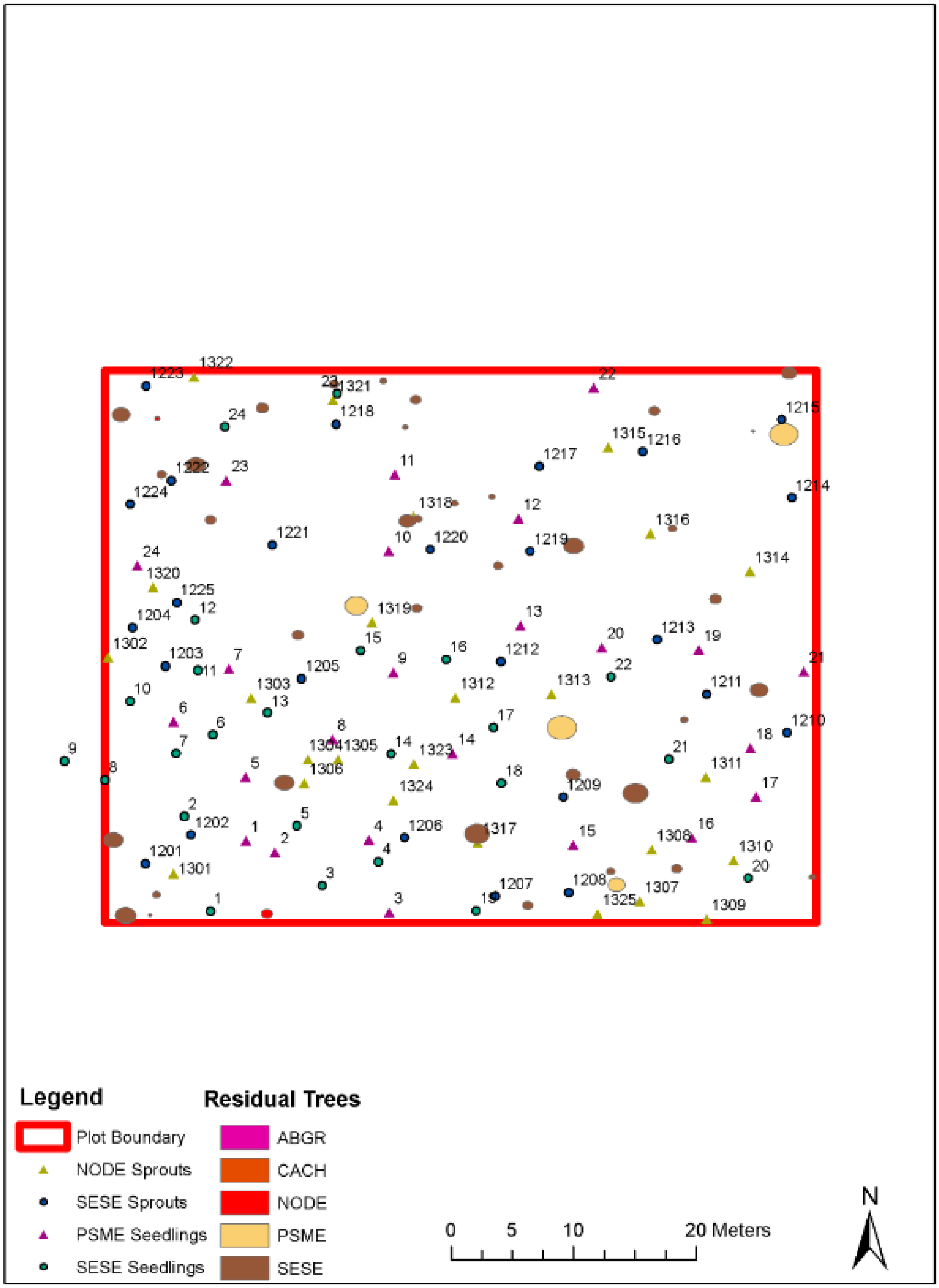

Figure 28. Stem map of high density dispersed treatment (2A) at Whiskey Springs in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

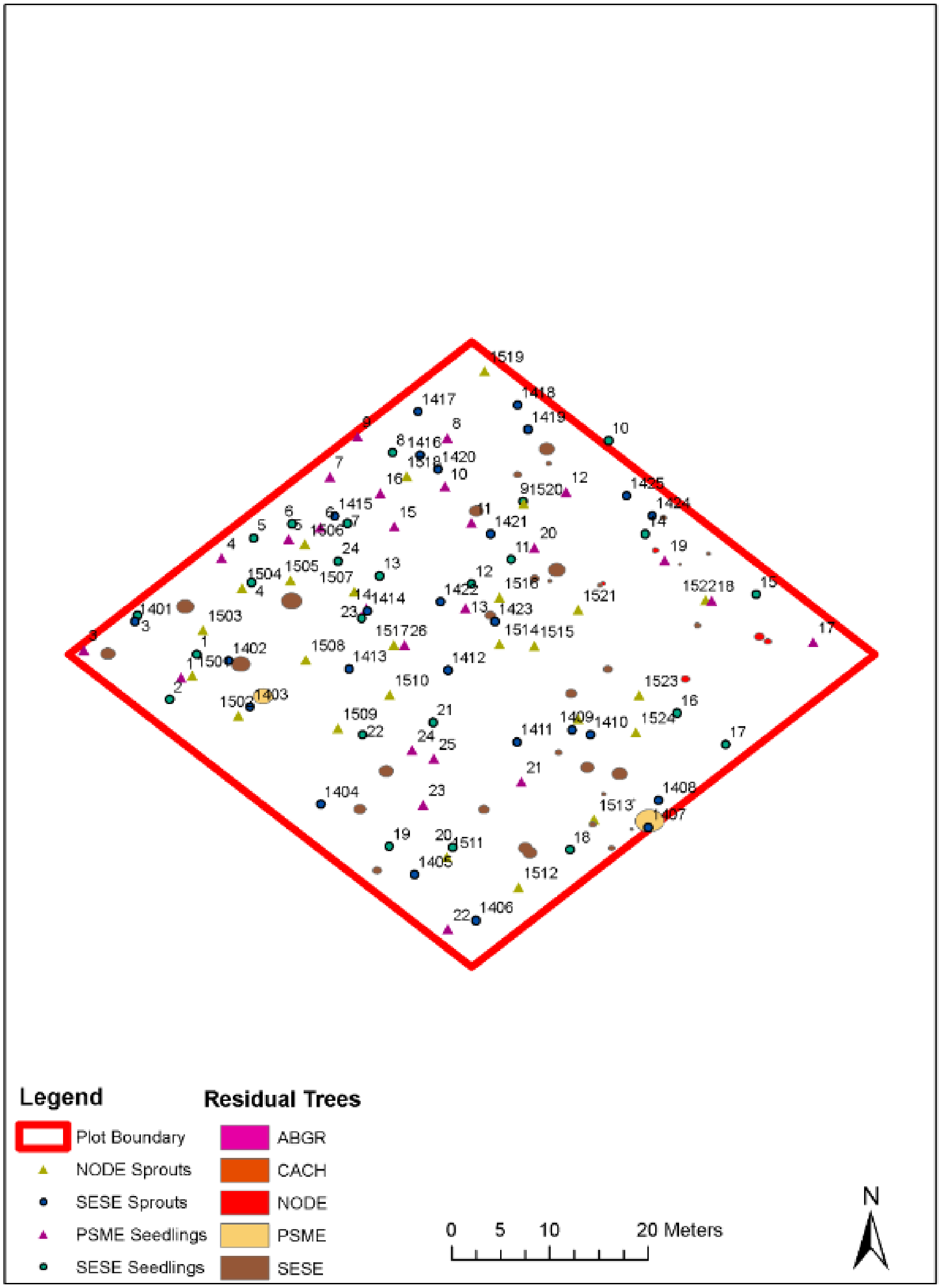

Figure 29. Stem map of high density dispersed treatment (2B) at Whiskey Springs in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

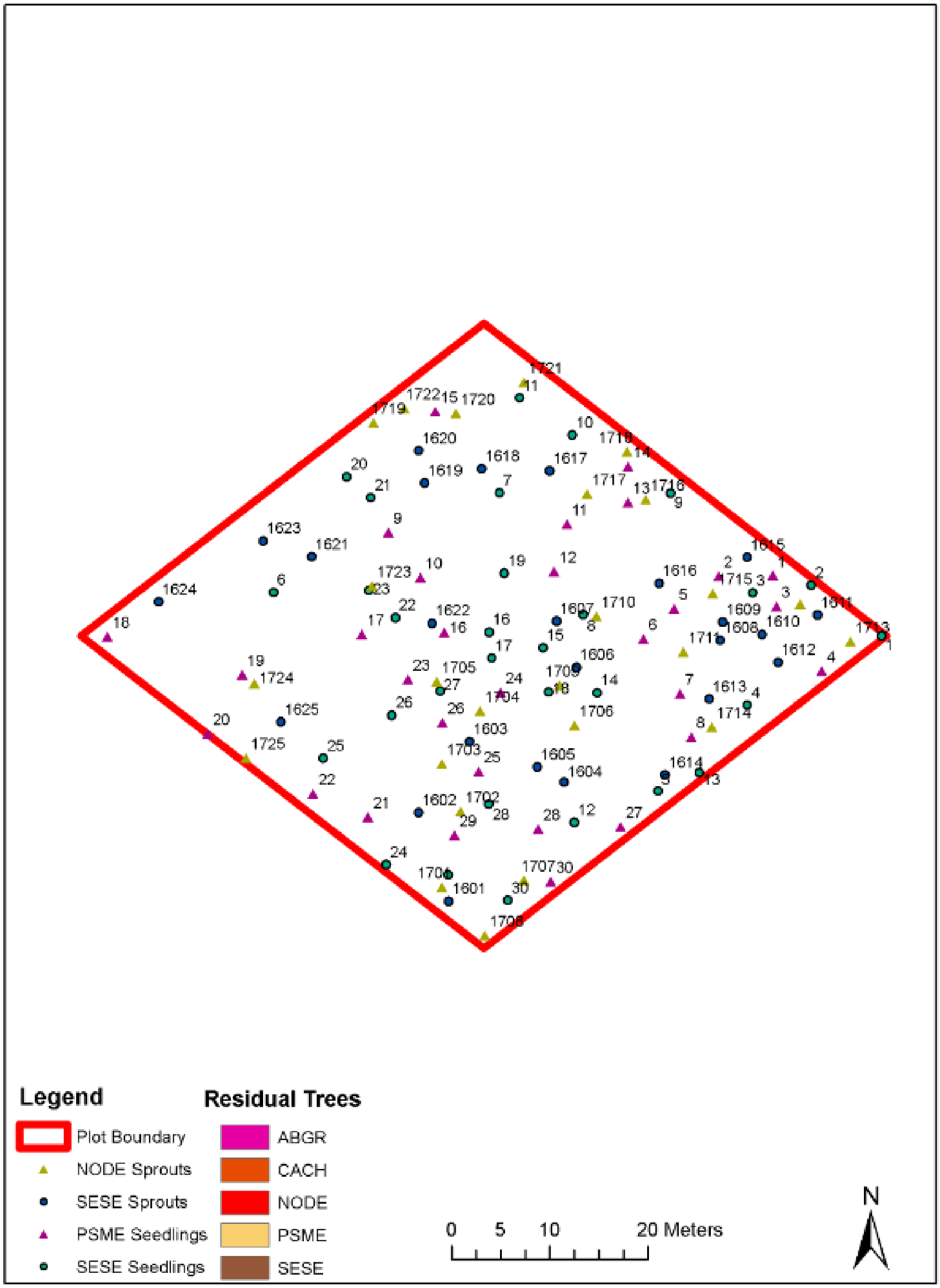

Figure 30. Stem map of group selection treatment at Whiskey Springs in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

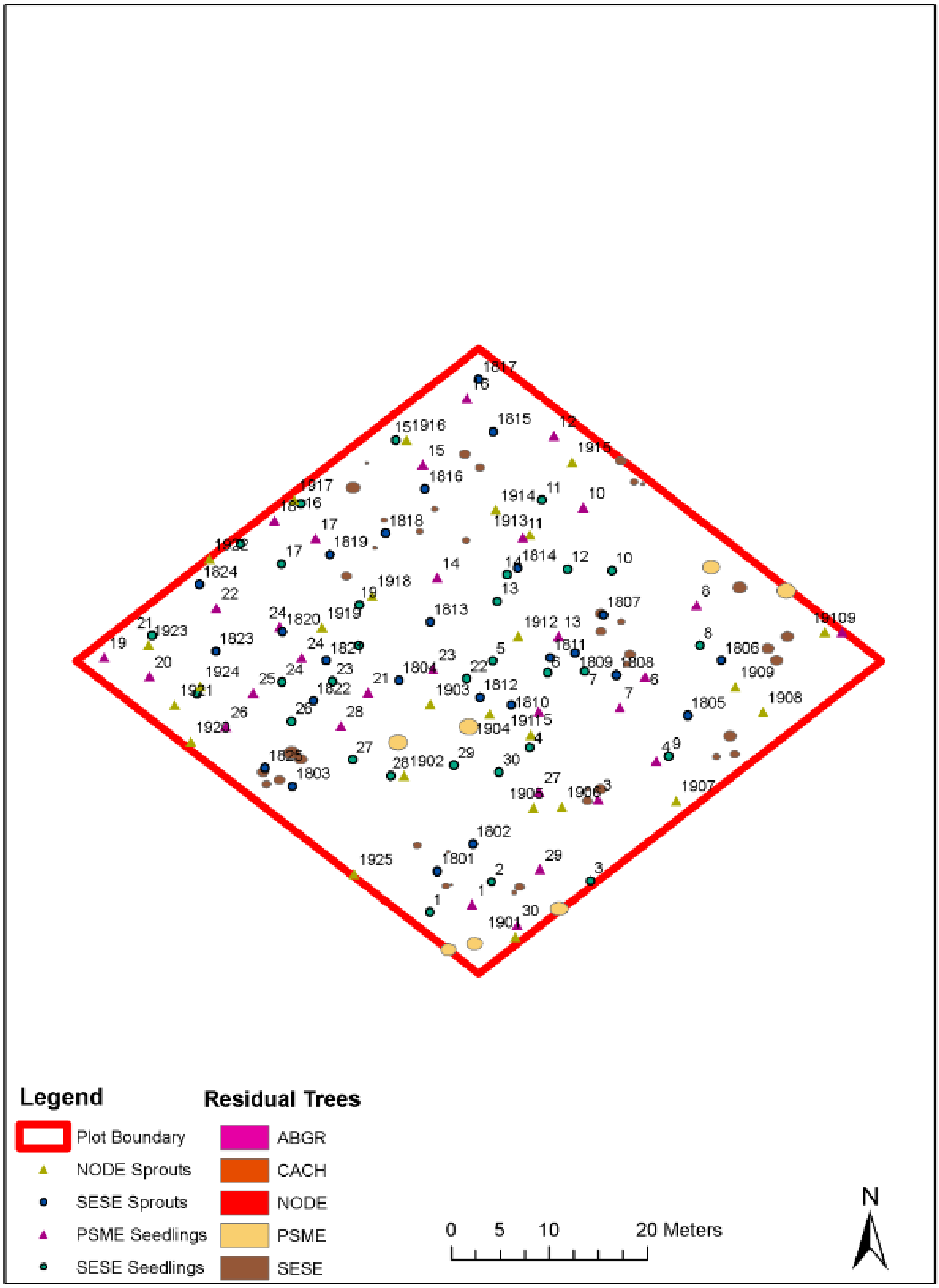

Figure 31. Stem map of high density aggregated treatment at Whiskey Springs in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

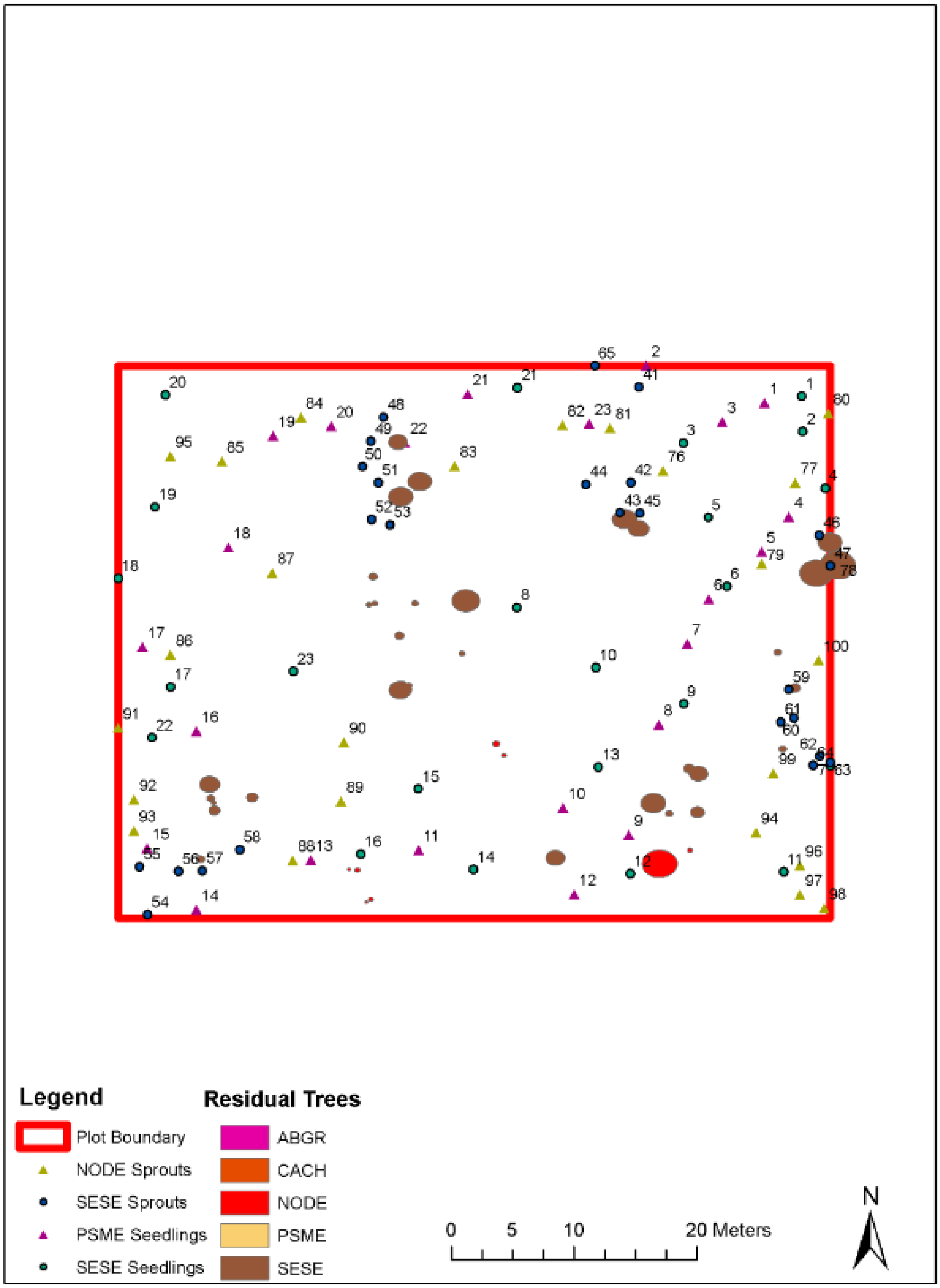

Figure 32. Stem map of high density aggregated treatment at Waldo North in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

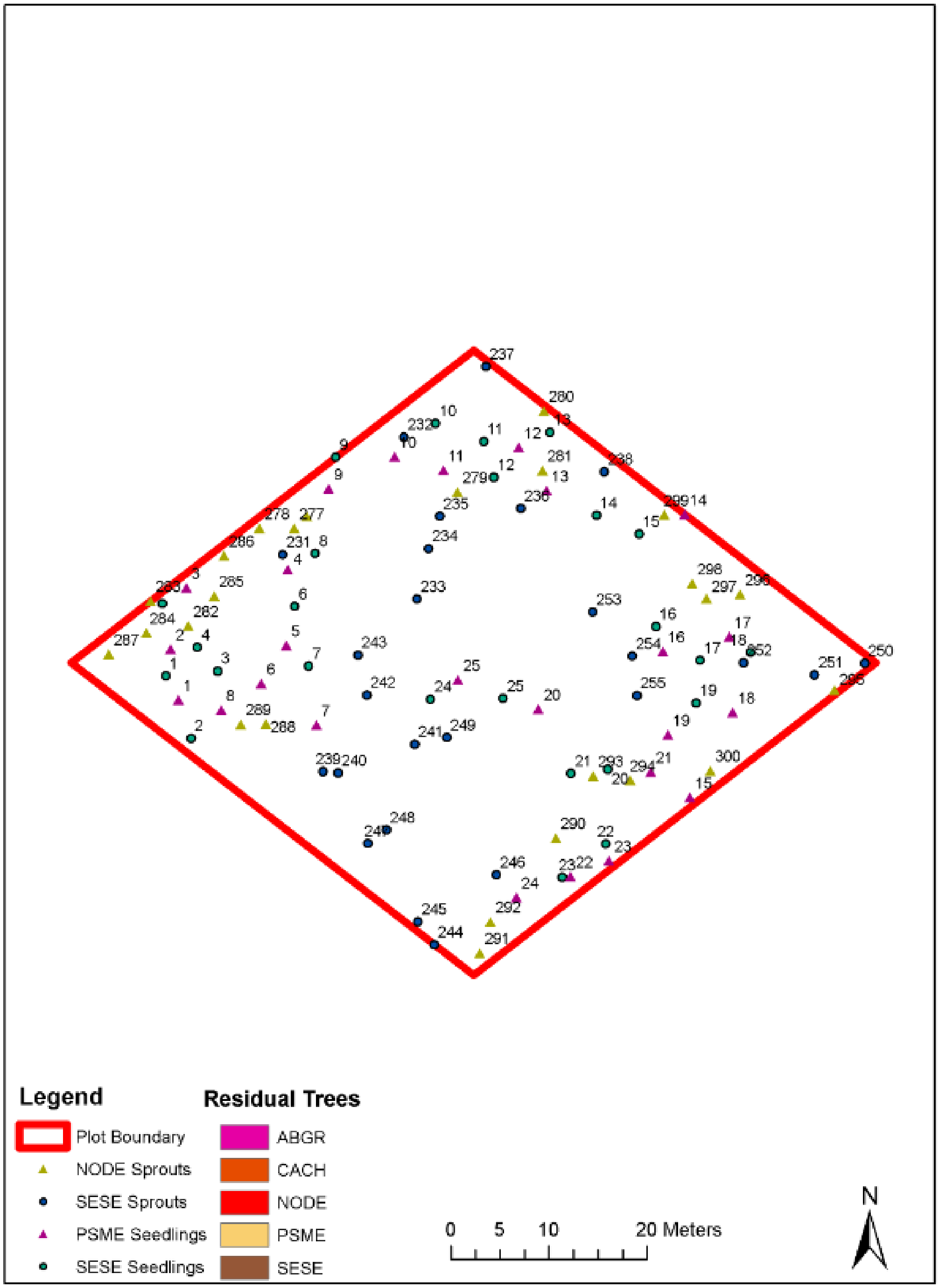

Figure 33. Stem map of group selection treatment at Waldo North in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

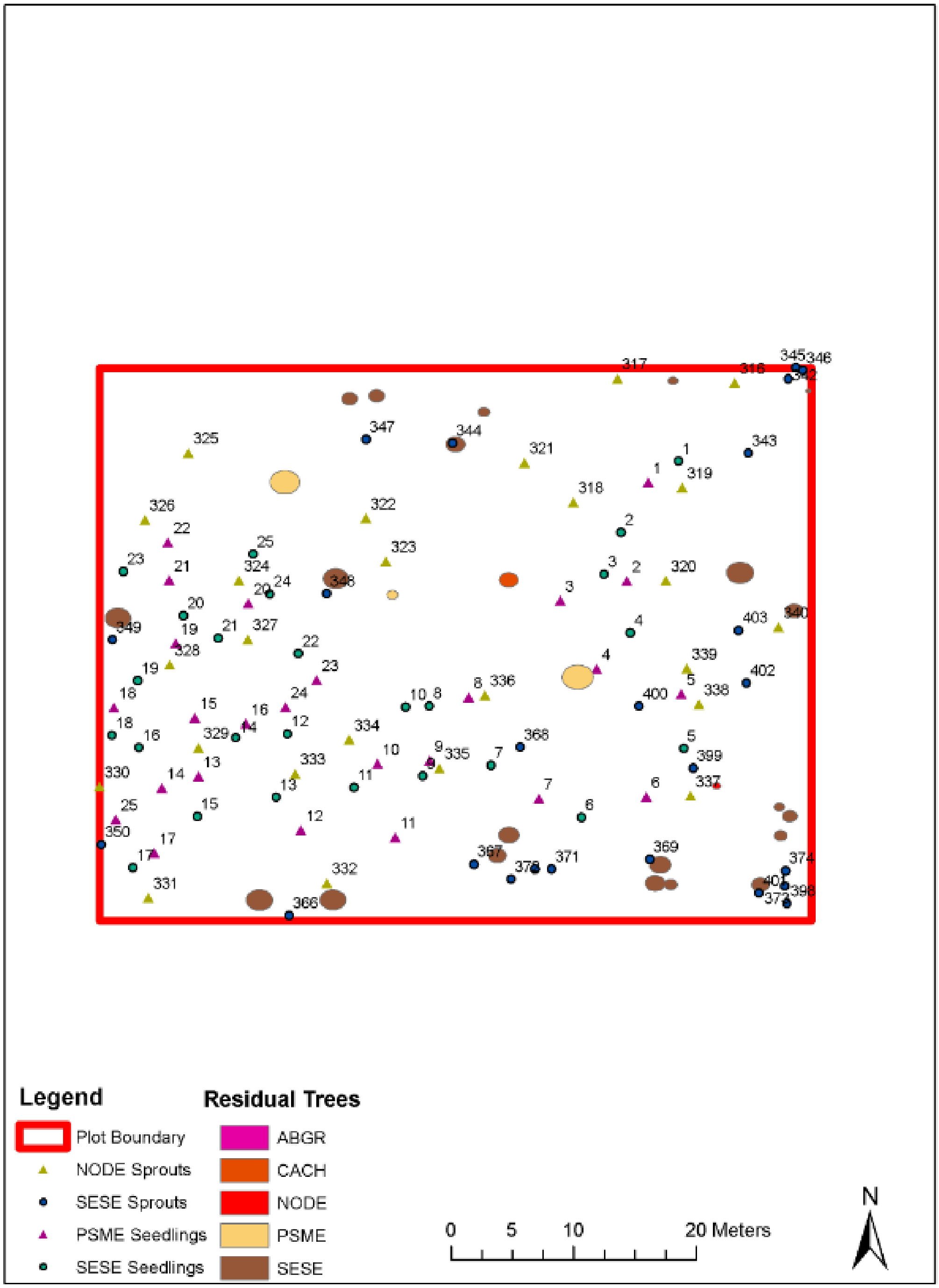

Figure 34. Stem map of high density dispersed treatment at Waldo North in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

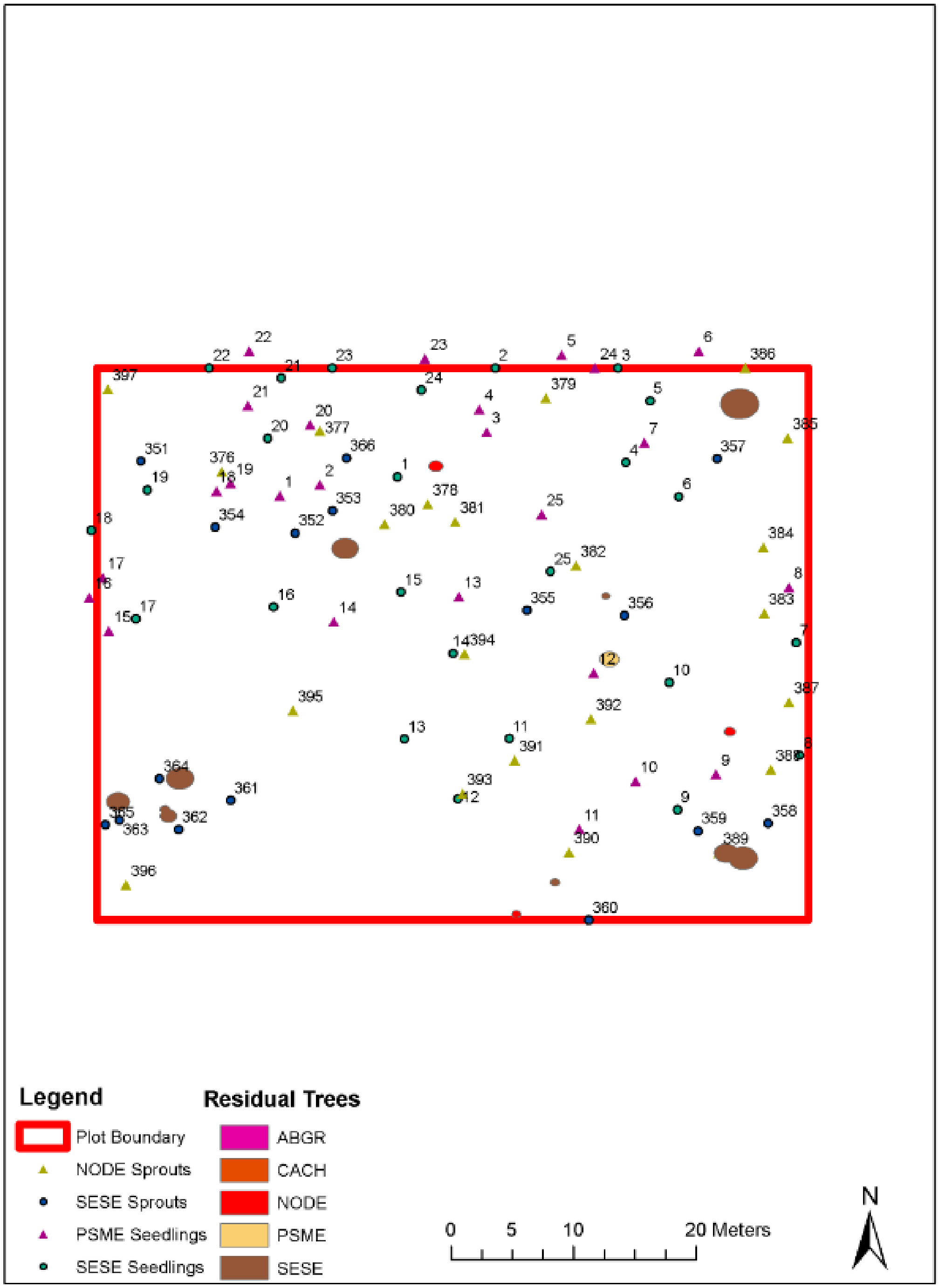

Figure 35. Stem map of low density dispersed treatment at Waldo North in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

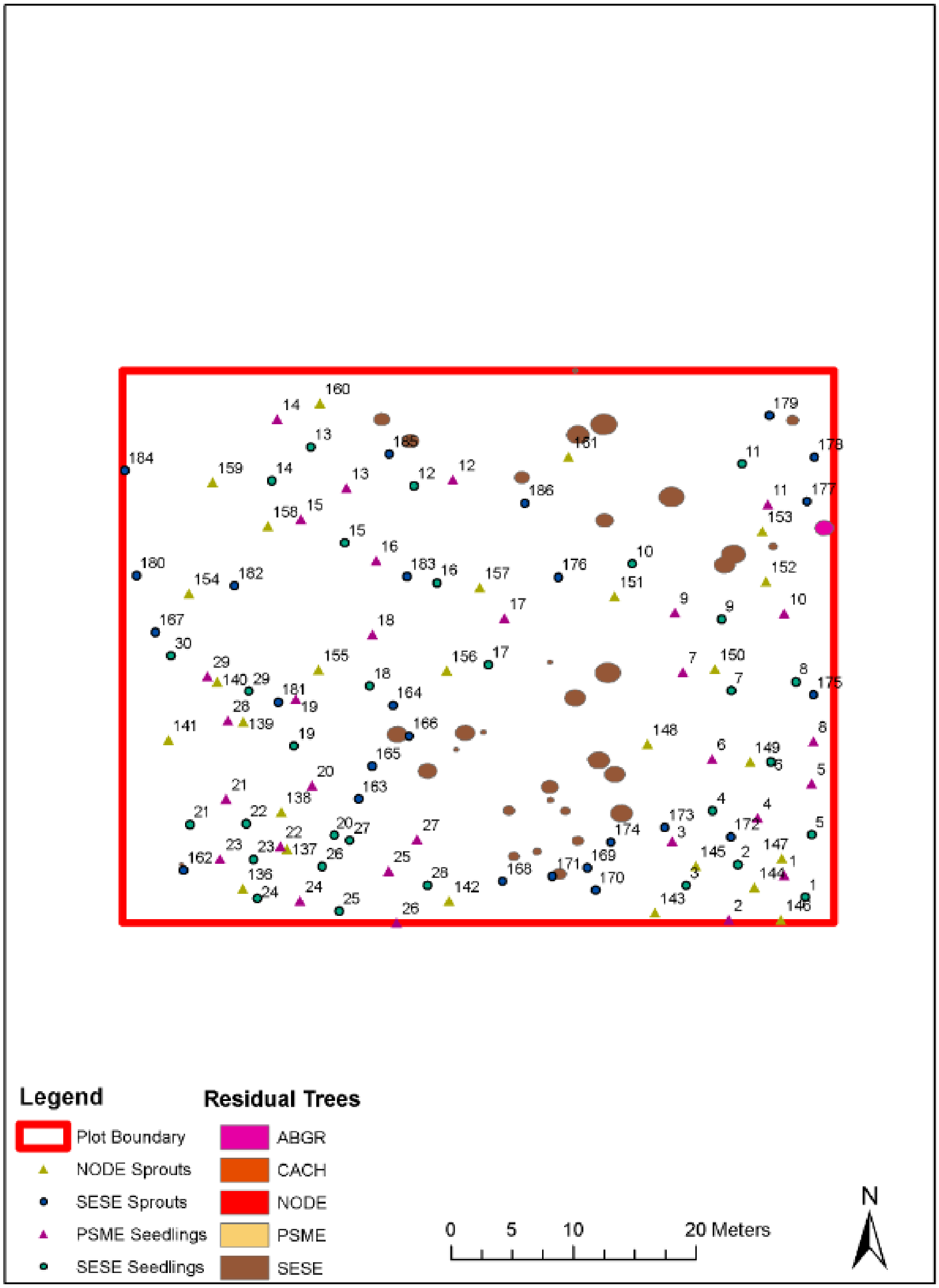

Figure 36. Stem map of high density aggregated treatment at Waldo South in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

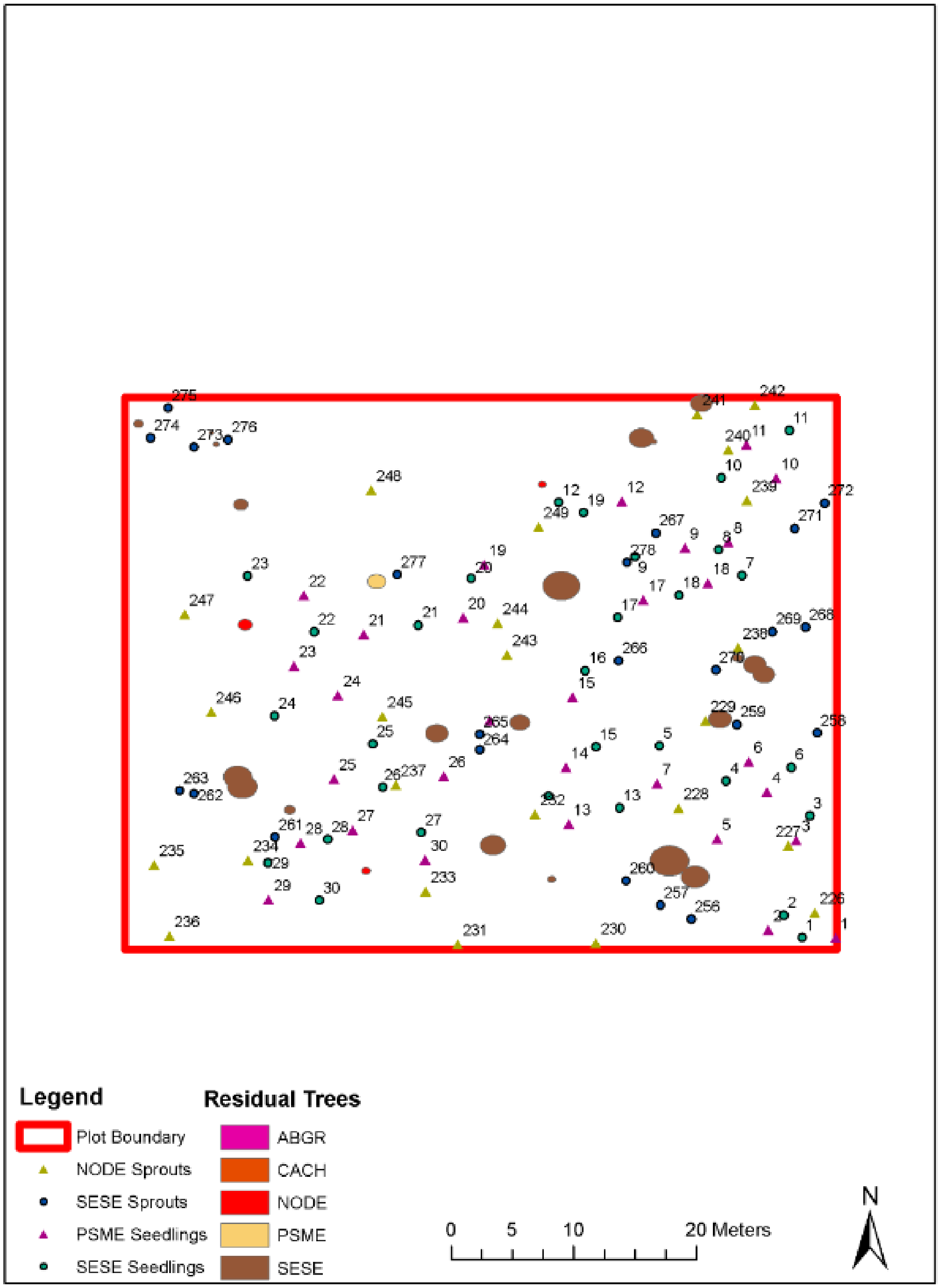

Figure 37. Stem map of high density dispersed treatment at Waldo South in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

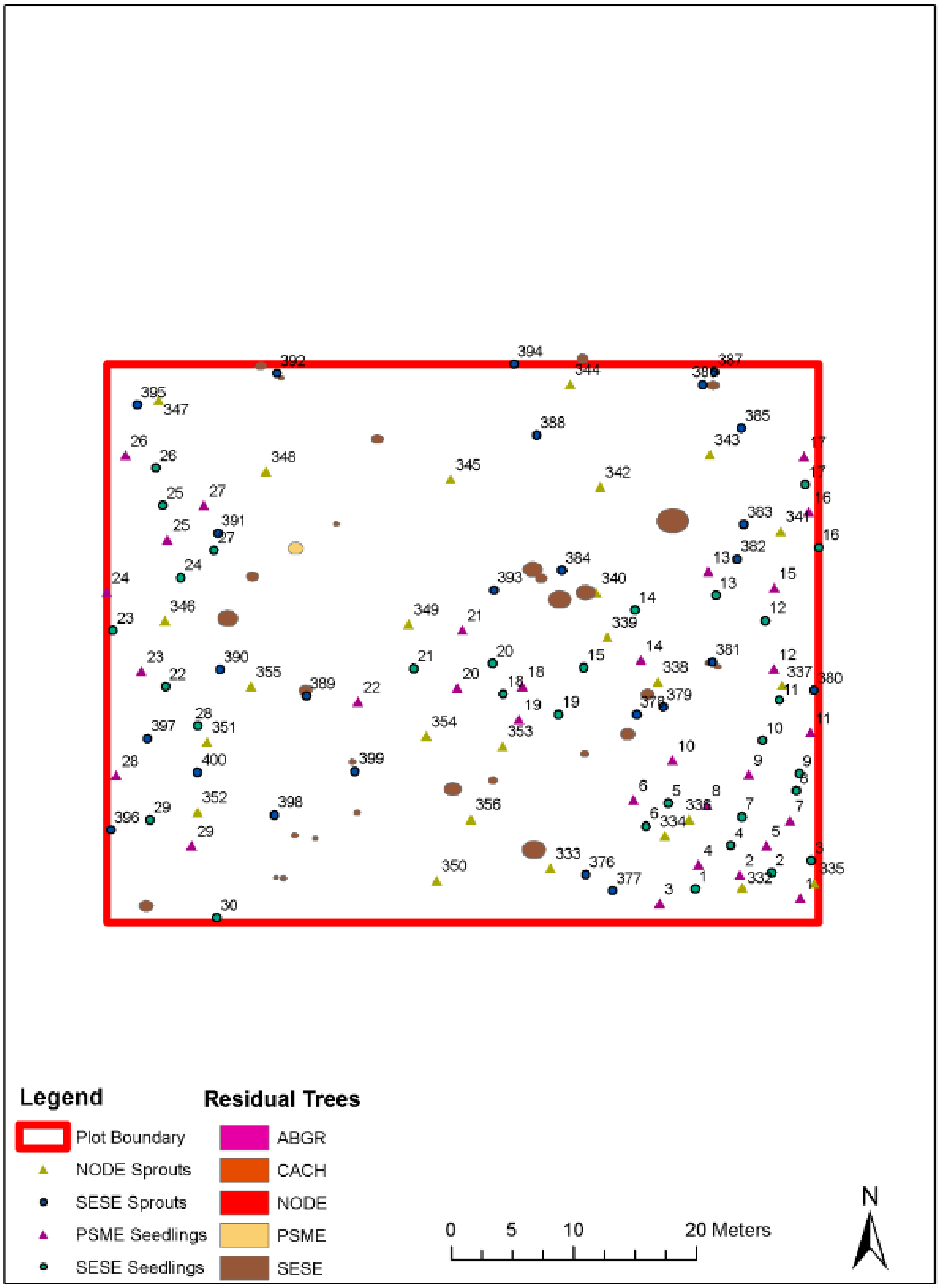

Figure 38. Stem map of low density dispersed treatment at Waldo South in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).

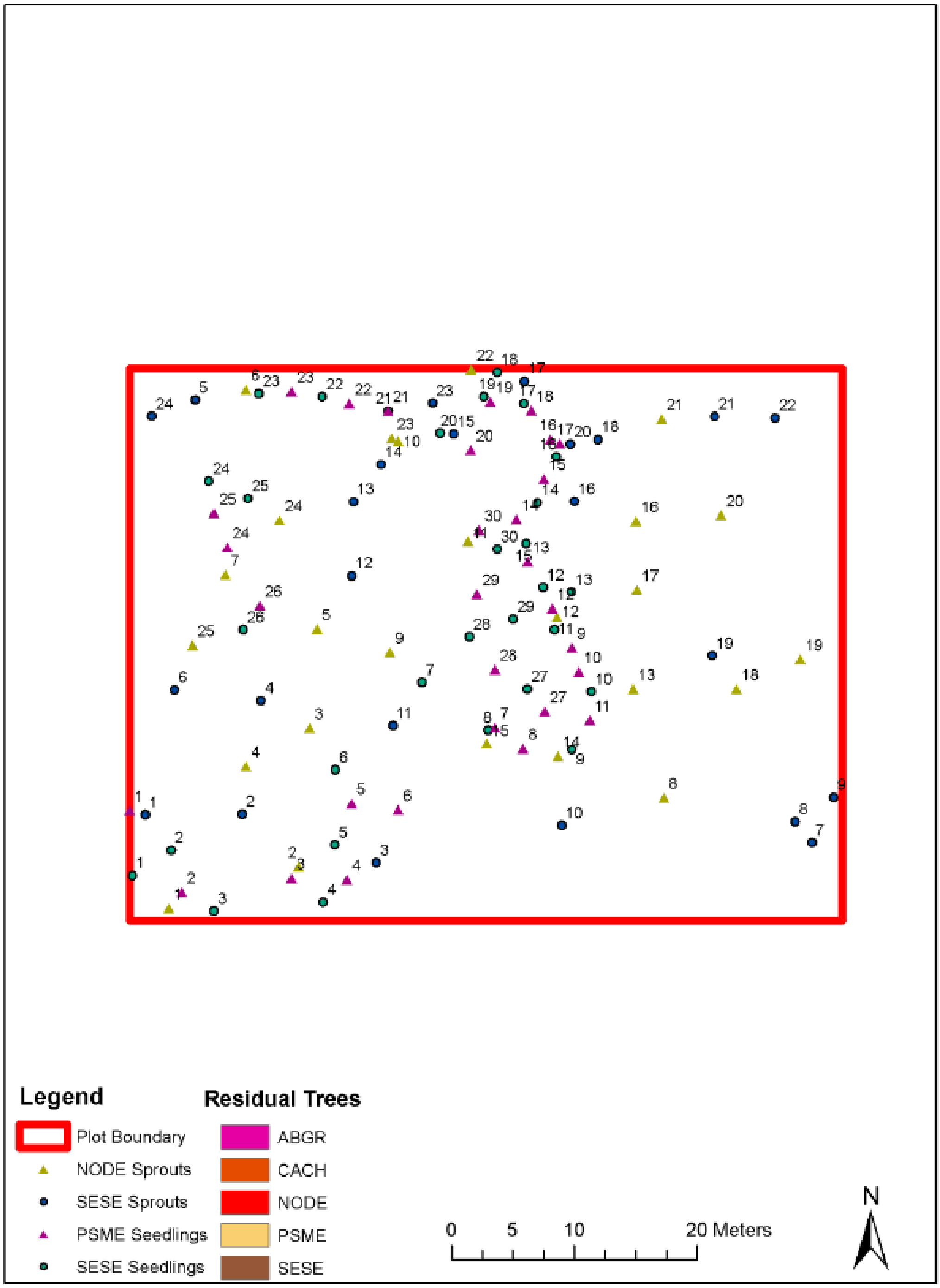

Figure 39. Stem map of group selection treatment at Waldo South in JDSF. Species include redwood (SESE), tanoak (NODE), Douglas-fir (PSME) grand fir (ABGR), and giant chinquapin (CACH).