

Overstory and Understory Dynamics in a Ponderosa Pine Plantation Vary with Stand Density in the Sierra Nevada: 40-Year Results

Jianwei Zhang, William W. Oliver, Martin W. Ritchie, and Donald L. Neal

Abstract: We periodically measured overstory ponderosa pine (*Pinus ponderosa*) growth and understory cover and abundance in a long-term study on the west slope of the Sierra Nevada, California, USA. The study was established in 1969 in a 20-year-old plantation, thinned to basal areas of 9, 16, 23, 30, and 37 m² ha⁻¹ and rethinned three times. The objective was to determine the effect of stand density regimes on productivity, understory vegetation, aboveground carbon storage, and mortality caused mainly by *Dendroctonus* infestations. Results showed that without mortality, basal area and volume increments were not affected by thinning the plantation to 16 m² ha⁻¹ from 37 m² ha⁻¹. With *Dendroctonus* actively attacking trees, the plantation could be thinned to 9 m² ha⁻¹ without sacrificing volume increment, because the level of mortality increased with stand density index. The thinning intensity did not affect the abundance of understory vegetation but did affect the cover of understory trees and graminoids. Intensively managed plantations could sequester and store the same amount of carbon as less intensively managed plantations. However, because fire is a major component in a pine-dominant ecosystem, carbon in larger diameter trees would be more resilient to wildfire than carbon in small diameter trees or understory vegetation. FOR. SCI. 59(6):670–680.

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MANAGING FORESTS FOR MULTIPLE ECOSYSTEM SERVICES has become increasingly important (Noble and Dirzo 1997, Canadell and Raupach 2008, Paquette and Messier 2010). As a part of provisioning services, traditional wood production cannot be overlooked because demand for wood products has been increasing significantly with the rapid growth of the world's population along with increasing standard of living (Food and Agriculture Organization [FAO] 2009, p. 62). For example, worldwide consumption of wood, excluding wood panel and paper products, has increased from 1.5 billion m³ in 1965 to 2.1 billion m³ in 2005, and is expected to reach 3.0 billion m³ in 2030 (FAO 2009, p. 62–44). The only way to meet the rising demands is to increase productivity of existing forests, convert more lands to tree plantations, or both. Regardless, forests sustainably managed for wood production are critical to meeting the global demand.

Ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) is one of the most widely distributed coniferous species in northwestern North America (Oliver and Ryker 1990). Ecosystems dominated by this species in the western United States play a significant role in wood production, water purification, climate regulation, and many other benefits to the society (Millennium Ecosystem Assessment 2005). Because limited information was available to manage young growth ponderosa pine forests 40 years ago, a series of levels-of-growing-stock (LOGS) studies was es-

tablished in young, even-aged stands throughout the range of ponderosa pine in the western United States by the USDA Forest Service using a common study plan (Myers 1967). The original objectives of these studies were “to determine (1) optimum stand densities for maximum growth of usable wood per tree and per acre over a range of site qualities and average diameters and (2) growth and yield obtainable with repeated thinning” (Myers 1967). For several decades, these studies have produced much needed information for managing even-aged ponderosa pine stands in the western United States. For example, Oliver (1979a, 1997) found that repeatedly thinning a stand to a stand density index (SDI) of 450 (number of trees ha⁻¹ indexed to a quadratic mean diameter of 25.4 cm [i.e., 10 in.]) resulted in the greatest stemwood productivity and least bark beetle-caused mortality on the west slope of the Sierra Nevada in California. Similar results were also found at other study sites (Barrett 1983, Cochran and Barrett 1995, Oliver 1995).

Besides wood production, ponderosa pine forests also provide important habitat for various wildlife species and forage for livestock grazing (Uresk and Severson 1989). Studies have found that appropriate density manipulation is a necessity for development of understory vegetation, which provides food and cover for a variety of wildlife in the Cascade and the southern Rocky Mountains (Riegel et al. 1995, Moore et al. 2006, Tappeiner et al. 2007, p. 100). Total production of grasses, sedges, and forbs increased

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significantly after thinning a dense ponderosa pine stand (Uresk and Severson 1989, Moore et al. 2006, Tappeiner et al. 2007, p. 108). In addition, preferred browse species along with understory species providing fruit increased after thinning (Wender et al. 2004, Moore et al. 2006). Some understory species are important sources of nutrition for cattle and deer. For instance, deerbrush (*Ceanothus integriramus* Hook. & Arn.) on the west slopes of the Sierra Nevada is an aggressive species after wildfires. Its current year's growth, flowers, and seed are highly palatable and nutritious to cattle and deer during the early and mid-summer grazing period (Sindel 1962). Based on a study soon after the Elliot Ranch, California, plantation was established, Sindel (1962) recommended using cattle to control this competing species to achieve successful plantation establishment.

Species diversity may also be influenced by stand density management in ponderosa pine ecosystems. For more than a century, logging, grazing, and fire suppression have altered stand structure, composition, and function (Covington et al. 1997). Density management by thinning has been historically used to change the stand structure and species composition. It may also increase plant diversity (Griffis et al. 2001, Moore et al. 2006), even though the plant community may also include exotic species (Bailey et al. 1998, Griffis et al. 2001). Information on exotic species is very important for forest managers to address public concerns from various stakeholders.

Treatments of young stands may not only affect biodiversity but also alter the carbon pools (Misson et al. 2005, Campbell et al. 2009, Zhang et al. 2010). Because forests play a significant role in carbon sequestration and storage (Canadell and Raupach 2008, FAO 2009, p. 76), the impact of stand density management on carbon pools must be better understood for foresters to effectively design a management regime that captures and stores the most atmospheric CO₂ by forests. This is particularly important in fire-dominated ecosystems such as ponderosa pine or mixed-conifer ecosystems in California (Agee 2007) because wildfires are frequent in the region. Carbon can be easily released back to the atmosphere if forest stands lack the capability to resist this disturbance.

In this study, we summarized data collected over 40 years from the Elliot Ranch installation, the most productive site for ponderosa pine among the LOGS studies. The objectives of the current study were to address the following four questions. (1) Have the original objectives been fulfilled in the long term by comparing the results of the previous reports (Oliver 1979a, 1997)? (2) How do stand densities affect understory vegetation development? (3) Does aboveground carbon sequestration and storage differ significantly among stand densities? (4) Can we improve stand health and resilience to wildfires and insects by manipulating stand density?

Materials and Methods

Study Site

The Elliot Ranch plantation is located 7.6 km northeast of Foresthill, Placer County, California (latitude 39°04' N,

longitude 120°45' W, elevation 1,180 m above sea level), on a gentle, south-facing slope on the west slope of the northern Sierra Nevada. Annual precipitation at Foresthill from 1940 to 2009 averaged approximately 1,270 mm (Figure 1), of which about 87% occurs from November through April. Average maximum temperature was 19.2° C, and minimum temperature was 8.2° C. Extreme high and low temperatures were 41.7° C and −8.3° C, respectively. The climate is typically Mediterranean with hot, dry summers and mild, wet winters (Oliver 1997).

Three soils occur within the study area. Underlying half of the area is Cohasset loam. One-third is underlain with Horseshoe gravelly loam, a Xeric Haplohumult developed from Tertiary Period river gravels. Covering the remaining area is an alluvial soil not easily classified as to series. Depth to parent material is at least 1.5 m in all three soils. Site index was estimated between 35 and 37 m at 50 years (Powers and Oliver 1978). The Horseshoe Series and alluvial soils show similar site quality and are slightly less productive than the Cohasset Series (Oliver 1997).

The study area was burned severely in 1936 by the McKenzie Mill Fire. From 1937 to 1940, portions of the area were planted, but the plantings were unsuccessful (Sindel 1962). On Sept. 8, 1949, the Elliot Ranch Fire burned the brush and snag field originating from the previous fire. In March and April of 1950, ponderosa pine 1-1 stock from the appropriate seed zone was hand planted at a density of 2,200 stems ha^{−1}. The experimental plots were installed in

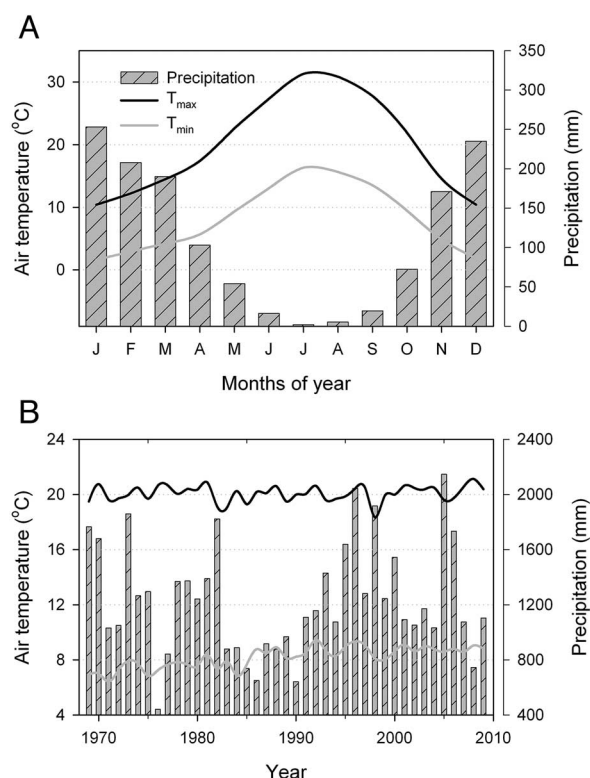


Figure 1. Monthly (A) and annual (B) precipitation and mean maximum and minimum temperature at Elliot Ranch LOGS study site. Temperature data were extrapolated from either Auburn or Foresthill, California. Precipitation data are originally from Foresthill (Western Regional Climate Center 2012).

1968 when the plantations were 20 years old. By that time, trees completely dominated the deerbrush understory; the average tree was 18 cm dbh (measured at 1.37 m above breast height) and 10 m tall. Detailed descriptions for the site can be found in Oliver (1979a, 1997).

Experimental Design

All of the of six ponderosa pine LOGS study sites used a common experimental design (Myers 1967). However, growing-stock levels (GSLs) varied based on specific site productivity. At the site used in this study, five GSLs were used. Each GSL was randomly assigned to one of three replicates of 0.2 ha each (i.e., an experimental unit, hereafter termed a “plot”), with basal area (BA) in English units of 40, 70, 100, 130, and 160 ft² ac⁻¹, approximately equivalent to 9, 16, 23, 30, and 37 m² ha⁻¹. At age 20 years, all plots were thinned to the targeted GSLs. The exception was plots with an assigned GSL of 37 m² ha⁻¹ because they did not reach this BA until age 25 years. All plots had a 10-m wide buffer strip around plot boundaries, and all thinnings were conducted using thinning from below (i.e., removing trees from lower crown classes to favor those in the upper crown classes).

The plots were thinned again to the assigned target GSLs at ages 25, 30, and 40 years. However, at ages 30 and 40, the target GSLs were redefined from a measure of BA to a SDI, based on the number of trees per unit area and the quadratic mean diameter indexed at 10 in. or 25.4 cm (Reineke 1933), because SDI is more independent of stand age and site quality. The SDI values equivalent to the original GSLs were 180, 320, 450, 590, and 720 trees ha⁻¹, representing 20, 35, 50, 65, and 80% of limiting SDI of 902 trees ha⁻¹ for ponderosa pine in northern California (Oliver 1997).

Overstory Tree Measurements

Dbh was measured on all trees before the GSLs were imposed. For each plot, the use of thinning from below resulted in retention of the most vigorous, well-formed trees with some consideration given to uniform spacing. Immediately after plots were initially thinned, all remaining trees were tagged and remeasured for dbh at age 20 years. Height was measured on every fifth tree. Then, dbh for all trees and total height for every fifth tree were remeasured every 5 years from ages 25 to 60 years (i.e., eight more times). As noted, plots were thinned again at ages 25, 30, and 40, and because all trees were numbered after the first thinning at age 20, all thinned and remaining trees were tracked before and after thinning. Trees that died were assumed not to have grown during the period encompassing tree death.

Mortality Including Bark Beetle Impacts

At each remeasurement, the tree condition was recorded for each tree including damage from insects and diseases, wind or snow, and stem deformity. Because bark beetles, including both mountain pine beetle (*Dendroctonus ponderosae*) and western pine beetle (*Dendroctonus brevicomis*), frequently attack ponderosa pine in the region (Oliver 1997), we recorded beetle presence for each tree. Because

these beetles only attack live trees, a dead tree with beetle presence was regarded as beetle-caused mortality.

Understory Vegetation Inventory

From 1970 to 1985 (ages 21–36 years), an inventory of understory vegetation was conducted approximately every 4 years in late summer on two randomly selected replicates of the lowest (GSL40), middle (GSL100), and highest (GSL160) growing stock levels. Twenty circular subplots, each with a radius of 1.6 m, were installed within each of the selected plots. The area of each plant was measured by projecting the plant onto the equivalent ground area during each inventory. To include all plant species possible in our inventories, we also measured plant skeletons for those herbaceous species that died in the early summer. Nevertheless, some small individuals could have easily dried up and blown away. Thus, our estimate of herbaceous species could be underestimated. Plant species were identified using Munz (1959) except for grasses that were simply categorized as graminoids. For each plant, the life form and status as a native or introduced species were based on the US Department of Agriculture (2012) plant identification Web site. Then, plant cover was calculated as plant area expressed as a percentage of plot size. Plant abundance was estimated from number of plants. The cover and abundance were categorized as forbs, graminoids, shrubs, and trees. In July 2004, because the original vegetation subplots could not be completely relocated, we measured plant species and cover at 55 temporarily established circular subplots each with a 0.4-m radius along two transects across each of 15 plots (i.e., all experimental units of all GSLs). Plant cover and abundance were estimated with the same method as used previously and then were summarized by averaging the plant cover and abundance by plot.

Aboveground Tree Biomass and Carbon Pools

Aboveground individual tree biomass (i.e., dry weight) was estimated from the dbh-based allometric equations developed for ponderosa pine in northern California (Zhang et al. 2010). Plot-level biomass was estimated by summing live trees within each plot for each measurement period. Carbon was estimated with the assumption that carbon concentration was approximately 50% using a standard of the Intergovernmental Panel on Climate Change (2003). The total aboveground carbon in standing live trees was then summarized for each plot and measurement.

Plot-Level Variables

The total stem volume inside bark was determined on a sample of 500 trees by using a Barr-Stroud FP15 optical dendrometer on standing trees to measure diameters outside bark, and diameters inside bark were obtained via application of a regional bark thickness equation (Cochran 1976). Trees were sampled from Elliott Ranch, Show Plantation, and Edson Creek, California. Another 113 trees were destructively sampled from the Long-Term Soil Productivity study sites in California (R.F. Powers, USDA Forest Service, unpubl. data, Mar. 30, 2010) and diameters inside bark

were measured directly on stem sections. Section volumes from both standing and felled trees were computed as frusta of cones. A tree-level inside-bark stem volume equation was then developed from all 613 sampled trees (Figure 2)

$$\hat{V} = 0.0000549 (\text{dbh})^{2.696} \quad (1)$$

where $\hat{V}$ (m^3) is volume inside bark and dbh is outside bark dbh in cm. Plot-level volume (Vol) was calculated by summing individual tree volumes in each plot for each measurement period.

SDI was estimated using a modified form from Reineke (1933) by converting English units to metric units

$$\widehat{\text{SDI}} = \text{TPH} \cdot (\text{QMD}/25.4)^b \quad (2)$$

where TPH is the number of trees ha^{-1} and QMD is a quadratic mean diameter in cm at the plot level. Although b is 1.605 for the general SDI relationship (Reineke 1933), 1.77 for b has been found to be a better fit for ponderosa pine in northern California (Oliver and Powers 1978) and was used here.

Plot-level variables were derived following Husch et al. (1982, p. 291–310) and Pretzsch (2009, p. 47) without considering in-growth, which were naturally regenerated seedlings. First, gross yield per ha for BA, Vol, and above-ground biomass (i.e., gross BA, gross Vol, and gross biomass) was calculated for nine times using all living trees for the first observation (after the GSL was applied), and for all subsequent observations, material removed from thinnings and mortality was included. Thus, we excluded any trees removed in the original thinning from these calculations. Second, we calculated periodic annual increment (PAI) for QMD (cm year^{-1}), average height (m year^{-1}), BA ($\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$), Vol ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$), and biomass ($\text{Mg ha}^{-1} \text{year}^{-1}$) using net increase; that is, the change based on trees at the end of the measurement period relative to those at the start of the measurement period. These were calculated for eight periods between measurement times by using the endpoint of each period as the corresponding age. Third, total BA, total V, and total biomass were calculated by gross accumulated yield at age 60 years including trees removed in the initial thinning. Finally, SDIs were calculated using all live trees at the endpoint of each period.

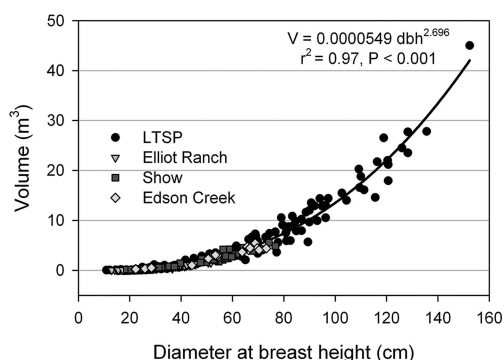


Figure 2. Measured and estimated individual tree volumes for ponderosa pine across California. LTSP, long-term soil productivity.

Effects of Growing Stock Levels on Plot-Level Variables

The effects of growing stock levels on a number of plot-level variables were assessed via a linear mixed-effects model fitted using SAS PROC MIXED (version 9.3; SAS Institute, Inc., Cary, NC), with age as a covariate and plot as the experimental unit. Because the relationship with age could have been nonlinear, additional powers of age were also considered, along with interactions between GSLs and the age variables. An autoregressive model with varying measurement times [i.e., SP(POW)] was used in all models to account for serial correlation resulting from repeated plot measurements over time. Using the notation from Littell et al. (2006, p. 334–339), the models are the following

$$y_{ijk} = \mu + \tau_i + \gamma_{ij} + \text{Age}_{ijk}(\beta_i + b_{ij}) + \varepsilon_{ijk} \quad (3.1)$$

$$y_{ijk} = \mu + \tau_i + \gamma_{ij} + \text{Age}_{ijk}(\beta_i + b_{ij}) + \text{Age}_{ijk}^2(\beta_{2,i} + b_{2,ij}) + \varepsilon_{ijk} \quad (3.2)$$

$$y_{ijk} = \mu + \tau_i + \gamma_{ij} + \text{Age}_{ijk}(\beta_i + b_{ij}) + \text{Age}_{ijk}^2(\beta_{2,i} + b_{2,ij}) + \text{Age}_{ijk}^3(\beta_{3,i} + b_{3,ij}) + \varepsilon_{ijk} \quad (3.3)$$

where y_{ijk} is the dependent variable measured for the i th GSL, the j th plot, and the k th age, μ is the overall mean, τ_i is the fixed effect of the i th GSL, Age_{ijk} is the k th age within the j th plot from the i th GSL, β_i is the slope for the i th GSL, b_{ij} is the random effect of the j th plot on the slope for the i th GSL with $b_{ij} \sim N(0, \sigma_b^2)$, γ_{ij} is the random effect of the j th plot from the i th GSL with $\gamma_{ij} \sim N(0, \sigma_\gamma^2)$, and $\text{Cov}(\varepsilon_{ijk}, \varepsilon_{i'j'k'}) = \sigma^2 |\text{Age}_{ik} - \text{Age}_{i'k'}|$ if $i = i', j = j',$ and $k \neq k',$ $\text{Cov}(\varepsilon_{ijk}, \varepsilon_{i'j'k'}) = \sigma^2$ if $i = i', j = j',$ and $k = k',$ and $\text{Cov}(\varepsilon_{ijk}, \varepsilon_{i'j'k'}) = 0,$ otherwise. Besides accounting for the repeated measures, these models allow for random deviations of the slopes and intercept by plot.

For the fixed effects we only consider estimable functions (Littell et al. 2006) so that restrictions such as requiring $\sum_i \tau_i = 0$ or $\tau_{160} = 0$ to obtain unique estimates all result in the same values for the estimable functions and the same values for testing the equality of fixed effects (such as $H_0: \tau_{40} = \tau_{70} = \tau_{100} = \tau_{130} = \tau_{160}$).

Two steps were taken to choose the most appropriate model for each variable. First, we evaluated Studentized residual plots and a normality plot of residuals to determine whether the variable should be transformed. We found that PAI QMD, PAI height, PAI BA, PAI Vol, and PAI biomass did not require any transformations. However, SDI required a square root transformation and a natural log transformation was applied to gross BA, gross Vol, gross biomass, and understory cover and abundance. Transformations yielded residuals that were approximately normal and with homogeneous variance across the predicted values. Second, after all models were fitted, the best fitted model was selected for each variable based on plots of the Studentized residuals and guided by the Akaike information criterion (AIC). All variables were compared by the Tukey-Kramer test by controlling for the overall $\alpha = 0.05$ after adjustment for the age covariates.

To examine changes in mortality among GSLs, we used

a generalized linear mixed-effects model with numbers of dead stems as the dependent variable and with GSL as a fixed effect. SAS PROC GLIMMIX was used to fit this mortality model using a negative binomial distribution and a log-link function. Random effects were specified as per the linear mixed-effects models. Data for the mortality analysis was pooled over age because of the large number of zeros for each plot/age/GSL combination and a model that included age did not produce a significant effect. In addition, plotting the sample means over time did not show any discernible pattern with age.

Results

Overstory Tree Growth

The GSL treatments affected all growth variables ($P < 0.05$) except for PAI height ($P = 0.39$) and PAI Vol ($P = 0.07$) (Table 1). The age effect was significant (i.e., as age, age squared, and/or age cubed) for all growth variables. During the initial 15 years after installation, the basal area increment (PAI BA) offset the amount removed by the repeated thinnings although the lowest density treatment (GSL40) produced considerably less basal area than the

other density treatments over 40 years (Figure 3A and B). During these periods, differences in PAI BA were not significant among the other four higher GSL treatments based on the Tukey-Kramer test (Figure 3B). A decreasing trend in PAI BA with increasing ages was observed for all stocking levels. The higher density treatments carried more basal area throughout all measurement periods except for the last one because of heavy mortality at age 60 (Figure 4).

As we expected, stand density affected diameter growth substantially with a mean diameter of approximately 80 cm in the lowest density treatments and approximately 45 cm in the highest density treatments at age 60 (Figure 3C). After installation of the experiment 40 years ago, average tree diameter was approximately 20 cm. The direct effect of three rethinnings on diameter was approximately 3.8 (3.1–4.2) cm among GSLs (Figure 3C). However, the mortality (Figure 5) did not cause a large fluctuation in QMD because mortality was mainly caused by bark beetles that attack trees across all diameter classes.

After the initial thinning, gross BA, gross Vol, and gross biomass during the study period from age 20 to age 60 (1969–2009) was higher at the higher density treatments than at lower density treatments (Figure 6A, B, and C). We

Table 1. P values of fixed effects and the estimates of the 1-year correlations (ρ) of measurements taken on the same plot for the best fitting model for PAI of QMD, height, BA, Vol, aboveground biomass, SDI, and gross BA, Vol, and biomass for overstory trees, and cover (%) and abundance for understory vegetation developed at various GSLs after the initial thinning at age 20.

	GSL	Age	GSL $\times$ age	Age ²	GSL $\times$ age ²	Age ³	GSL $\times$ age ³	
Overstory trees								
PAI QMD (cm yr ⁻¹)	0.01	0.01		0.01				0.048
PAI height (m yr ⁻¹)	0.399	0.01		0.01		0.01		0.027
PAI BA (m ² ha ⁻¹ yr ⁻¹)	0.01	0.01						0.674
PAI Vol (m ³ ha ⁻¹ yr ⁻¹)	0.067	0.01		0.01				0.053
PAI biomass (Mg ha ⁻¹ yr ⁻¹)	0.035	0.01		0.01				0.060
SDI (trees ha ⁻¹)*	0.01	0.01	0.01	0.01				0.042
Gross BA (m ² ha ⁻¹)†	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.889
Gross Vol (m ³ ha ⁻¹)†	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.831
Gross biomass (Mg ha ⁻¹)†	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.878
Understory plants								
Cover (%)†								
Forbs	0.182	0.01						0.003
Graminoids	0.024	0.01						0.463
Shrubs	0.820							0.001
Trees	0.018	0.01						0.435
Abundance (no. ha ⁻¹)†								
Forbs	0.490	0.038						0.002
Graminoids	0.096							0.003
Shrubs	0.258	0.01						0.001
Trees	0.309	0.01						0.146

Definition of hypotheses being tested for each column (based on notation from Equations 3.1, 3.2, and 3.3):

GSL: $H_0: \tau_{40} = \tau_{70} = \tau_{100} = \tau_{130} = \tau_{160}$.

Age: $H_0: \bar{\beta} = \frac{(\beta_{40} + \beta_{70} + \beta_{100} + \beta_{130} + \beta_{160})}{5} = 0$.

GSL $\times$ age: $H_0: \beta_{40} = \beta_{70} = \beta_{100} = \beta_{130} = \beta_{160} = \bar{\beta}$.

Age²: $H_0: \bar{\beta}_2 = \frac{(\beta_{2,40} + \beta_{2,70} + \beta_{2,100} + \beta_{2,130} + \beta_{2,160})}{5} = 0$.

GSL $\times$ age²: $H_0: \beta_{2,40} = \beta_{2,70} = \beta_{2,100} = \beta_{2,130} = \beta_{2,160} = \bar{\beta}_2$.

Age³: $H_0: \bar{\beta}_3 = \frac{(\beta_{3,40} + \beta_{3,70} + \beta_{3,100} + \beta_{3,130} + \beta_{3,160})}{5} = 0$.

GSL $\times$ age³: $H_0: \beta_{3,40} = \beta_{3,70} = \beta_{3,100} = \beta_{3,130} = \beta_{3,160} = \bar{\beta}_3$.

: $H_0: = 0$.

* Analyses were based on square root transformation.

† Analyses were based on natural log transformation.

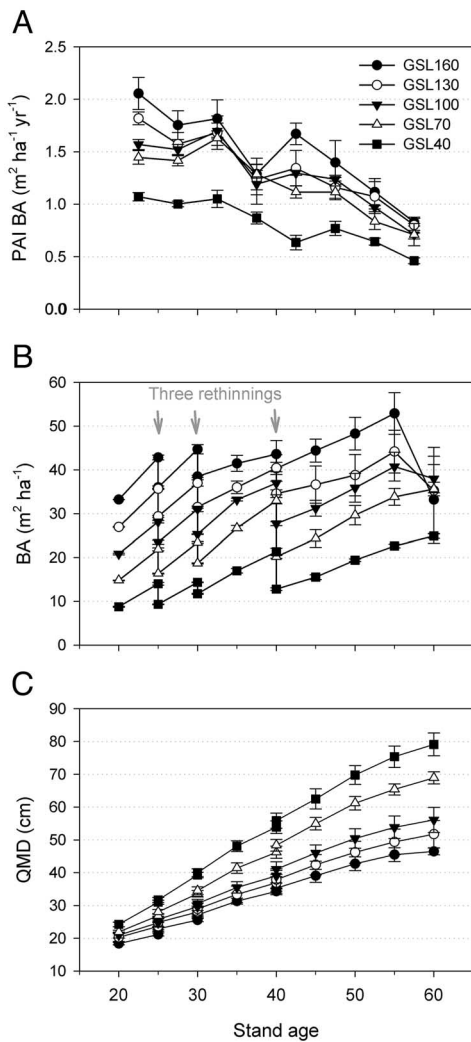


Figure 3. Living tree PAI BA (A), BA (B), and QMD (C) from age 20 to 60 (1969–2009) by growing stock levels after initial thinning in a 20-year-old ponderosa pine plantation in northern California. They were rethinned at ages 25, 30, and 40.

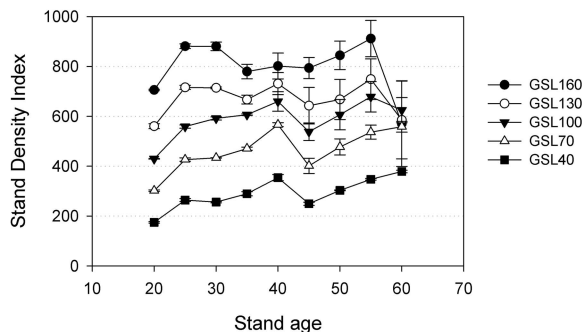


Figure 4. SDI (trees ha^{-1}) by growing stock levels after initial thinning in a ponderosa pine plantation in northern California from age 20 to 60.

found that gross BA differed between any two GSLs at all measurement ages except for the following comparisons: GSL100 versus GSL130 at ages 50, 55, and 60, GSL70 versus GSL160 at age 60, and GSL130 versus GSL160 at age 60. Similarly, gross Vol and gross biomass differed between the GSLs before age 35. Although GSL40 was

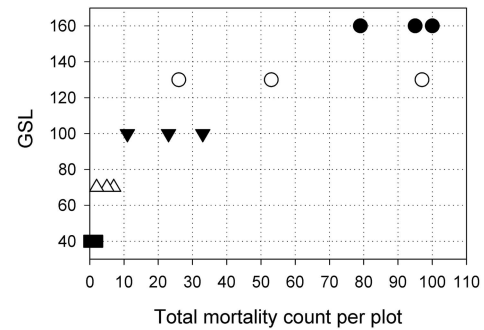


Figure 5. Total plot-level mortality count by growing stock levels after initial thinning in a ponderosa pine plantation in northern California from age 20 to 60.

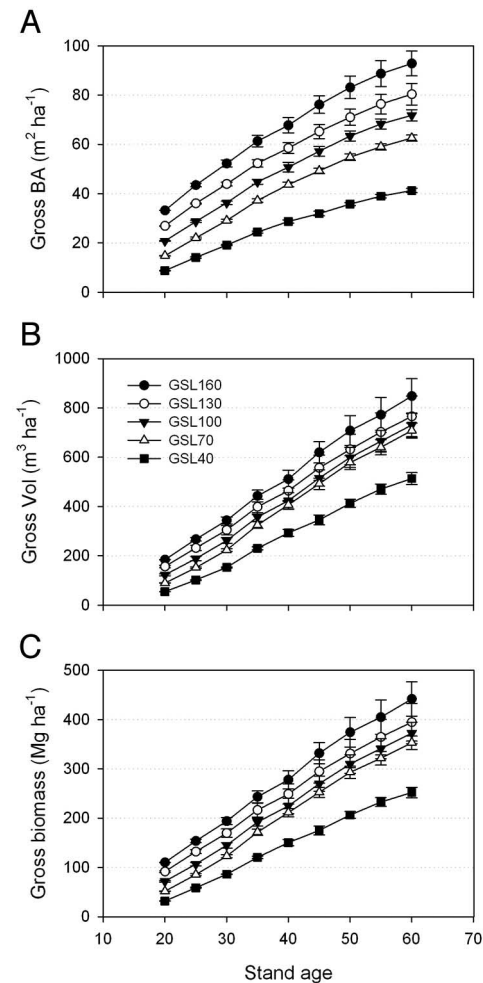


Figure 6. Means (± 1 SE, $n = 3$) for gross BA (A), Vol (B), and aboveground biomass (C) by growing stock levels after initial thinning in a ponderosa pine plantation in northern California from age 20 to 60.

lower than other GSLs during these years, nonsignificant differences between any other two GSLs emerged at age 35. Ultimately, there was no difference among any two GSLs in gross Vol after age 40 and in gross biomass after age 50 (Figure 6B and C). GSL70 was substantially lower than GSL160 for most years. If the trees removed from the initial thinning were included, the overall density effect in total BA production at age 60 was significant ($P = 0.056$)

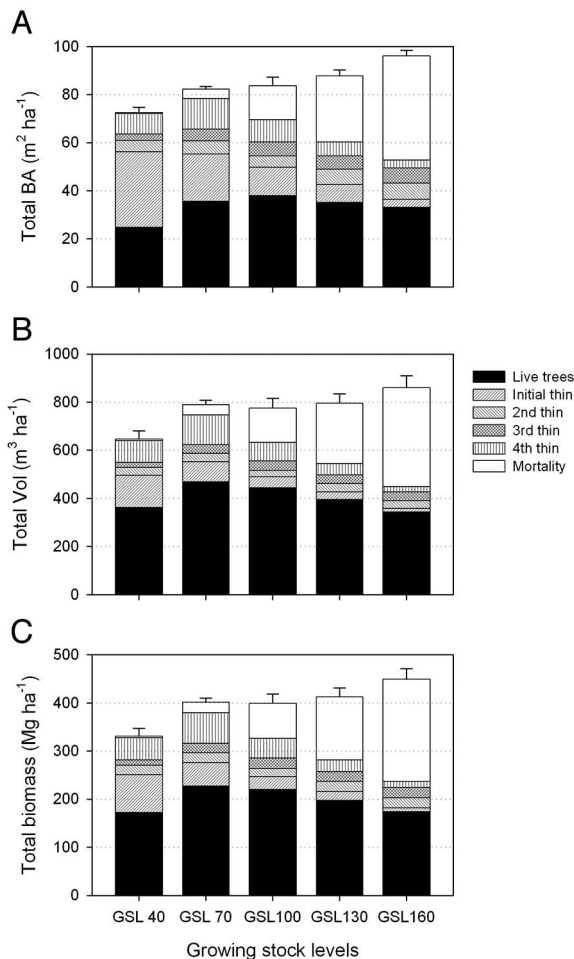


Figure 7. Means and overall stand errors of total production of basal area (A), volume (B), and aboveground biomass (C) including initial thinning by growing stock levels at age 60.

(Figure 7A). Multiple mean comparisons showed that BA only differed between GSL40 and GSL160. For both total volume and total aboveground biomass, density effect was not substantial ($P = 0.15$). No differences were found between any level of GSLs (Figure 7B and C).

Substantial height growth occurred over these 40 years. For most years, trees grew at least 0.5 m year^{-1} , regardless of GSLs. The mean height at age 50 for the top 20 dominant and codominant trees from a sample of plots averaged 38.1 m, which was greater than the site indices of 35–37 m predicted by Powers and Oliver (1978).

SDI and Mortality

The SDIs varied significantly among GSLs and among ages because of rethinnings and mortality (Table 1; Figure 4). Before age 60, SDI was significantly different among GSLs except for that between GSL100 and GSL130 at ages 45, 50, and 55, between GSL70 and GSL100 at age 55, and between any combinations among GSL100, GSL130, and GSL160 at age 55. Because of the heavy mortality before age 60, only GSL40 differed from the other GSLs. Both lowest density treatments were at $\text{SDI} \leq 568 \text{ trees ha}^{-1}$ and the highest density treatments were at $\text{SDI} \geq 568 \text{ trees ha}^{-1}$ throughout these 40 years.

Heavy mortality occurred in the two densest treatments (Figure 5). The two periods with the most mortality due to high beetle activity were between ages 30 and 35, immediately after the second rethinning, and between ages 55 and 60, after the highest SDI that trees experienced in these treatments (Figure 4). There was no or very light mortality in the two lowest density treatments (GSL40 and GSL70), consistent high mortality in GSL160, and more variation in mortality in GSL130. With use of the generalized linear mixed-effects model, differences in mortality among GSLs were detected ($P = 0.005$).

Understory Vegetation

The GSLs significantly affected cover of graminoids ($P = 0.024$) and trees ($P = 0.018$), but not the cover of forbs and shrubs (Table 1). However, there was no significant difference in abundance of understory vegetation among life forms. It appeared that abundance of all species increased with plantation ages although increasing rate was much slower in graminoids (Figure 8A). In addition, all life forms except for shrub cover significantly responded to age (Table 1).

A total of 44 understory plant species were found on these plots except for graminoids that were not identified individually. All plants identified were native species except two: *Rubus leucodermis* and *Stachys arvensis*. Of all plants at age 55, stems of forbs, graminoids, shrubs, and

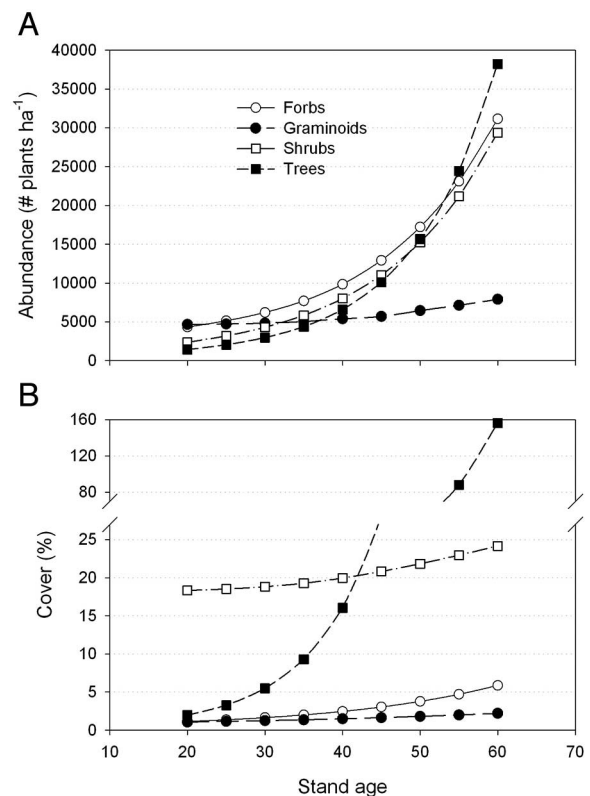


Figure 8. Modeled mean plant abundance (A) and cover percentage (B) of forbs, graminoids, shrubs, and regenerated trees in a ponderosa pine plantation in northern California during last 40 years. The overstory trees were rethinned at ages 25, 30, and 40 after initial thinning at age 20.

trees accounted for 31.9, 11.8, 32.5, and 23.8%, respectively. Of shrub stems, 60% were deerbrush. Incense cedar (*Calocedrus decurrens* [Torr.] Florin), ponderosa pine, and white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) were the major regenerated tree species with 29.0, 27.5, and 20.4%, respectively. Three other common tree species were sugar pine (*Pinus lambertiana* Douglas), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), and California black oak (*Quercus kelloggii* Newberry). These species appeared in all density levels. For the non-native species, we found one *R. leucodermis* plant at the GSL40 plot and 109 *S. arvensis* plants across all plots.

Discussion

Stand Density and Overstory Dynamics

We found a general trend that PAI QMD increased as stand density decreased from GSL160 to GSL40 during the last 40 years and that PAI BA, PAI Vol, and PAI biomass were just the opposite in the earlier stages after the thinning. These results are consistent with previous studies (Oliver 1979, 1995, Barrett 1983, Cochran and Barrett, 1995, 1999, Zhang et al. 2006). An average for GSLs without mortality was at least $9.3 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ and as high as $20.1 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$, which were within the range in yield of $8\text{--}35 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ cited for intensively managed pine plantations in the world (*sensu* Paquette and Messier 2010). Early results suggest that growth augments the amount of basal area removed by repeated thinning (Figure 3A and B), although periodic annual increments decreased considerably after age 35 (1984). This phenomenon might be explained in part as age-related decline (Ryan et al. 1997) as was observed here during the period of age 35–40 (Figure 3A). After these plots were rethinned at age 40, PAI growth during the age period of age 40–45 not only failed to recover from the previous period but also further declined. This reduction might be attributed to a drought from 1982 to 1991 (Figure 1B) and bark beetle mortality (Figure 5). Stands recovered some after age 45 (Figure 3A). However, PAI BA never again reached the levels of the first 10 years. Therefore, it appears to be very unlikely that the decline can be attributed to a single hypothesis as noted by Weiner and Thomas (2001).

The growth rate of ponderosa pine at Elliot Ranch on the west slope of the Sierra Nevada was much higher than that observed in the central Oregon and eastern Oregon LOGS installations. For example, diameter growth for these plots averaged 0.6 cm year^{-1} in the densest GSLs and 1.4 cm year^{-1} in the lowest density GSLs, whereas growth rates were all less than 0.5 cm year^{-1} in the Blue Mountains (Cochran and Barrett 1995) and were less than 0.8 cm year^{-1} at Lookout Mountain (Barrett 1983) in their lowest density plots with basal areas of $6.9 \text{ m}^2 \text{ ha}^{-1}$. Thinning the 20-year-old Elliot Ranch plantation to a stand density of $9.2 \text{ m}^2 \text{ ha}^{-1}$ (the lowest density) resulted in an increase of 54.9 cm in QMD from the start of the study, with 3.3 cm due to three rethinnings from below (Figure 3C). In contrast, the thinning to $36.7 \text{ m}^2 \text{ ha}^{-1}$ produced an increase in QMD of only 28.1 cm , with 4.2 cm due to three re-thinnings during the same period.

One of the main objectives was “to determine optimum stand densities for maximum growth of usable wood per tree and per acre over a range of site qualities and average diameters” (Myers 1967). From another study and earlier data from this study, Oliver (1979a, 1979b, 1997) found that stands with 23 and $32 \text{ m}^2 \text{ ha}^{-1}$ should have low bark beetle-caused mortality and have vigorous growth. The results from this study after 40 years suggest that a stand could be thinned to as low as $16 \text{ m}^2 \text{ ha}^{-1}$ without sacrificing any loss of basal area or volume at age 60 (Figure 7A and B). This is particularly true in this area with high population levels of *Dendroctonus* (personal observations). Therefore, the optimal density regime for total production in such systems is a compromise between maximizing growth production per unit area and minimizing mortality from bark beetles by reducing density and, subsequently, potential total production per unit area. If forests were managed primarily for timber, stands of lower density would produce greater commercial volume than higher density stands (board-foot data are not included). The trends hold even if we eliminate mortality effects by examining total production from these density treatments during the last period (Figure 7). Results showed no difference in cumulative total volume production among stocking levels. The general relationship of increasing stand growth with increasing growing stock was clearly disrupted by bark beetle mortality.

Understory Vegetation Responses to Stand Densities

The lack of difference in both abundance for all understory vegetation and cover for forbs and shrubs was unexpected among GSLs (Table 1). Because the variation was extremely high both between and within GSLs, there might not have been sufficient replications to detect differences of practical importance. However, understory appeared to follow the overstory dynamics along developmental stages. During the earlier years after the initial thinning, abundance of forbs and graminoids was higher than the abundance of shrubs and tree species (Figure 8A). Over 40 years, all vegetation types but graminoids increased exponentially with overstory development. The abundance of graminoids increased slowly, however, as did the cover of all vegetation types except for tree species, which have the potential to add another layer in the forest stand structure (Figure 8B). Mixed results have been reported for responses of understory cover and abundance to overstory density in various forest ecosystems (Hughes and Fahey 1991, Harrington and Edwards 1999, Zenner et al. 2006, Adrian et al. 2009, Cole et al. 2010). Various explanations were proposed such as light, water, nutrient, or pretreatment history. In ponderosa pine stands, Moore and Deiter (1992) found a significant negative relationship between SDI and forage production. This relationship was also reported for aboveground biomass in the Black Hills LOGS installations (Uresk and Severson 1989) and elsewhere in ponderosa pine forests (McConnell and Smith 1965, Clary and Ffolliott 1966, Riegel et al. 1995). However, delayed or no response of shrubs to thinning was also found in Washington (McConnell and Smith 1965) and Oregon (Riegel et al. 1995),

suggesting that certain species might be more limited by nutrients than by light (Riegel et al. 1991).

Exotic species invasion seems not to explain the increases of both abundance and cover in this study. Griffis et al. (2001) found that an increase in understory abundance with disturbance intensity was largely due to a dramatic increase in the abundance of exotic species, both forbs and graminoids. In the current study, only one exotic forb species was found. If there were some exotic graminoids, they would not affect our abundance trends because grasses were regarded as one category. Most species appeared to respond to enhanced light, water, and nutrient availability after thinning (Riegel et al. 1995, Kaye et al. 2005).

Results showed that tree regeneration was abundant among GSLs (Figure 8) in 20 years after the last rethinning. Unfortunately, no unthinned control was included in this study and, as a result, we could not observe response in the absence of disturbance. However, these tree species and patterns of regeneration were the same as the regeneration in any typical mixed-conifer forests in the Sierra Nevada (Oliver and Dolph 1992). More shade-tolerant white fir and incense cedar were observed in higher density stands, and pines were more abundant in the lower density stands.

Stand Resilience to Biotic Disturbance at Different Densities

In ponderosa pine stands throughout western North America, several *Dendroctonus* species are important ecosystem components (Furniss and Carolin 1977). They have been regarded as ubiquitous regulators of density in young, even-aged stands of ponderosa pine (Sartwell and Stevens 1975), although their periodic outbreaks have the potential to cause widespread mortality of older trees in mature forests within large areas (Fettig et al. 2007). In California, *Dendroctonus* spp. cause considerable mortality in ponderosa pine forests (Oliver 1997). By analyzing 155 permanent plots in even-aged ponderosa pine stands, Oliver (1995) found that self-thinning started when SDI reached 568 trees ha⁻¹ (230 trees ac⁻¹) and significant mortality occurred when SDI reaches 902 trees ha⁻¹ (365 trees ac⁻¹). This value (902 trees ha⁻¹) was considerably below the maximum SDI of 1,060–1,236 trees ha⁻¹ (429–500 trees ac⁻¹) used by foresters in the West. However, Oliver (1995) argued that a limiting SDI of 902 trees ha⁻¹ is the result of increased bark beetle activity. In this study, we found substantially more dead trees in the higher density treatments than in the lower density treatments (Figure 5). The results were supported by the fact that the lowest density treatments (GSL40 and GSL70) were at or below SDI 568 trees ha⁻¹ and that the highest density treatments (GSL130 and GSL160) were above SDI 568 trees ha⁻¹ throughout these 40 years (Figure 4). A similar result was also reported in Oregon (Cochran and Barrett 1995).

Although SDI is related to stand susceptibility to bark beetle attack and/or mortality, the mechanistic rationale has not been resolved (Tappeiner et al. 2007, p. 170–171). The current study supports the hypothesis that lower density plots enhanced tree vigor (Figure 3C) with an attendant increase in water and nutrient availability (Long 1985, Jack

and Long 1996). Increasing tree vigor and growth decreases bark beetle attacks on individual trees (Feeney et al. 1998), possibly due to an increase of phloem thickness and resin production (Kolb et al. 1998, Wallin et al. 2008). There might be other benefits to preventing bark beetle infestations by thinning stands to lower densities, which need to be investigated (Fettig et al. 2007).

We did not test the resilience to abiotic disturbance such as wildland fire. Given the history of frequent wildfires in this region, the stands with fewer and larger diameter trees should be more resistant to fire damage and subsequent mortality (Agee 1993, p. 124, Zhang et al. 2008). By running a fire model with typical summer weather conditions for two densities at this site, Zhang et al. (2010) estimated tree mortality to be 36.6% in the GSL70 density plots and 61.5% in the GSL160 plots at age 55.

Stand Density and Carbon Sequestration

Plantations could play a significant role in sequestering CO₂ from the atmosphere and storing it in forests or products (Canadell and Raupach 2008, Malmsheimer et al. 2008). Results from this study show that aboveground living tree carbon was similar among different stand densities (Figure 7C). However, aboveground net primary productivity (ANPP) was relatively higher in the GSL160 plots (8.3 Mg biomass ha⁻¹ year⁻¹ $\approx$ 415 g C m⁻² year⁻¹) than in the GSL40 plots (5.5 Mg biomass ha⁻¹ year⁻¹ $\approx$ 275 g C m⁻² year⁻¹) (calculated from Figure 6C). All the intermediate density plots showed similar ANPP with 7.5 Mg biomass ha⁻¹ year⁻¹. These numbers were very comparable with ANPP reported in Campbell et al. (2009), who found that aggregate ANPP including shrubs was 435 g C m⁻² year⁻¹ in unthinned plots, 216 g C m⁻² year⁻¹ in plots thinned 3 years earlier, and 341 g C m⁻² year⁻¹ in plots thinned 16 years earlier at a study site located a few miles from the current study. Misson et al. (2005) found similar trends in a younger ponderosa pine plantation south of the current site. In addition, had we considered understory vegetation, lower density plots would have been found to store more C than the higher density plots. ANPP could have been the same or even greater in the lower density plots (GSL70–GSL130) than in GSL160.

We cannot account for a complete forest carbon pool without considering wildfires in the fire-dominant ecosystems (Powers 2010, Zhang et al. 2010). Ponderosa pine grown under the Mediterranean climate is surely such a system. Large diameter trees with the major weight of carbon in the stem represent a more stable form of carbon storage than smaller diameter trees if understory vegetation is similar (Zhang et al. 2010). Therefore, lower density plots provide more such carbon than the high-density plots.

Conclusions

To address the four questions that we posed earlier, we found that the optimal stand density would be 16 m² ha⁻¹, in terms of optimizing wood production and potential understory development and disturbing resilience, if the plantation could be thinned four times starting at age 20 during

a 60-year rotation. This number is lower than the 23 m² ha⁻¹ proposed by the previous report (Oliver 1997) because of an increase in bark beetle-caused mortality in recent years. The best reentry time seemed to be when SDI reached approximately 600 trees ha⁻¹. The thinning intensity did not affect the abundance of understory vegetation but did affect the cover of understory trees and graminoids. Except for the lowest density treatment (GSL40), there appeared to be no differences in aboveground carbon stock among overstory stand densities at age 60. However, carbon in larger diameter trees in the lower density treatments would be more resilient to wildfires than carbon in small diameter trees. In addition, bark beetles tended to attack trees in high-density treatments. The dead plant materials accumulated in the high-density treatments can become hazardous fuels and present a fire risk in the forests. Overall, our study supports the management of stands to improve health and resilience to wildfires and insects by manipulating stand density.

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