



Long-term thinning alters ponderosa pine reproduction in northern Arizona



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ARTICLE INFO

Article history:

Received 4 March 2016

Received in revised form 25 April 2016

Accepted 27 April 2016

Keywords:

Pinus ponderosa

Regeneration

Seedling establishment

Silviculture

Soil water content

ABSTRACT

The future of ponderosa pine (*Pinus ponderosa* var. *scopulorum*) forests in the southwestern United States is uncertain because climate-change-induced stresses are expected to increase tree mortality and place greater constraints on regeneration. Silvicultural treatments, which include thinning, are increasingly being used to address forest health concerns by restoring ponderosa pine forests to more open conditions representative of historical forest structure. In light of the greater use of thinning and mounting concerns about the future of the species at the southern edge of its range, further investigations about impacts of thinning on ponderosa pine regeneration and underlying mechanisms are needed. We used a long-term (>50 years) experiment in northern Arizona to investigate impacts of repeated stand thinning that maintained different growing stock basal areas (0, 7, 14, 23, 34, 66 m² ha⁻¹) on early seedling survival, growth, and microenvironment. Seedling survival for the first two years after germination (2013–2015), which had above-average precipitation, was higher than reported in several earlier studies and ranged between 4 and 21% among all basal areas. Seedling density exhibited a negative quadratic relationship with basal area and was positively associated with litter cover. Growing stock levels that fostered the highest seedling survival and density were those with a low density of overstory trees, low canopy cover, high cone production, coverage of soil by a thin layer of litter, and high soil water content at a depth of 15–30 cm. Overstory basal area was positively associated with seedling height but negatively associated with seedling diameter. During this relatively wet period, all basal area treatments supported higher average seedling densities than those previously recommended to produce a multi-aged stand or presettlement structure in the southwestern United States. Our results show that long-term maintenance of low to intermediate basal areas (7–23 m² ha⁻¹) by thinning over the last 50 years led to a favorable microenvironment for early seedling establishment of ponderosa pine.

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1. Introduction

Tree mortality has increased and expanded in western North American forests as a result of increasing drought, warmer temperatures, and associated disturbance by wildfire and insect attacks (Westerling et al., 2006; van Mantgem et al., 2009; Allen et al., 2010; Meddens et al., 2012; Williams et al., 2013; Cohen et al., 2015). Greater drought intensity in the 21st century is projected to contribute to increases in tree mortality and shift the distribution of dominant trees (Choat et al., 2012; McDowell and Allen, 2015) and vegetation communities (Jiang et al., 2013). Given these forecasts for higher forest turnover rates, better understanding of

controls over tree regeneration is important to predict future tree species distribution and abundance. Seedlings are often more sensitive than adult trees to environmental stressors (e.g., drought) caused by climate change (Thuiller et al., 2005; Bell et al., 2014). Therefore, we may not be able to predict seedling responses on the basis of mature tree responses.

The future of ponderosa pine (*Pinus ponderosa* var. *scopulorum*) forests in the southwestern United States is unclear in the face of expected future increases in stresses caused by climate change. Models predict suitable climate space for ponderosa pine will be reduced by 50% in the next century, with 77% of the contemporary climate space lost at the rear (southern) edge of the species' distribution (Rehfeldt et al., 2014). Natural regeneration of ponderosa pine is already heavily constrained by climate (Heidmann et al., 1982; Heidmann, 2008; Petrie et al., 2016) and favorable opportunities

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for regeneration may become more limited in the future due to climate warming and deforestation caused by fire, insect outbreaks, and intense drought (Savage et al., 2013; Williams et al., 2013; Allen et al., 2015; Ouzts et al., 2015; Rother et al., 2015). Germination and establishment of ponderosa pine are influenced by precipitation and temperature (Schubert, 1974; Savage et al., 1996; Petrie et al., 2016), soil type (Heidmann and Thorud, 1976; Heidmann and King, 1992; Puhlick et al., 2012), and competing vegetation (Pearson, 1942, 1950; Heidmann et al., 1982; Heidmann, 2008). Within months of germination seedling roots of ponderosa pine can grow to depths of 50 cm in soil with abundant moisture (Larson, 1963), but only grow to half that depth or less when soil moisture is low (Larson and Schubert, 1969). Many southwestern ponderosa pine forests exhibit episodic recruitment linked to the combination of favorable climate conditions of above-average precipitation and high May temperatures (Pearson, 1933; Savage et al., 1996; League and Veblen, 2006), and well as heavy seed production, low occurrence of surface fire during the seedling stage (Brown and Wu, 2005), and openings in the canopy (Schubert, 1974).

Ponderosa pine forests are currently stressed by legacies of past exploitation and management. Prior to Euro-American settlement in the late 1800s southwestern ponderosa pine forests were described as open stands characterized by widely spaced older trees and sparse pockets of younger trees interspersed with openings of abundant herbaceous cover (Cooper, 1960). After logging removed most large trees by the early 1900s, a combination of factors led to an increase in tree density. The natural frequent-fire regime was disrupted through active fire suppression, and heavy domestic livestock grazing that denuded herbaceous cover created an environment relatively free of fire and herbaceous competition that promoted establishment of a large number of seedlings following years of ample seed production (Arnold, 1950; Cooper, 1960; Covington and Moore, 1994; Savage et al., 1996). As a result, many current stands contain thickets of slow-growing trees, heavy accumulations of litter and woody materials, and low understory vegetation cover (Harrington and Sackett, 1992; Covington and Moore, 1994). These conditions have led to forest health concerns about increased risks of deforestation caused by wildfires, insect outbreaks, and drought (Covington and Moore, 1994; Covington et al., 1997; Allen et al., 2010).

Silvicultural treatments are increasingly being used in the southwestern United States to restore ponderosa pine forests to more open conditions representative of historical forest structure (Arno et al., 1995; Covington et al., 1997), to reduce fuels and reduce wildfire severity (Agee and Skinner, 2005), to enhance growth and resilience of residual trees (Skov et al., 2004; Kerhoulas et al., 2013), and to increase water supply to trees and from forests to streams and aquifers (Grant et al., 2013; Robles et al., 2014). Few studies, however, have investigated impacts of treatments on ponderosa pine regeneration (Bailey and Covington, 2002) and investigations of regeneration under field conditions are notably rare (Petrie et al., 2016). Whereas several studies show that forest treatments can increase soil water availability to plants, most of these studies investigated soil water only for the first several years after treatment and focused only on mature trees (e.g., Stone et al., 1999; Simonin et al., 2007). Information about the relationship between ponderosa pine regeneration and both stand structure and abiotic conditions is needed to develop management strategies that promote successful ponderosa pine regeneration.

We used a long-term (>50 years) experiment at Taylor Woods in northern Arizona, USA, to investigate impacts of different overstory basal areas (cross-sectional area of all trees measured at 1.37 m height) on early seedling survival, growth, and microenvironment. Taylor Woods is one of several level-of-growing-stock (GSL) studies initiated in young, even-aged ponderosa pine stands

throughout the western United States (Schubert, 1971; Ronco et al., 1985). Our study focused on a cohort of seedlings that established in 2013 following heavy cone and seed production and during an unusually wet summer. For this cohort we investigated impacts of six basal area levels (0, 7, 14, 23, 34 and 66 m² ha⁻¹) on seedling density, survival, and growth; tree reproductive output; soil water content; light availability; and understory litter and vegetation. Our investigation of this suite of responses in a long-term thinning experiment is unique as far as we know. We hypothesized that the lower basal area levels (7 and 14 m² ha⁻¹) would have the highest seedling density, survival, and growth, and that differences in seedling performance among basal areas would be associated with tree reproductive output, understory microenvironment, and soil water availability.

2. Materials and methods

2.1. Study area

Taylor Woods is a subdivision of the Fort Valley Experimental Forest located about 14.5 km northwest of Flagstaff, Arizona within the Coconino National Forest on the Colorado Plateau. Mean annual precipitation is 56.4 cm and is distributed in a bimodal pattern with approximately half of this precipitation falling as snow during winter (November–March) and the other half falling during the remaining months. About 29% of precipitation falls during the late-summer monsoon season (July–August). This region also experiences regular drought during May and June. Average daily temperatures range from −3.9 °C in January to 17.2 °C in July (Ronco et al., 1985). The stand has flat topography and is located at approximately 2266 m elevation. The soils at the study site are characterized as a montmorillonitic complex of frigid Typic Argiborolls (USDA, 1975) derived from volcanic material, primarily basalt parent material (Ronco et al., 1985). The soil has a shallow A horizon (about 10 cm), but the soil profile extends from 114 to more than 152 cm in depth before a fractured basalt bedrock occurs (Ronco et al., 1985).

Seasonal precipitation during our study varied from long-term normals in each year. In 2013 when the seedlings we studied germinated and started to establish, precipitation in the study site region (Flagstaff Airport NOAA station) was 70% of average in winter, 20% of average in spring, but 200% of average in summer. In 2014, the first full year of seedling establishment, precipitation was 30% of average in winter, 60% of average in spring, but 160% of average in summer. In 2015, the second year of seedling growth, precipitation was 125% of average in winter, 220% of average in spring, and 85% of average in summer. Thus, the years included in our study had unusually high spring (2015) or summer (2013, 2014) precipitation.

Prior to the implementation of the GSL study in 1962 the stand consisted of overstory sawtimber-sized trees (>50 cm diameter at breast height [DBH]) and dense sapling and pole-sized trees primarily originating in 1919 (Schubert, 1971; Ronco et al., 1985). In 1962 all sawtimber was harvested in a removal cut to leave a dense, even-aged stand consisting of mostly 43-year-old small-diameter saplings and poles. Remaining trees were tagged and measured and thinning slash was lopped and scattered (Schubert, 1971). All plots in the GSL study are within a 36.4 ha stand on a gentle (4%) southwest-facing slope in the *P. ponderosa*/*Festuca arizonica* habitat type (Ronco et al., 1985). Site index is 22 based on height in meters at a base age of 100 (Minor, 1964; Ronco et al., 1985).

Taylor Woods includes six GSLs (34, 28, 23, 18, 14 and 7 m² ha⁻¹) as well as unthinned control and clearcut treatments. Each treatment is replicated in three plots, which range in size

from 0.30 to 0.50 ha. The GSLs are target basal areas that are maintained by rethinning once per decade, which resulted in removal of trees in 1972, 1982, 1992, and 2003 (Bailey, 2008; McDowell et al., 2007). At the time of our study in 2014–2015, 12 years of growth had occurred since the last thinning. Regeneration in 1999 in the two lowest GSLs (14 and 7 m² ha⁻¹) was 41 and 18 seedlings ha⁻¹, respectively (Bailey and Covington, 2002).

2.2. Experimental and sample design

We investigated four (34, 23, 14, and 7 m² ha⁻¹) GSLs plus the unthinned control and the clearcut treatment, for a total of six treatments that span the range of basal area and tree density at Taylor Woods. We included all three replicates of each treatment for a total of 18 plots (6 GSLs × 3 replicates).

In April 2014 we installed a network of 10 systematically located subplots (1 m² quadrats) within each of the 18 plots (Barbour et al., 1987; Fidelibus and MacAller, 1993) to measure biotic and abiotic characteristics related to ponderosa pine seedling density, survival, and growth. The subplots were installed in a systematic design in the middle of each plot with a 10 m buffer from all plot edges. Subplots were marked by rebar, flagging, and GPS for repeated measurements during the 2014 and 2015 field seasons.

2.3. Plot basal area, tree density, and canopy index

In June 2015 we measured current basal area and tree density by counting and measuring DBH of all trees within three 0.04047 ha circular plots (11.3 m radius) in each treatment plot. The unthinned plots were an exception; measurements were made using one or two 0.04047 ha circular plots per treatment plot because of the small size of the unthinned plots (0.3 ha).

We measured canopy cover in July 2014 at all subplots with a LiCor LAI-2000 Plant Canopy Analyzer (LiCor, Inc., Lincoln, NE). Because the LAI-2000 measures all light-blocking objects, we define this measurement as canopy area index (CAI). We did not adjust these measurements to remove cover by woody tissues because we were interested in total cover by foliar and woody tissues. For these measurements we followed the LAI-2000 instruction manual to obtain readings in paired open and below-canopy environments for each subplot. We used a 270° view cap to hide the operator from the sensor, and accounted for small plot sizes by using the C2200 computer program provided by Li-Cor to compute CAI without data from the outer ring.

2.4. Understory microenvironment

We visually assessed by ocular estimation the percentage of ground coverage by graminoids, forbs, shrubs, pine litter, bare soil, dead woody material, and rock in each subplot after the monsoon season (September) in 2014 to quantify the understory environment of seedlings. Plant cover was separated into categories (graminoids grasses, forbs, and shrubs). For analysis of the data we pooled graminoid cover and forb cover together as one response variable termed herbaceous plant cover.

We measured the depth of duff and litter in each subplot once in summer 2014. Each 1 m² subplot was split into quarters and litter and duff depths were measured with a ruler in the middle of each quarter and averaged for the subplot. We defined litter and duff following the USDA Forest Service definitions (USDA Forest Service, FIA, 2011). Duff (humus) was considered as the soil layer dominated by organic material derived from the decomposition of plant and animal litter and deposited on either an organic or a mineral surface. Duff was characterized by the presence of original organic material which has undergone sufficient decomposition

that the source of the material is no longer identifiable. Litter was defined as the undecomposed or only partially decomposed organic material that can be readily identified (e.g., pine needles).

2.5. Soil water content

We measured volumetric soil water content (SWC) in all plots using time domain reflectometry (Trace TDR System 1, 6050X1, Soilmoisture Equipment Corp., Santa Barbara, CA) (Rundel and Jarrell, 1989). We measured SWC at depths of 0–15 cm and 0–30 cm from the surface of the mineral soil using probes installed at the beginning of the study which remained in the same location for the duration of the study. A set of 15 and 30 cm probes was installed in two locations (beneath a canopy drip line and in a canopy opening) in each of the 18 plots. Data from the two locations were averaged to produce SWC for the plot. We measured SWC every two weeks from May to November in 2014 and from May to October in 2015.

2.6. Cone production

We measured tree reproductive output of cones three ways. First, we counted cones present on the forest floor in each subplot in summer 2014. Cone counts were expressed as number per unit land area (m⁻²) for each plot. Second, we measured cone size as dry weight in summer 2014. We collected ten cones from the top of the forest floor adjacent to each subplot for a total of 50 cones per stand per class, and then measured their dry weights after oven-drying at 70 °C for three days. Third, we estimated current production of cones in trees growing in each plot. We counted the number of branch tips per 100 branches (mid canopy) that had mature cones in October 2015 and calculated the proportion of cone-bearing branches. We counted ten trees per stand in the 7, 14, 23, and 34 GSLs. In the unthinned plots we stratified cone counts by tree diameter class because diameter is highly variable among trees and because tree stem diameter is an important determinant of ponderosa pine cone production (Krannitz and Duralia, 2004). We separated trees in each unthinned plot into diameter size classes at the 25, 50, 75 and 90% quantiles. We counted cone production on five trees within 2.54 cm of each of the quantiles' mean diameter for a total of 20 trees per plot in the unthinned treatment. Cone counts were averaged over all trees for each unthinned plot.

2.7. Seedling density, survival, and growth

We investigated new pine seedlings that germinated in the summer and fall of 2013 after a large cone crop in 2012 and ample monsoon rains in 2013, which led to a large population of seedlings in the region. All new seedlings in each 1 m² subplot were identified and mapped in April 2014 using a 20 cm by 20 cm grid. The status (dead, live) of each seedling present in each subplot at the start of the study in April 2014 was recorded in June and October of 2014, and April, July, and October of 2015. From these data we calculated seedling density for each plot as the number of live seedlings per m². In October 2015 we measured diameter (1 cm above the forest floor) using a digital caliper and height using a ruler on all live seedlings.

2.8. Data analysis

All data collected in the subplots were averaged to produce a single value for each plot (n = 18) to avoid pseudoreplication (Hurlbert, 1984). We checked assumptions of distribution and homogeneous variance and residuals before analyzing data and when necessary used distributions other than normal (e.g.,

negative binomial) or rank-based non-parametric tests. We analyzed all data with JMP software (SAS Institute, Inc., Cary, NC). We used correlation and regression to investigate relationships among plot-level values of overstory and understory metrics and seedling characteristics. We compared measurements made once in the study, or once each year, among GSLs with one-way ANOVAs and Tukey-Kramer HSD tests (e.g., litter and duff depth, seedling height and diameter, cone density and dry weight) or with non-parametric Kruskal-Wallis and Dunn All Pairs for Joint Ranks tests (e.g., herbaceous and litter cover, proportion cone-bearing branches). Seedling density data exhibited overdispersion (variance exceeded the mean) (Ver Hoef and Boveng, 2007), but was not zero-inflated, so we used a GLM with a negative binomial distribution. We analyzed the SWC data for each year and depth with repeated measures ANOVA to test the effects of date, GSL, and the interaction between date and GSL. When the SWC data met the assumption of sphericity, we used the univariate unadjusted epsilon test for these effects. When the data did not meet this assumption, we used the univariate adjusted G-G test. When the GSL main effect was significant in the repeated measures ANOVA (significance value = 0.05), we used contrasts to identify differences among GSLs in mean SWC across the growing season of each year. Also, we used one-way ANOVAs and Tukey-Kramer HSD tests on each individual measurement date to investigate differences between GSLs at each date.

We used survival analysis to assess whether GSL affected seedling survival between April 2014 and October 2015. The outcome variable was time until seedling death. We measured survival time using season in each year (spring, summer, and fall in 2014 and in 2015) as the unit of time. Our survival data were interval- and right-censored. Data are interval-censored when the exact time of death is only known to have occurred within a particular time duration (Singh and Totawattage, 2013). Right-censored data are a particular case of interval-censored data when the time of the event does not occur within the study period, as is the case when seedlings survive past the end of the study (Harrell, 2001; Singh and Totawattage, 2013). We used Kaplan-Meier survival curves to show differences in survival among GSLs through time (Harrell, 2001) and a log-rank test to evaluate the strength of differences in survival among GSLs.

We used model selection on plot-level data ($N = 18$) to investigate the role of the canopy, understory, and SWC on seedling survival, density, and growth. In the first step we investigated correlations among all candidate explanatory variables and selected four variables that collectively represent canopy characteristics (basal area), understory characteristics (litter cover), and soil water (SWC_{0-15} , SWC_{15-30}). These four variables were not strongly correlated ($r < 0.75$) with each other, but were strongly correlated ($r > 0.75$) with other variables. For example, litter cover was strongly correlated with other understory metrics such as herbaceous cover ($r = -0.89$) and litter depth ($r = 0.82$), and basal area was strongly correlated with CAI ($r = 0.92$) and tree density ($r = 0.83$). Values of SWC_{0-15} and SWC_{15-30} were averaged over the growing season of both years for this analysis. Next, we ran all possible one-, two-, three-, and four-variable models and used minimum Akaike Information Criterion (AIC_c) (Akaike, 1973) to select the strongest and most parsimonious models. We did not include interactions in these models due to small sample size ($N = 18$).

3. Results

3.1. Overstory

Basal area at Taylor Woods in 2015 was greater than the GSL targets by 2–8 $m^2 ha^{-1}$ depending on the target because the last thinning occurred in 2003. Basal area ranged between 13.6 and

65.7 $m^2 ha^{-1}$ (Table 1). Tree density ranged between 97 and 2933 trees ha^{-1} (Table 1). Plot-level basal area was strongly and positively related to tree density (quadratic regression: $r^2 = 0.79$, $P < 0.0001$) and CAI (quadratic regression: $r^2 = 0.92$, $P < 0.0001$).

3.2. Understory

Litter depth (Fig. 1a), duff depth (Fig. 1b), and litter cover (Fig. 1c) differed significantly among GSLs and generally increased with increasing GSL with the largest increases between the 0 and 7 GSLs. Herbaceous cover was significantly different between 0 and unthinned GSLs with decreasing cover as GSL increased, especially between the 0 and 7 GSLs (Fig. 1d).

3.3. Soil water content

In 2014 water content of surface soil (SWC_{0-15}) varied significantly over GSLs and dates ($P = 0.0392$ and < 0.001 , respectively). The SWC_{0-15} averaged over all 2014 dates was significantly greater in the 14 GSL (22.0, SE = 1.55) than in the 0 (18.7 SE = 1.8), 7 (18.3 SE = 1.7), and 23 (18.8 SE = 1.6) GSLs, and was significantly greater in the 34 GSL (21.3 SE = 1.8) than the 7 GSL (18.3 SE = 1.7). The SWC_{0-15} decreased between May and June of 2014 and increased in response to monsoon rains starting in July (Fig. 2a). Results for the date \times GSL interaction ($P = 0.125$) indicates that this seasonal pattern was generally similar for all GSLs (Fig. 2a). One-way ANOVAs at each sampling date in 2014 revealed that the 0 GSL had lower SWC_{0-15} than the 14 GSL on two dates in June, and the 7 and 23 GSLs had lower SWC_{0-15} than the unthinned GSL in early July after a heavy rain (Fig. 2a).

In 2015 SWC_{0-15} again varied significantly over GSLs and dates ($P = 0.0351$ and < 0.0001 , respectively) with evidence of a marginal difference among GSLs in changes in SWC_{0-15} over time (GSL \times date interaction $P = 0.0732$). The seasonal pattern of SWC_{0-15} in 2015 differed from 2014 in that depletion of spring soil water was more gradual in 2015 and recharge from summer rains did not occur until the middle of August, as compared with early July in 2014 (Fig. 2a and b). Average SWC_{0-15} in 2015 was lower in the 0 GSL (15.2 SE = 1.7) than the 14 (18.9 SE = 1.4), 23 (16.3 SE = 1.5), 34 (19.3 SE = 1.4), and unthinned (19.2 SE = 1.6) GSLs. Low SWC_{0-15} in the 0 GSL occurred most often during the drydown between June and August (Fig. 2b).

Water content of deep soil (SWC_{15-30}) varied significantly over dates in both years ($P < 0.0001$) with similar seasonal dynamics as measured in surface soil (Fig. 2). While average SWC_{15-30} over 2015 was similar for all GSLs ($P = 0.7120$ in 2014, 0.8602 in 2015), results for the GSL by date interaction ($P = 0.0429$ for 2014, 0.1405 for 2015) suggest a difference among GSLs in the

Table 1

Mean (1 SE) basal area, tree density, and canopy area index (CAI) in the growing stock level plots in 2015. The average basal area of unthinned plots in 2015 is shown in parenthesis.

| Growing stock level ($m^2 ha^{-1}$) | Basal area ($m^2 ha^{-1}$) | Tree density ($\# ha^{-1}$) | CAI ($m^2 m^{-2}$) |
|---------------------------------------|------------------------------|-------------------------------|----------------------|
| 0 | 0.0 (0.00) | 0 (0.0) | 0.01 (0.005) |
| 7 | 13.6 (1.07) | 156 (44.7) | 0.77 (0.186) |
| 14 | 16.3 (0.13) | 97 (5.5) | 0.88 (0.014) |
| 23 | 28.2 (1.88) | 278 (36.7) | 1.07 (0.140) |
| 34 | 42.0 (1.73) | 619 (19.4) | 1.34 (0.093) |
| Unthinned (66) | 65.7 (5.86) | 2933 (639.9) | 1.85 (0.071) |

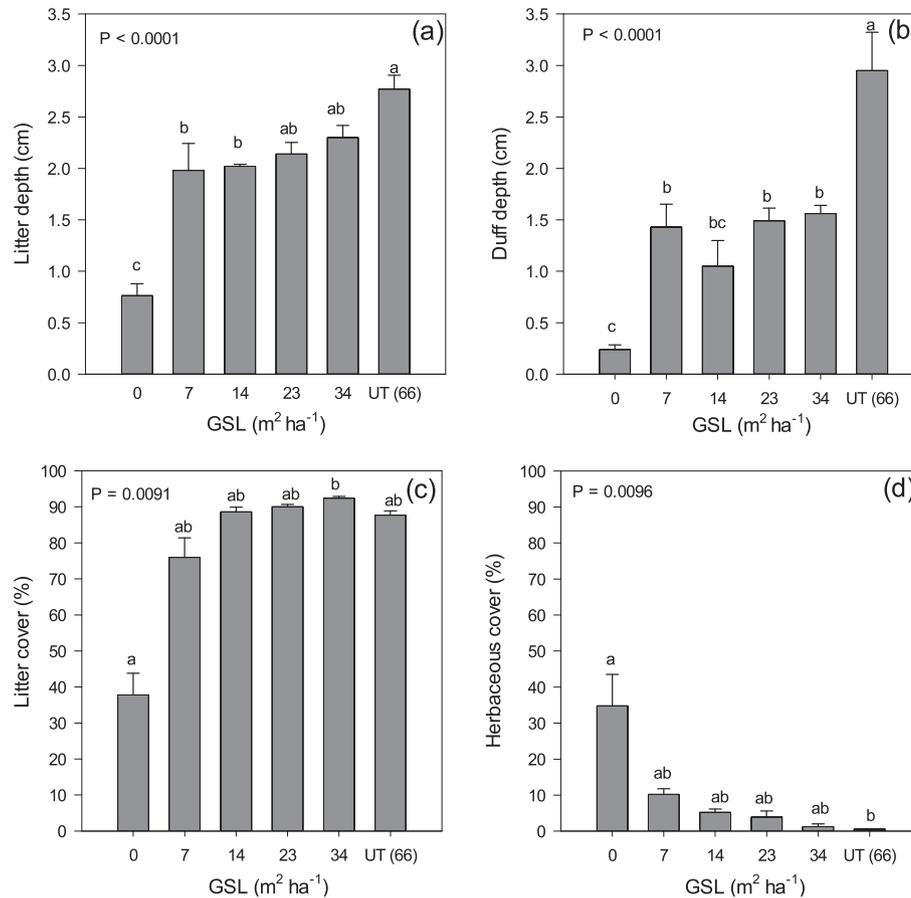


Fig. 1. Mean and 1 SE (vertical bar) understory characteristics at six growing stock levels (GSL): (a) litter depth analyzed with ANOVA and GSLs compared with Tukey's HSD test; (b) duff depth analyzed with ANOVA and GSLs compared with Tukey's HSD test; (c) litter cover analyzed with Kruskal-Wallis test and GSLs compared with Dunn All Pairs for Joint Ranks; (d) herbaceous cover analyzed with Kruskal-Wallis test and GSLs compared with Dunn All Pairs for Joint Ranks. Bars with different letters differ significantly ($P \leq 0.05$). UT is the unthinned treatment and its basal area in 2015 is in parentheses.

change in SWC_{15-30} over time. In 2014 the 0 GSL had the highest SWC_{15-30} of all GSLs in May and October but not in other periods (Fig. 2c). The 34 GSL often had the lowest SWC_{15-30} of all GSLs during dry periods of both years, and the unthinned GSL had the highest SWC_{15-30} of all GSLs during summer rains in 2015 (Fig. 2c and d).

3.4. Cone production

Cone density on the forest floor tended to decrease with increasing GSL but the differences were not significant (Fig. 3a). Cone dry weight (Fig. 3b) and the proportion of cone-bearing branches (Fig. 3c) varied significantly among GSLs and generally decreased with increasing GSL with the largest decreases at GSLs greater than 14. The lowest GSLs (7 and 14) had the highest cone density on the forest floor, heaviest cones, and greatest proportion of cone-bearing branches. The proportion of cone-bearing branches was near zero in the 34 and unthinned GSLs (Fig. 3c). Negative quadratic regressions with basal area explained about 30% of variation in cone density on the forest floor (Fig. 4a) and at least 62% of variation in plot-level cone dry weight (Fig. 4b) and proportion of cone-bearing branches (Fig. 4c). We found no significant difference in proportion of cone-bearing branches between different-sized trees in the unthinned plots; all were near zero. We found a lower proportion of cone-bearing branches in large diameter trees growing in the unthinned GSL (90th percentile DBH 23.0, 23.1, 34.2 cm, for each of the three unthinned plots) compared with trees of similar diameter in the 23 GSL, which had average DBH of 34.0 cm (Chi

square $P = 0.0121$). The average proportion of cone-bearing branches was 0.0003 (SE 0.00003) by trees in the 0 GSL and 0.0397 (SE 0.00765) by trees in the 23 GSL.

3.5. Seedling density

Seedling density differed significantly ($P < 0.001$) among GSLs at all sampling dates and at the conclusion of the study in October 2015 was highest in the 7, 14, and 23 GSLs (Fig. 5). Seedling density in the 0, 34, and unthinned GSLs was less than 0.5 seedlings m^{-2} at the end of the study. Seedling density exhibited a marginally significant ($P = 0.07$) negative quadratic relationship with plot-level basal area when data from the 0 GSLs were omitted from the regression (Fig. 6a). The relationship was weaker and not significant ($P > 0.25$) when data from the 0 GSLs were included in regression analysis. The highest ranked model of seedling density was:

$$\text{Seedling Density} = -3.21475 - 0.084723_{BA} + 0.0922788_{\text{Litter Cover}} + \varepsilon$$

The AIC_c between this model and all other models was >3.33 , which shows the superiority of this model (Appendix A).

Additionally, plot-level seedling density was significantly and positively correlated with cone dry weight ($r = 0.687$, $P = 0.005$) and the proportion of cone-bearing branches ($r = 0.603$, $P = 0.017$), but not with cone density on the forest floor ($r = 0.374$, $P = 0.169$).

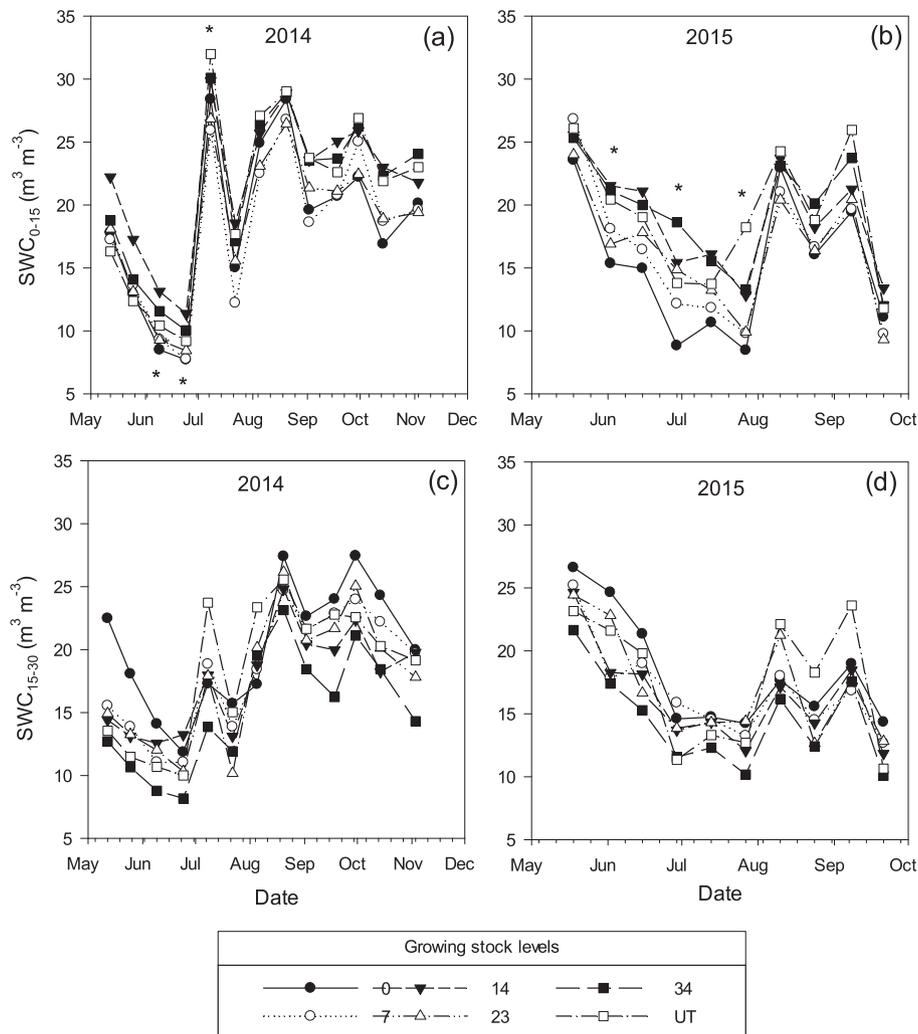


Fig. 2. Mean soil water content (SWC; $\text{m}^3 \text{m}^{-3}$) at depths of 0–15 cm (a, b) and 15–30 cm (c, d) in 2014 (a, c) and 2015 (b, d) at six growing stock levels (GSLs). Dates with significant differences among GSLs are marked by *. UT is the unthinned treatment.

3.6. Seedling survival

Survival of the 2013 seedling cohort at the end of the study in October 2015 differed significantly among GSLs ($P < 0.001$ log-rank test). Kaplan-Meier estimates of survival for new seedlings ranged from 4.2% in the 0 GSL to 21.4% in the 23 GSL. Survival curves showed two distinct groups of GSLs that differed in survival by the end of the study (Fig. 7). The two groups separated into the 0, 34, and unthinned GSLs with low survival and the 7, 14 and 23 GSLs with high survival (Fig. 7). Plot-level seedling survival was highest at basal areas between 10 and 30 $\text{m}^2 \text{ha}^{-1}$ (Fig. 6b), but the relationship between survival and basal area could not be accurately described by linear or quadric regressions ($P > 0.19$). The top-ranked model of seedling survival was:

$$\text{Seedling Survival} = -10.52008 - 0.36078_{BA} + 0.3567186_{(\text{litter cover})} + \varepsilon$$

The AIC_c between this model and the second-ranked model, which added SWC_{15-30} to basal area and litter cover, was 1.944 (Appendix A), which indicates similar explanatory skill of both models. We also investigated correlations between plot-level seedling survival and cone characteristics and found evidence of a weak positive trend with cone dry weight ($r = 0.443$, $P = 0.098$), but no significant

relationships with cone density on the forest floor ($r = 0.203$, $P = 0.468$) and the proportion of cone-bearing branches ($r = 0.266$, $P = 0.337$).

3.7. Seedling growth

At the end of the study in October 2015 average seedling height ranged from 23.3 mm (0 GSL) to 41.5 mm (unthinned GSL) and differed significantly among GSLs ($P = 0.0127$). Height in the unthinned GSL was significantly taller than in the 0, 7 and 14 $\text{m}^2 \text{ha}^{-1}$ GSLs (Fig. 8a). Height was positively and linearly related to plot-level basal area (Fig. 6c). The top-ranked model of height was:

$$\text{Height} = 22.865742 + 0.2112889_{BA} + \varepsilon$$

The AIC_c between this model and all other models was >3.5 , which shows the superiority of this model (Appendix A).

Average seedling diameter differed significantly among GSLs in October 2015 ($P = 0.0066$) and ranged from 1.89 mm (14 GSL) to 1.12 mm (unthinned GSL). Seedlings in the 0 and 14 GSLs had significantly greater diameter than seedlings in the 34 and unthinned GSLs (Fig. 8b). Seedling diameter was negatively and linearly

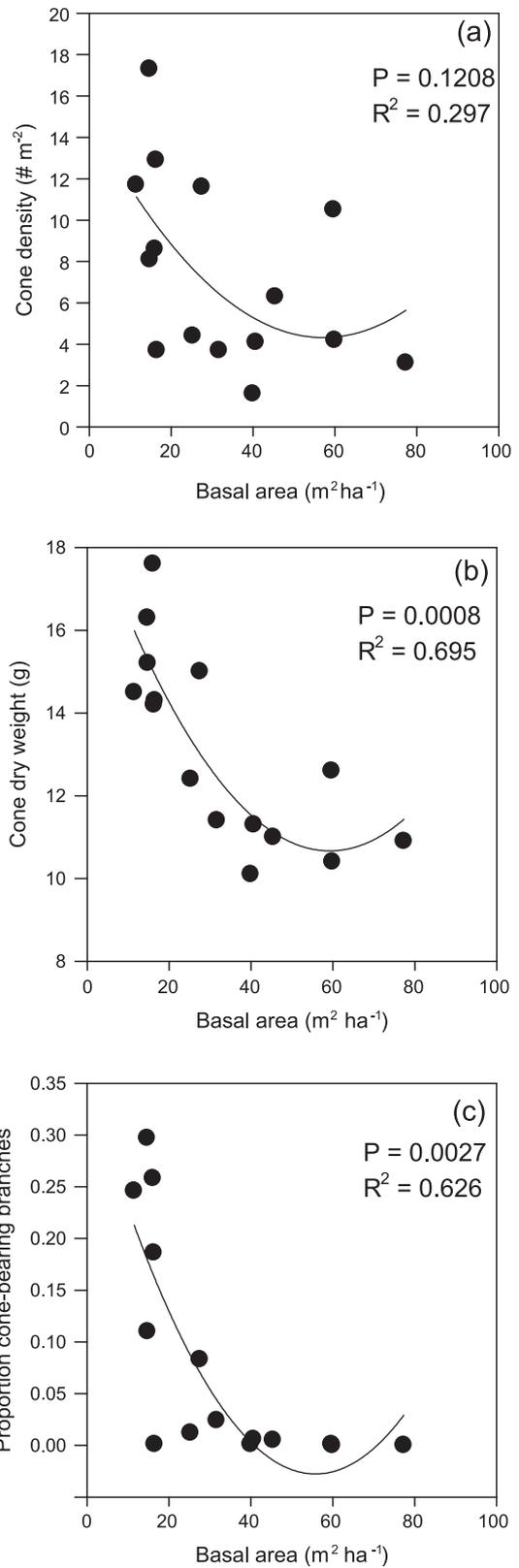
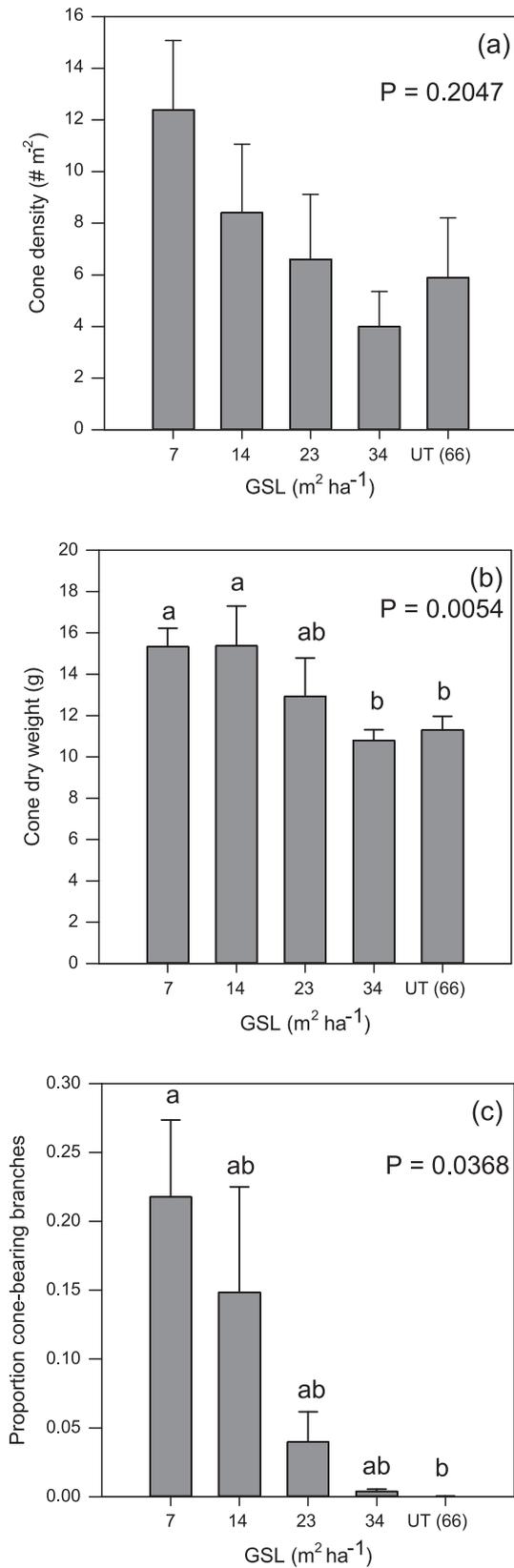


Fig. 3. Mean and 1 SE (vertical bar) cone characteristics at six growing stock levels (GSL): (a) density of cones on forest floor analyzed with ANOVA; (b) dry weight of recent cones analyzed with ANOVA and GSLs compared with Tukey's HSD test; (c) proportion of cone-bearing branches analyzed with Kruskal-Wallis test and GSLs compared with Dunn All Pairs for Joint Ranks test. Values with different letters differ significantly ($P \leq 0.05$). UT is the unthinned treatment and its current basal area is in parentheses.

Fig. 4. Best-fit regressions between cone characteristics and plot basal area (BA). (a) Density of cones on forest floor = $11.39930 - 0.15645 * BA + 0.00325 * (BA - 33.15870)^2$. (b) Dry weight of recent cones = $16.28819 - 0.12157 * BA + 0.00233 * (BA - 33.15870)^2$. (c) Proportion of cone-bearing branches = $0.21919 - 0.00555 * BA + 0.00122 * (BA - 33.15870)^2$.

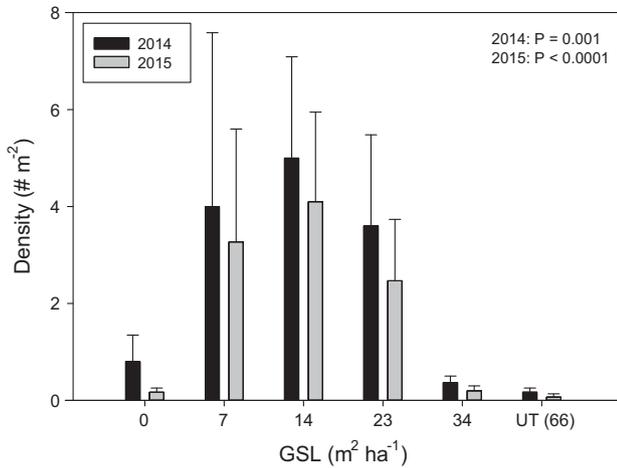


Fig. 5. Mean (1 SE) seedling density in fall 2014 and 2015 in six growing stock levels (GSL). UT is the unthinned treatment and its basal area in 2015 is in parentheses. P values are for the GSL effect from a GLM using a negative binomial distribution.

related to plot-level basal area (Fig. 6d). The strongest model of seedling diameter was:

$$\text{Diameter} = 1.9206484 - 0.011091_{BA} + \varepsilon$$

The AIC_c between this model and all other models was >3.2 which shows the superiority of this model (Appendix A).

4. Discussion

Our results show that long-term maintenance of low basal area by mechanical thinning supported higher ponderosa pine seedling establishment and survival for the first two years after germination. The growing stock levels at Taylor Woods provide an ideal opportunity to examine regeneration response to stand structure. Basal area in 2015 was greater than the GSL targets due to recruitment of previously established seedlings into the sapling category and 12 years of diameter growth in overstory trees since the most recent thinning in 2003. The larger increase in basal area over this period in the 7 m² ha⁻¹ GSL and in the 14 m² ha⁻¹ GSL was a result of the sapling-size regeneration greater than breast height (1.37 m) that was included in measurement of basal area. The 7 and 14 m² ha⁻¹ GSLs were the only treatments where we observed regeneration greater than 20 cm height. The presence of older regeneration is evidence of historically greater regeneration in the 7 and 14 m² ha⁻¹ GSLs, which is consistent with our results for 2014 and 2015 seedling density and survival, and with findings in an earlier study of large (>20 cm height) seedlings (Bailey and Covington, 2002) as well as the lack of surface fire in the study area.

Our finding of a marginally significant (P = 0.07) quadratic relationship between seedling density and stand basal area is consistent with results from Publick et al. (2012) for larger seedlings (≥ 15.2 cm height) in northern Arizona where maximum pine seedling density occurred at a basal area of approximately 27 m² ha⁻¹. In our study seedling density two years after germination was highest

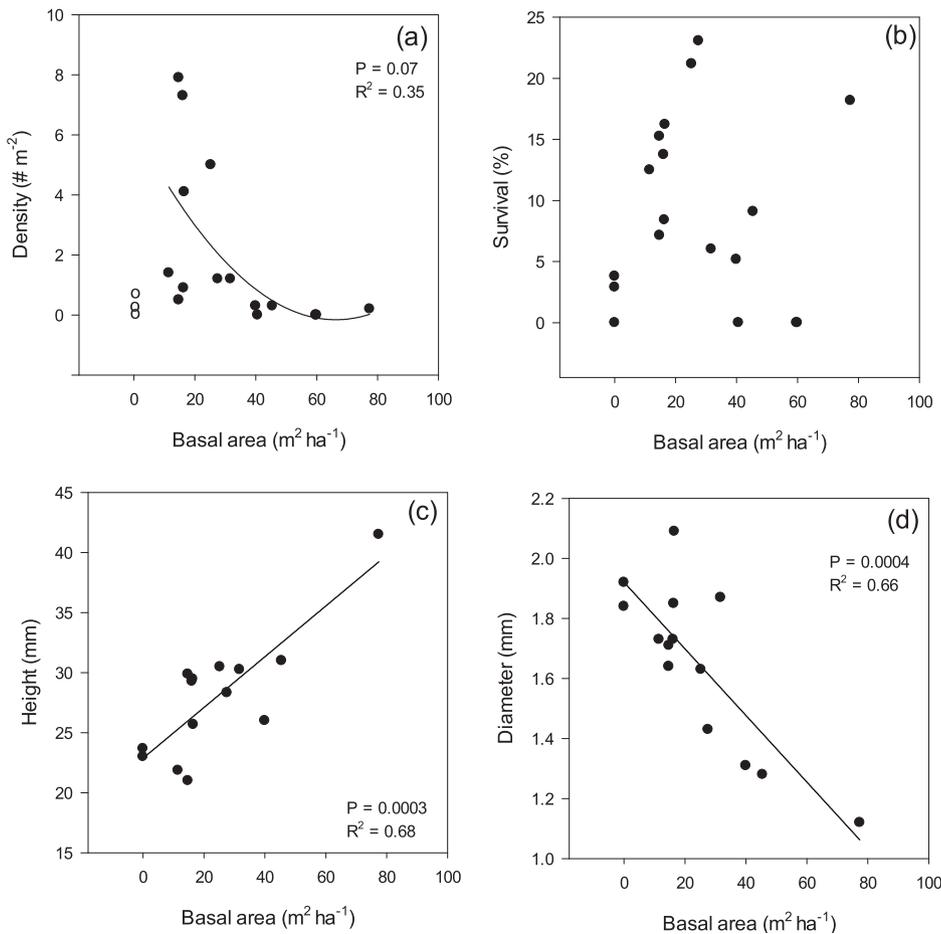


Fig. 6. Best-fit regressions between seedling characteristics and plot basal area (BA). (a) Seedling density = 6.3076 – 0.1950 * BA + 0.0015 * (BA²), for data with clearcut plots (BA = 0, open circles) removed; no models were significant (P > 0.25) when clearcut plots were included. (b) Survival; no models were significant (P > 0.19) with or without clearcut plots. (c) Height = 22.865742 + 0.2112889 * BA. (d) Diameter = 1.9206484 – 0.0110913 * BA.

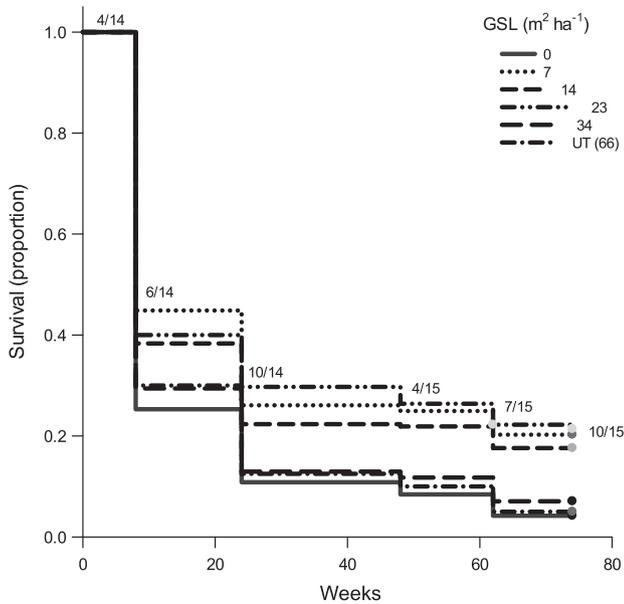


Fig. 7. Seedling survival proportion between April 2014 and October 2015 in six growing stock levels (GSL). UT is the unthinned treatment and its basal area in 2015 is in parentheses. The month and year of each census is shown above the top curve (e.g., 4/14 is April 2014).

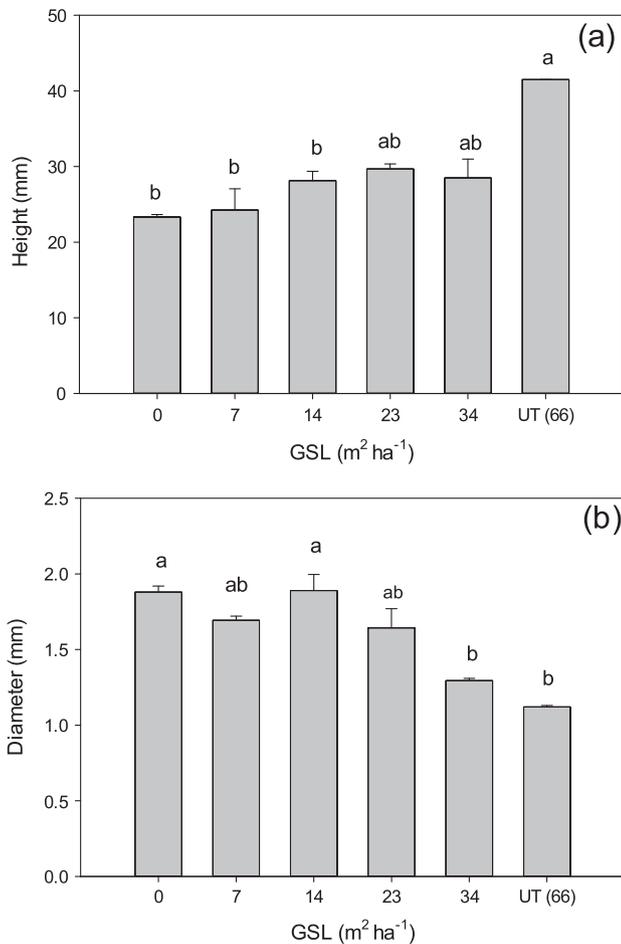


Fig. 8. Seedling height (a) and diameter (b) in fall 2015 in six growing stock levels (GSL). UT is the unthinned treatment and its basal area in 2015 is in parentheses. GSL values with different letters are significantly different.

in the $14 \text{ m}^2 \text{ ha}^{-1}$ GSL and seedling survival was highest in the $23 \text{ m}^2 \text{ ha}^{-1}$ GSL. Low initial seedling density and subsequent survival in the clearcut GSL and the two GSLs with highest basal area ($34 \text{ m}^2 \text{ ha}^{-1}$, unthinned control) resulted in few seedlings two years after germination. These results provide insight into possible mechanisms influencing early establishment of ponderosa pine regeneration and suggest that forest thinning will be useful for enhancing forest regeneration under future climatic conditions.

Our results suggest an influence of litter and herbaceous cover on seedling density and survival. The two GSLs with deepest litter and duff ($34 \text{ m}^2 \text{ ha}^{-1}$ and unthinned) had low seedling survival and density. The deep litter may have kept soil too cold for seed germination (Sackett, 1984) or may have impeded the ability of seedling roots to reach mineral soil and soil water (Pearson, 1950; Stein and Kimberling, 2003). The model selection showed a small positive effect of litter cover on seedling density and survival. The potentially beneficial impact of light mulching by litter on ponderosa pine regeneration may occur through the prevention of excessive soil drying during germination (Krauch, 1936; Pearson, 1950) or protection from high surface soil temperatures (Graham et al., 1990). Understorey herbaceous cover was highest in the clearcut treatment (35%), where herbaceous species likely competed with seedlings for soil moisture (Pearson, 1942; Larson and Schubert, 1969). The bunchgrass Arizona fescue (*F. arizonica*), which occurs at Taylor Woods, is considered one of the most aggressive competitors with ponderosa pine seedlings (Pearson, 1942).

Soil water content (SWC) during the growing season was significantly influenced by GSL at the 0–15 cm depth, but not at the 15–30 cm depth. The dates with significant differences in SWC_{0-15} among GSLs in both 2014 and 2015 all occurred toward the end of the spring drought in late June, when SWC was lowest, and just after the start of the monsoon season in July. Significant differences among GSLs occurred during the driest portion of the growing season, which is similar to results reported by Feeney et al. (1998) and Stone et al. (1999) at a nearby ponderosa pine forest in Northern Arizona. Aside from these periods, SWC at the 0–15 cm depth was similar in all GSLs and stayed above the percentage at which soil water becomes unavailable for root uptake in basalt-derived soil (10%; Heidmann and King, 1992). Although there were no significant differences in SWC among GSLs at the 15–30 cm depth, the $34 \text{ m}^2 \text{ ha}^{-1}$ GSL consistently had the lowest SWC in both 2014 and 2015. This may be a result of high stocking levels of trees (and commensurately high CAI; Table 1) that are actively transpiring water from the soil in the $34 \text{ m}^2 \text{ ha}^{-1}$ GSL. Overall, we conclude that GSL has little effect on surface SWC in years of average to above-average precipitation such as in 2014 (year: 94.6% of normal) and 2015 (125% of normal).

Thinning increased individual-tree reproductive output. Greater cone production and cone mass occurred in the lower GSLs (7, 14, and $23 \text{ m}^2 \text{ ha}^{-1}$) that also produced the greatest number of seedlings. Further, plot-level seedling density was positively associated with cone mass and the proportion of cone-bearing branches. Our results support previous findings of higher cone production in ponderosa pine trees growing in openings and at low densities rather than in dense stands (Curtis and Lynch, 1956; Heidmann, 1983) and in large diameter, vigorous trees (Larson and Schubert, 1970; Linhart and Mitton, 1985). We found greater cone production in trees with similar diameter in the $23 \text{ m}^2 \text{ ha}^{-1}$ GSL compared with the unthinned stand, suggesting that differences in cone production among GSLs were at least partly the result of inter-tree competition. Our results at Taylor Woods are consistent with previous reports (Schubert, 1974) of little cone production in trees smaller than 41 cm DBH in two experimental forests (Fort Valley and Long Valley) in northern Arizona.

Several microenvironmental variables were significantly associated with seedling density and survival in this study. Our model selection identified basal area (–) and litter cover (+) as important explanatory variables for both seedling density and survival. Basal area was positively related to canopy area index (CAI) and thus negatively related to light intensity at the forest floor. Pine seedlings in dense shade rarely survive more than a few years (Pearson, 1950). High basal area also increases litter and duff depths and may increase competition for deep soil water from mature trees. Litter cover can protect the soil surface from temperature extremes (Graham et al., 1990) and evaporation, and prevents excessive soil drying during germination (Krauch, 1936; Pearson, 1950). SWC at 15–30 cm was an explanatory variable in the second-best models for seedling density and survival, which suggests importance of high moisture content in deep soil to seedling establishment given the deep rooting potential of ponderosa pine seedlings.

Our survival results for ponderosa pine seedlings (2–21% depending on GSL) are greater than Stein and Kimberling's (2003) report of 0% survival the first year after germination (1987–1988) in northern Arizona, and Keyes et al.'s (2007) report of 3% survival after two years in central Oregon under more normal precipitation conditions than the wet years included in our study. Seedling mortality of ponderosa pine is high in the first two years (Stein and Kimberling, 2003; Shepperd et al., 2006; Keyes et al., 2007) and continues at slower rates until approximately seven years of age (Shepperd et al., 2006). Stein and Kimberling (2003) attributed much of the mortality of young seedlings to failure of roots to reach the soil due to deep litter, and to desiccation, herbivory, and winterkill. Despite the relatively wet conditions during 2014–2015, the majority of seedling mortality in our study was attributed, via visual observation, to desiccation, with lesser impacts from trampling by animals (e.g., elk) and herbivory.

All GSLs in our study had average ponderosa pine seedling densities higher than recommended to produce a multi-aged stand or presettlement structure in the southwestern United States. Mast et al. (1999) recommended 17 ponderosa pine seedlings ha^{-1} , or 3.6 trees establishing $\text{ha}^{-1} \text{decade}^{-1}$, to eventually produce presettlement structure or for multi-aged management. Heidmann et al. (1982) recommended 1000 seedlings ha^{-1} over 70% of a treatment area to achieve full stocking in an even-aged management objective on sedimentary soils. In our study on basalt-derived soils, seedling density ranged from 70 seedlings ha^{-1} in the unthinned control to 4100 seedlings ha^{-1} in the 14 $\text{m}^2 \text{ha}^{-1}$ GSL and averaged 1713 seedlings ha^{-1} over all thinning treatments. These densities, however, are based on seedlings that are less than three years old, less than 5 cm in height, and occurred in years of average yearly precipitation and above-average summer precipitation. "Seedling" is a loose term encompassing individuals from new germinants to trees shorter than breast height (1.37 m). Tree height-age relationships have shown that naturally established ponderosa pine remains in a seedling stage for up to 25 years before reaching sufficient height (breast height) to classify as a sapling (Shepperd et al., 2006; Puhlick et al., 2013). The only previous work regarding regeneration at Taylor Woods measured the density of seedlings older than those measured in our study. Bailey and Covington (2002) conducted a 100% survey of the 7 and 14 $\text{m}^2 \text{ha}^{-1}$ GSLs for ponderosa pine seedlings at least 20 cm in height and found 41 and 18 seedlings ha^{-1} , respectively. They concluded that these seedling densities, although low by some management objectives, were adequate for the goal of ecological restoration to pre Euro-American settlement forest structure (3.6 trees establishing $\text{ha}^{-1} \text{decade}^{-1}$ over multiple decades).

In the context of long-term sustainability of low-density ponderosa pine forests, Taylor Woods currently appears to have ample seedlings in all GSLs, but further investigation of mortality between years two and ten when seedling mortality continues to be high (Shepperd et al., 2006) is needed to confirm this tentative conclusion. Our results contribute insight into how thinning practices and stand structure in the southwestern U.S. affect regeneration. However, future monitoring of seedlings in the next several years will be necessary to more fully understand long-term impacts of thinning on regeneration success in this period of climate warming. The ample establishment of seedlings from the 2013 cohort documented in our study could lead to overly dense forests in the future without subsequent density management or natural mortality of seedlings.

Growing stock level also affected early seedling height and diameter growth. Seedling height was positively associated with basal area and seedlings were tallest in higher GSLs. Faster height growth in high-shade environments with deep litter is likely a result of allocation of resources to growth to increase light capture in dense stands (Schubert, 1974; Franklin, 2008). Stem diameter exhibited the opposite trend; the largest diameters were found in the clearcut treatment and diameter generally decreased with increasing basal area. Basal area was the only explanatory variable included in the best regression model for seedling diameter and was negatively related to diameter. Seedlings growing in heavily thinned stands with low basal area received more light than seedlings growing in high-basal-area stands, which may have shifted allocation of growth to diameter and away from height.

5. Conclusions

Managing ponderosa pine forests for adequate regeneration will become increasingly important given climate model predictions of increasing aridity and drought-induced mortality of mature trees (Williams et al., 2013; McDowell et al., 2015). We found that long-term maintenance of low to intermediate GSLs (7–23 $\text{m}^2 \text{ha}^{-1}$) over the last 50 years led to a favorable microenvironment for early seedling establishment of ponderosa pine. High seedling density and survival at low GSLs resulted from high cone production by residual trees and changes in microenvironment, including an increase in light and higher soil water content. Using thinning to create and maintain ponderosa pine stands of low to intermediate overstory tree density promotes regeneration in addition to increasing mature tree growth and water uptake (Schubert, 1971; Kolb et al., 1998; Stone et al., 1999; Skov et al., 2005). Given concerns about the future climatic niche space of ponderosa pine in the southwestern U.S. (e.g., Rehfeldt et al., 2014), stand thinning that creates a stage to facilitate future ponderosa pine regeneration in the uncommon years when ample seed production and favorable weather events coincide may be warranted.

Acknowledgements

The project described in this publication was supported by Grant/Cooperative Agreement Number G13AC00268 from the United States Geological Survey to Northern Arizona University. JBB was supported by the USGS Ecosystems mission area and the Climate and Landuse Change mission area. We thank Ashley Wildeman and Megan Sullivan for help with data collection, and two anonymous reviewers for their helpful suggestions. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A

Top regression models of seedling density, survival, height, and diameter ranked by AIC_c (corrected Akaike's information criterion). BA = plot basal area, SWC_{0–15} = soil water content 0–15 cm depth, SWC_{15–30} = soil water content 15–30 cm depth.

| Model (Seedling density) | AIC _c | ΔAIC _c | R ² |
|--|------------------|-------------------|----------------|
| BA + Litter Cover | 85.594 | 0.000 | 0.325 |
| BA + Litter Cover + SWC _{15–30} | 88.930 | 3.336 | 0.300 |
| BA + Litter Cover + SWC _{0–15} | 89.437 | 3.843 | 0.280 |
| BA | 90.046 | 4.461 | 0.023 |
| Litter Cover | 90.224 | 4.640 | 0.013 |
| SWC _{0–15} | 91.388 | 5.754 | 0.053 |
| SWC _{15–30} | 91.456 | 5.822 | 0.057 |
| Litter Cover + SWC _{0–15} | 92.626 | 6.992 | 0.002 |
| Litter Cover + SWC _{15–30} | 93.198 | 7.564 | 0.030 |
| BA + Litter Cover + SWC _{0–15} + SWC _{15–30} | 93.308 | 7.674 | 0.257 |

| Model (Seedling survival) | AIC _c | ΔAIC _c | R ² |
|--|------------------|-------------------|----------------|
| BA + Litter Cover | 112.521 | 0.000 | 0.505 |
| BA + Litter Cover + SWC _{15–30} | 114.465 | 1.944 | 0.531 |
| BA + Litter Cover + SWC _{0–15} | 115.692 | 3.171 | 0.496 |
| BA + Litter Cover + SWC _{0–15} + SWC _{15–30} | 117.409 | 4.888 | 0.548 |
| Litter Cover | 121.038 | 8.517 | 0.064 |
| Litter Cover + SWC _{15–30} | 121.430 | 8.909 | 0.164 |
| SWC _{15–30} | 121.945 | 9.424 | 0.013 |
| BA | 122.288 | 9.767 | 0.008 |
| SWC _{0–15} | 123.169 | 10.648 | 0.061 |
| Litter Cover + SWC _{0–15} + SWC _{15–30} | 123.332 | 10.811 | 0.210 |

| Model (Seedling height) | AIC _c | ΔAIC _c | R ² |
|---|------------------|-------------------|----------------|
| BA | 77.394 | 0.000 | 0.649 |
| BA + SWC _{15–30} | 80.903 | 3.509 | 0.632 |
| BA + Litter Cover | 81.354 | 3.96 | 0.620 |
| BA + SWC _{0–15} | 81.409 | 4.015 | 0.618 |
| BA + Litter Cover + SWC _{15–30} | 85.680 | 8.286 | 0.603 |
| BA + SWC _{0–15} + SWC _{15–30} | 85.960 | 8.566 | 0.595 |
| BA + Litter Cover + SWC _{0–15} | 86.396 | 8.975 | 0.582 |
| Litter Cover | 89.086 | 11.665 | 0.191 |
| SWC _{0–15} | 90.317 | 12.896 | 0.117 |
| Litter Cover + SWC _{0–15} | 92.006 | 14.585 | 0.186 |

| Model (Seedling diameter) | AIC _c | ΔAIC _c | R ² |
|--|------------------|-------------------|----------------|
| BA | –3.999 | 0.000 | 0.630 |
| BA + SWC _{15–30} | –0.765 | 3.234 | 0.619 |
| BA + Litter Cover | –0.116 | 3.883 | 0.601 |
| BA + SWC _{0–15} | 0.010 | 4.009 | 0.597 |
| BA + SWC _{0–15} + SWC _{15–30} | 4.142 | 8.141 | 0.585 |
| BA + Litter Cover + SWC _{15–30} | 4.264 | 8.263 | 0.582 |
| BA + Litter Cover + SWC _{0–15} | 4.927 | 8.926 | 0.561 |
| Litter Cover | 8.465 | 12.464 | 0.098 |
| SWC _{0–15} | 8.894 | 12.893 | 0.070 |
| BA + Litter Cover + SWC _{0–15} + SWC _{15–30} | 10.638 | 14.637 | 0.593 |

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