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ARTICLE

Thinning ponderosa pine (*Pinus ponderosa*) stands reduces mortality while maintaining stand productivity

Jianwei Zhang, Martin W. Ritchie, Douglas A. Maguire, and William W. Oliver

Abstract: We analyzed 45 years of data collected from three ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) levels-of-growing-stock installations in Oregon (OR) and northern California (CA), USA, to determine the effect of stand density regimes on stand productivity and mortality. We found that periodic annual increment (PAI) of diameter, basal area (BA), volume, and aboveground dry mass were significantly related to stand density index (SDI) and stand age at start of the period; the quadratic trends varied among sites. Precipitation departure from the normal for each period explained a significant amount of residual variation in all PAI variables except diameter. BA production did not change significantly as SDI exceeded 270 trees·ha^{-1} at the OR sites and 320 trees·ha^{-1} at the CA site. Stand productivity was the highest at Elliot Ranch (CA) and the least at Blue Mountains (OR). A similar trend held in growth efficiency under lower stand densities (SDI < 600). Most of the mortality was caused by *Dendroctonus* bark beetles in stands that exceeded SDI of 500 trees·ha^{-1}. Limiting SDI was about 900 trees·ha^{-1}, although plots at Elliot Ranch reached much higher than that. The results demonstrate that silvicultural control of stand density can be a powerful tool for reducing bark beetle caused mortality without sacrificing stand productivity.

Résumé : Nous avons analysé les données de 45 ans provenant de trois dispositifs de densité de peuplements de pin ponderosa (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) établis en Oregon (OR) et au nord de la Californie (CA), aux États-Unis, dans le but de déterminer l'effet du régime de densité des peuplements sur leur production et leur mortalité. Nous avons trouvé que les accroissements annuels périodiques (AAP) en diamètre, en surface terrière (ST), en volume et en biomasse aérienne anhydre étaient significativement reliés à l'indice de densité des peuplements (IDP) et à l'âge du peuplement au début de la période; les tendances quadratiques variaient selon la station. Les écarts de précipitation par rapport à la normale de chaque période expliquaient une partie importante de la variation des résidus de tous les AAP, à l'exception de celui du diamètre. La production en ST ne changeait pas de façon significative lorsque l'IDP excédait 270 arbres·ha^{-1} sur les stations de l'OR et 320 arbres·ha^{-1} sur la stations de la CA. La productivité des peuplements était la plus forte sur la station du Ranch Elliot (CA) et la plus faible sur la station des Montagnes Bleues (OR). L'efficacité de croissance montrait une tendance similaire pour les densités de peuplement plus faibles (IDP < 600). Une grande partie de la mortalité était causée par le dendroctone du pin ponderosa dans les peuplements dont l'IDP était supérieur à 500 arbres·ha^{-1}. La valeur limite de l'IDP était d'environ 900 arbres·ha^{-1} bien que l'IDP de placettes de la station du Ranch Elliot atteignît des valeurs beaucoup plus élevées. Les résultats indiquent que le contrôle sylvicole de la densité des peuplements peut constituer un outil puissant pour diminuer la mortalité causée par le dendroctone du pin ponderosa sans sacrifier la productivité des peuplements. [Traduit par la Rédaction]

Introduction

Stand density impacts not only stand productivity, but also the structure and function of forest ecosystems. Thinning can therefore be employed to achieve a variety of ecosystem management goals (Tappeiner et al. 2007). One goal may be to maximize total stem volume production while removing some trees to enhance growth on remaining trees, while another might be the creation of structural diversity. The Ponderosa Pine Level-of-Growing-Stock (PPLOGS) study was initiated in the mid-20th century, when management of young-growth ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) forests was in its infancy (Oliver 2005). Mixed results from a few previous studies provided only limited insight into the potential response of ponderosa pine to thinning (Myers 1967; Schubert 1971). Growth responses were needed over a wider range of stand and site conditions and with a minimum of operational restrictions to yield comprehensive strategies for meeting a variety of management objectives.

The PPLOGS study is a west-wide investigation initiated by several western research stations of the United States (US) Forest Service under a common design (Myers 1967). Six installations were established from 1964 to 1969, including two in Black Hills, South Dakota, in 1964 (Boldt 1970) and one on the Coconino Plateau, Arizona (Schubert 1971; Ronco et al. 1985). We have continued measuring the remaining three sites, two in Oregon (OR) and one on the western side of the Sierra Nevada of California (CA). The original objectives were "to determine (*i*) optimum stand densities for maximum growth of usable wood per tree and per acre over a range of site qualities and average diameters and (*ii*) growth and yield obtainable with repeated thinning" (Myers 1967). Since their installation, reports have been published on individual installations or pooled results from several installations (Barrett 1983; Ronco et al. 1985; Cochran and Barrett 1995, 1999; Oliver 1979, 1997, 2005). Among the more consistent conclusions are the following: (1) regardless of stand age and stand origin (natural stand or plantation), ponderosa pine responded to thinning immediately, (2) average tree diameter at breast height (dbh) and crown length and width increased with decreasing residual stand density, (3) periodic annual increment for basal area and stem volume increased with increasing stand density during at least the first 20 years of study (in later years, responses were complicated by mortality caused by *Dendroctonus* bark beetles), and

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Table 1. Site characteristics of the three Ponderosa Pine Level-of-Growing-Stock installations in eastern and central Oregon and northern California.

	Blue Mountains	Lookout Mountain	Elliot Ranch
National forest (NF)	Malheur NF	Deschutes NF	Tahoe NF
County, State	Grant, Oregon	Deschutes, Oregon	Placer, California
Latitude (N)	44°35′	43°46′	39°09′
Longitude (W)	118°28′	121°43′	120°45′
Elevation (m)	1340	1520	1240
SI* (m @ 100 years)	15–24	28	49
Annual precipitation (mm)	500	530	1270
Annual mean temperature (°C)	5.3	5.6	13.7
Study establishment year	1968	1966	1970
No. of growth periods	8	9	8
No. of plots	18	18	15
No. of trees measured	2371	1602	2003
No. of dead trees	357	129	535
No. of thinned trees	589	720	1070

*Site index based on Meyer (1938).

(4) mortality increased substantially with increasing stand density. These results, based on treatment densities as categorical variable, have been widely applied in managing even-aged ponderosa pine stands in the western US.

In this study, we report on stand dynamics over the 45 years by adding a 15-year period since last assessment of the two Oregon installations, Blue Mountains and Lookout Mountain, and the California installation, Elliot Ranch. Differing from the analyses of previous reports (Barrett 1983; Cochran and Barrett 1995, 1999; Oliver 1979, 1997; Zhang et al. 2012), we analyzed the pooled data using residual stand density measured by stand density index (SDI; trees·ha^{-1} indexed to a quadratic mean diameter (QMD) of 25.4 cm (i.e., 10 in.); Reineke 1933) as a continuous variable to quantify the growth – growing stock relationship to address the four following questions.

(1) Were the trends over this 15-year period consistent with previous trends at both the stand and tree level?
(2) How did stand aboveground net primary production, besides basal area and volume as usually measured in the previous reports, respond to stand densities?
(3) How did site quality influence the relationship between stand density and growth dynamics?
(4) To what degree does stand density influence forest resilience to natural disturbances?

These questions address the objectives for which the PPLOGS study was established, but also consider wider implications about the efficacy of stand density management for achieving ecosystem management objectives faced by forest managers today.

Materials and methods

Study site

One of the PPLOGS installations was located in the Blue Mountains of eastern Oregon, one at Lookout Mountain near the eastern slope of the Cascade Range in central Oregon, and one on the western slope of the northern Sierra Nevada in California (Table 1). The PPLOGS installations were established in relatively young, even-aged stands throughout the range of ponderosa pine in the western US following a common study plan (Myers 1967). Details of each site can be found in several previous publications (e.g., Barrett 1983; Oliver 1979, 1997; Cochran and Barrett 1995, 1999). A brief stand and treatment history for the three installations included in the current analysis follows.

Blue Mountains

The Blue Mountains (BM) site was located near Crawford Creek, about 30 km northeast of Prairie City, OR. The climate is continental, but the rain shadow effect of the Cascade Range limits annual precipitation to only approximately 500 mm, with most precipitation falling as winter snow.

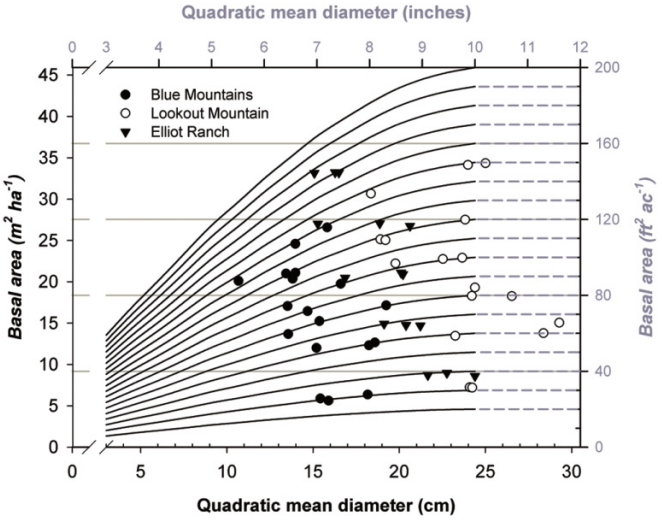
The overstory of natural forests consists primarily of ponderosa pine, with some widely scattered western larch (*Larix occidentalis* Nutt.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Two different understory plant associations are present in the general areas on which plots were established, the ponderosa pine – Idaho fescue (*Festuca idahoensis* Elmer) association and the Douglas-fir – elk sedge (*Carex geyeri* Booth) association. Soils are well-drained loamy-skeletal Bennettcreek–Fivebit or Bennettcreek–Bocker associations with loam and clay loam surface layers 15 to 40 cm deep and 12% to 65% gravels and cobbles. The parent material is Mazama volcanic ash mixed with colluvium overlying colluvium and residuum derived from andesitic basalt. Before study establishment, the overstory was a natural 60-year-old pure ponderosa pine stand averaging 5260 trees·ha^{-1} with 41.0 m^2·ha^{-1} of basal area and a QMD of 9.9 cm.

Thirteen 0.2 ha and five 0.16 ha plots were established in three blocks at the BM site. Within each block, each plot was randomly assigned to the following five growing stock levels (GSLs): 6.9, 13.8, 18.4, 23.0, 27.6, and 32.1 m^2·ha^{-1} (30, 60, 80, 100, 120, and 140 ft^2·acre^{-1}, respectively). These nominal GSLs represented the residual basal areas after thinning on plots with QMD ≥ 25.4 cm. For plots that had not yet reached this QMD, residual stand density was specified as the basal area that would allow the plot to reach its assigned nominal GSL at the same time that it attained a QMD of 25.4 cm (Myers 1967; Fig. 1). Plots and their corresponding 10 m wide buffer strips were initially thinned to the prescribed levels in 1967 and rethinned back to the originally targeted GSLs after the 1977 measurement. In 1986, plots were rethinned, but residual stand densities were specified by the following SDIs: 136, 272, 363, 452, 544, and 635 trees·ha^{-1}. These residual SDIs were equivalent to the original GSLs assuming a quadratic mean diameter of 25.4 cm.

Lookout Mountain

The Lookout Mountain site (LM) is on the south-facing slope of Lookout Mountain just east of the Cascade Range crest. This site is located within Pringle Falls Experimental Forest, about 21.0 km northwest of La Pine, OR. Annual precipitation is 530 mm and falls primarily as winter snow, with snowpacks commonly reaching 90 cm (Table 1). Summers are dry with hot days and cool nights; frost may occur at any time of year. The soil is a deep, well-drained loamy Typic Cryorthent formed from dacite pumice originating from the eruption of Mount Mazama (Crater Lake). The pumice depth averages 90 cm and is underlain by sandy loam material developed in older volcanic ash containing some cinders and basalt fragments. The current plant community is characterized by a

Fig. 1. Residual basal area and quadratic mean diameter (QMD) for each plot after initial thinning in the Blue Mountains, Lookout Mountain, and Elliot Ranch installations of the Ponderosa Pine Levels-of-Growing-Stock study. Solid lines represent the combinations of residual basal area and QMD that were expected to allow plots to attain their nominal GSL level when QMD reached 25.4 cm (Myers 1967).



Pinus ponderosa overstory and *Ceanothus velutinus* shrub layer, but the climax overstory species at this site is *Abies concolor* (Simpson 2007).

The initial ponderosa pine stand was 65 years old and had regenerated naturally. Eighteen 0.2 ha measurement plots with 10 m buffers comprised the experimental units. Initial conditions of these plots in 1965 averaged 2800 trees·ha^{-1} with a QMD of 16.0 cm and basal area of 55.1 m^2·ha^{-1}. Each of the following six nominal GSLs were randomly assigned to three plots: 6.9, 13.8, 18.4, 23.0, 27.6, and 34.4 m^2·ha^{-1} (30, 60, 80, 100, 120, and 150 ft^2·acre^{-1}, respectively). Because residual QMD on some of plots at LM exceeded 25.4 cm, residual basal area corresponded to the nominal GSL; in other plots with QMD < 25.4 cm, residual basal areas were lower and were again designed to allow the plots to reach the nominal GSL and QMD of 25.4 cm simultaneously (Fig. 1). Plots and buffer strips were rethinned to the prescribed GSL levels in 1975. In the 1985 rethinning, target residual densities were defined by converting the nominal GSLs to SDIs of 136, 272, 363, 452, 544, and 680 trees·ha^{-1}. However, the lowest GSL plots were not thinned this time because few residual trees remained on these plots.

Elliot Ranch

The Elliot Ranch (ER) site is located 7.6 km northeast of Foresthill, CA, on a gentle, south-facing aspect on the western slope of the northern Sierra Nevada. The Mediterranean climate has typical hot, dry summers and mild, wet winters, with annual precipitation of 1270 mm falling mostly as winter snow (Table 1).

Plots are located across an area containing three general soil types. Approximately one-half of the area is underlain by a Cohasset loam, one-third by a Horseshoe gravelly loam (a Xeric Haplohumult developed from Tertiary Period river gravels), and the remaining one-sixth by an alluvial soil not easily classified as to series. Depth to parent material is at least 150 cm in all three soil types. The Horseshoe Series and alluvial soil show similar site quality and are slightly less productive than the Cohasset Series (Oliver 1997).

The study area was burned severely in 1936 and reburned in 1949. In spring of 1950, ponderosa pine 1-1 stock from the appropriate seed zone was hand-planted at a density of 2200 trees·ha^{-1}. By age 20, when the plots were installed, trees completely dominated the *Ceanothus intergerrimus* understory and the stand carried a BA of 35.4 m^2·ha^{-1}. Ponderosa pine QMD averaged 18 cm and total height averaged 10 m.

The following five nominal GSLs were randomly assigned to three plots each: 9.2, 16.1, 23.0, 29.8, and 36.7 m^2·ha^{-1} (40, 70, 100, 130, and 160 ft^2·acre^{-1}, respectively). Experimental units were established in 1969 and followed the same design as at BM and LM, i.e., a 0.2 ha measure plot with 10 m buffer. Plots were rethinned guided by the initial GSLs in 1974. In 1979 and 1989, plots were rethinned to SDIs of 180, 316, 452, 588, and 724 trees·ha^{-1}.

Measurements

Prior to thinning, all trees on the measurement plots were measured for dbh. Thinnings were implemented from below to leave the most vigorous, well-formed trees, with additional consideration given to uniform spacing. Immediately after the initial thinning, all residual trees were tagged and dbh was recorded by tree number. Plots were generally measured every 5 years, with only occasional deviation. In the early inventories, height was measured on every fifth tree at ER site. At both BM and LM sites, height was measured on 15 trees on each plot. Selection of these trees was made across a diameter distribution series for each plot. For the last two measurements, height was measured for all trees in the plots at three sites. A volume equation was established from measurements taken by optical dendrometer on six trees per plot for several measurement years (Barrett 1983; Oliver 1997; Cochran and Barrett 1995, 1999). In addition, tree condition was recorded to characterize damage from insects and diseases, wind or snow, stem deformity, etc. Because bark beetles, including both mountain pine beetle (*D. ponderosae*) and western pine beetle (*D. brevicomis*), frequently attacked the ponderosa pine in the region (Oliver 1997; Cochran and Barrett 1995, 1999), we recorded bark beetle presence for each tree. Because these bark beetles only attack live trees, a dead tree with beetle presence was regarded as bark beetle caused mortality.

Data analysis

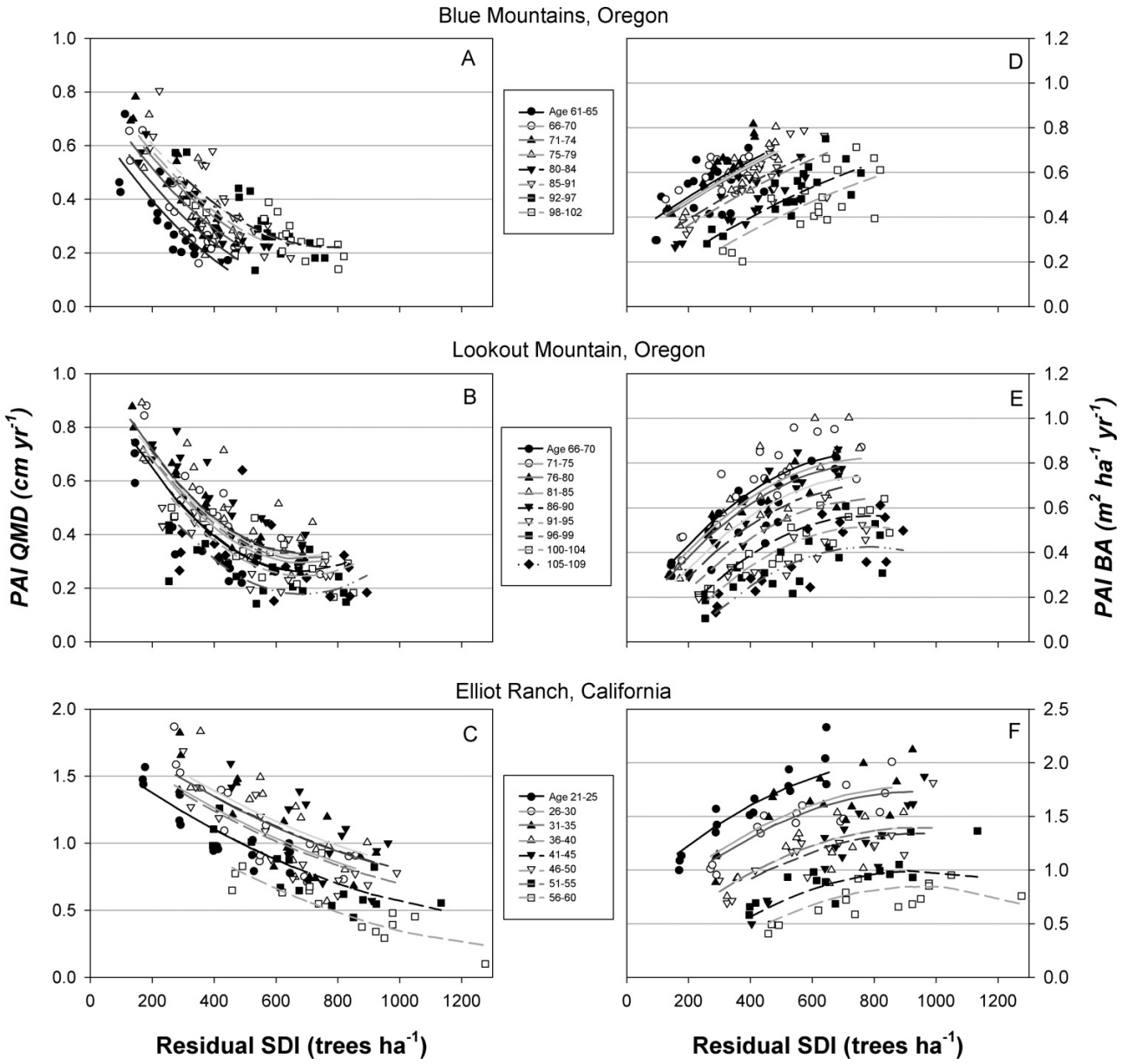
Stand-level characteristics

Stand QMD, basal area, total stem volume, and aboveground biomass were calculated from tree dimensions for each year of measurement. Volume inside bark from groundline to tip for those trees measured with optical dendrometer was calculated by a modified version of Grosenbaugh's (1974) STX program, using Cochran's (1976) bark thickness equations for Oregon sites and Powers' (1969) equations for Elliot Ranch. A local volume equation was therefore developed for each site, and tree volumes (m^3) were estimated from dbh only (Cochran and Barrett 1995, 1999; Zhang et al. 2012). Aboveground biomass (oven-dry kg) was estimated for each tree using an allometric equation developed for northern California (Zhang et al. 2010). Stand-level aboveground biomass (oven-dry Mg·ha^{-1}) was determined by summing estimates of aboveground biomass for all trees in the plot. Repeated measurement of these permanent plots allowed estimation of periodic annual increment in QMD (PAI QMD), basal area (PAI BA), stem volume (PAI Vol), and aboveground biomass (PAI AGDW), that is, the annual change based on trees at the end of the measurement period relative to those at the start of the measurement period. Trees that died were assumed not to have grown during the period encompassing tree death. Then, growth efficiency, defined as the PAI BA expressed as a percentage of initial BA at each measuring period for each plot across the sites, was calculated.

Stand density index (SDI) was calculated with a localized version of Reineke's (1933) formula as follows:

$$[1] \quad SDI = TPH \times (QMD/25.4)^b$$

Fig. 2. Periodic annual increment (PAI) of quadratic mean diameter (QMD) and basal area (BA) in relation to residual stand density index (SDI; number of trees per hectare indexed to a QMD of 25.4 cm) and stand age for each measurement period in the Ponderosa Pine Levels-of-Growing-Stock study plots installed at Blue Mountains, Lookout Mountain, and Elliot Ranch. Symbols are data directly calculated from inventories and lines are predictions from model 2 (parameter estimates in Table 3). The ranges in SDI covered by each measurement period are indicated by the ranges of the data points and lines, and observed ages are indicated in the legend.



where TPH is the number of trees per hectare and QMD is in centimetres. Although b was originally established as 1.605 across numerous species (Reineke 1933), this parameter has been applied as 1.77 for ponderosa pine in Oregon (DeMars and Barrett 1987) and northern California (Oliver and Powers 1978).

Precipitation

Water availability is one of the most important factors limiting tree growth in both continental and Mediterranean climatic regions of the western US, where summer drought is the norm. Soil water is recharged almost exclusively through winter rain or snow, with only minimal recharge during the growing season. To account for the variation in tree growth caused by annual fluctuations in precipitation, precipitation records were compiled from the nearest weather stations: Austin for BM, Wickiup Dam for LM, and Iowa Hill for ER (http://www.wrcc.dri.edu/). Because precipitation has historically differed among the three sites (Table 1), and because each site was established in different years, the percentage departure from normal precipitation (PDfN) was computed as a potential covariate. Normal precipitation was defined as the average annual precipitation over all years for which data were available at each weather station. A percentage departure was calculated for each year. The PDfN was an average of the percentage departures over those years, usually five, covered by each measuring period. Departures from normal precipitation were as high as 28% and as low as –35%.

Statistical analysis

A test of nominal GSL treatment effects was relatively uninteresting because residual basal area differed with GSL levels for

Table 2. *P* values of fixed effects, estimates of residual variance (σ^2), and fit statistics for response of periodic annual increment (PAI) of quadratic mean diameter (QMD), basal area (BA), stem volume (Vol), and aboveground dry mass (ABDW) to residual stand density index (SDI) and stand age (Age) at three installations of the Ponderosa Pine Level-of-Growing-Stock study (Blue Mountains and Lookout Mountain, Oregon, and Elliot Ranch, California).

	Num df	Den df	PAI QMD (cm·year^{-1})	PAI BA (m^2·ha^{-1} year^{-1})	PAI Vol (m^3·ha^{-1} year^{-1})	PAI AGDW (Mg·ha^{-1} year^{-1})
***P* values of fixed effects**						
Site	3	48	0.0002	<0.0001	0.0026	0.0482
SDI × Site	3	360	<0.0001	<0.0001	<0.001	<0.0001
(SDI/100)^2 × Site	3	360	<0.0001	<0.0001	0.0524	0.0060
Age	3	360	<0.0001	0.0198	<0.0001	<0.0001
(Age/10)^2 × Site	3	360	<0.0001	<0.0001	<0.0001	<0.0001
PDfN × Site	3	360	0.6534	<0.0001	<0.0001	<0.0001
Estimates of residual variance						
Residual σ^2			0.0091	0.0122	1.1495	0.5551
Random plot σ^2			0.0069	0.0057	2.1574	0.2652
Fit Statistics						
–2 Res log-likelihood			–512.44	–411.40	1705.38	1147.53
AIC			–508.44	–407.40	1709.38	1151.53
BIC			–510.24	–409.20	1707.58	1149.72
Generalized χ^2			3.71	4.97	880.23	226.48

Note: Num df, degrees of freedom numerator; Den df, degrees of freedom denominator; PDfN, percentage departure from normal precipitation; AIC, Akaike information criterion; BIC, Bayesian information criterion.

many of the growth periods (Figs. 1, 2, and 3). Therefore, residual stand density was regarded as a continuous variable to quantify the growth – growing stock relationship, specifically the effect of residual stand density on PAI QMD, PAI BA, PAI Vol, PAI AGDW, and mortality. Because SDI was the measure of stand density in later rethinnings at all sites, SDI was selected to represent stand density at the beginning of each growth period. Due to the widely recognized effects of tree and stand age on growth, initial age for each growth period was introduced as another covariate. Finally, PDfN was introduced into the statistical model to account for variation caused by periodic fluctuations in annual precipitation.

During the model fitting process, linear, quadratic, and cubic terms of SDI and age were tested and final models included only linear and quadratic terms, which were selected on the basis of residual plots and change of Akaike information criterion adjusted for small sample size (ΔAICc) (Burnham and Anderson 2002, p. 70). The model for productivity (PAIs) was:

$$[2]\quad y_{ijt} = \beta_{0i} + \beta_{1i} \times \mathrm{SDI}_{ijt} + \beta_{2i} \times (\mathrm{SDI}/100)^2_{ijt} + \beta_{3i} \times \mathrm{Age}_{it} + \beta_{4i} \times (\mathrm{Age}/10)^2_{it} + \beta_{5i} \times \mathrm{PDfN}_{it} + \gamma_{j(i)} + \varepsilon_{ijt}$$

where $i = 1, 2, 3$ indexes site (1 = BM, 2 = LM, and 3 = ER); $j = 1, 2, \ldots$, 15 or 18 indexes plot within site; $t = 1, 2, \ldots$, 8 or 9 indexes growth period; y_{ijk} is the dependent variable (PAI QMD, PAI BA, PAI Vol, and PAI AGDW) measured at plot j within site i at growth period t. SDI is the stand density index and Age is total stand age, both are at the start of the growth period. PDfN is precipitation departure from normal during the growth period, usually five years. These terms were assumed to be fixed effects. The effect $\gamma_{j(i)}$ due to plot j nested in site i, and the residual error of the response ε_{ijt} for the plot j within site i at growth period t, were both assumed to be random effects and normally distributed. The coefficients, intercept β_{0i}, and slopes β_{ki} ($k = 1, 2, \ldots, 5$) were estimated using the GLIMMIX procedure (SAS 9.2; SAS Institute Inc., Cary, North Carolina, USA).

For mortality, a negative binomial regression was fitted with total number of trees died as a dependent variable and maximum SDI (SDI_{max}) ever reached at each plot as an independent variable. A reduced model $y_{ij} = \beta_{0i} + \beta_1 \times \mathrm{SDI}_{ij} + \varepsilon_{ij}$ was used to estimate coefficients with the GENMOD procedure (SAS Institute Inc.) using the log-likelihood method with a log-link function and offset of plot size.

Results

Quadratic mean diameter response

Periodic annual increment of tree diameter responded significantly to SDI and stand age (Table 2). PDfN provided no additional significant predictive power ($P > 0.63$). Not surprisingly, the PAI of QMD declined with increasing initial growth period SDI across all three sites (Table 3; Fig. 2) with a caveat that our model may overestimate PAI QMD, especially at Lookout Mountain, OR (Fig. 2B). Across the three sites, the PAI QMD clearly reflected the site quality measured with site index (Tables 1 and 4), with PAI at Elliot Ranch about twice the PAI at the other two sites for a given initial SDI, and Lookout Mountain about a third higher than the Blue Mountains site (Fig. 2).

Basal area response

In contrast to PAI QMD, PAI BA increased with increasing initial SDI (Tables 2, 3, and 4), especially at lower levels of SDI (Figs. 2D–2F). PAI BA started to decline after SDI reached about 700 trees·ha^{-1} at both Lookout Mountain and Elliot Ranch, with a less pronounced effect at the Blue Mountains site. Elliot Ranch produced almost twice the basal area increment as Lookout Mountain, and the Blue Mountains site produced the least basal area annually. PAI BA generally declined with increasing age (Tables 3 and 4; Fig. 2) and increased with increasing precipitation at Elliot Ranch and the Blue Mountains site (Table 3).

Volume and aboveground dry mass response

Both PAI Vol and PAI AGDW showed trends similar to PAI BA (Tables 2 and 4; Fig. 3). However, the relative increase in these PAIs was smaller per unit increase in SDI relative to PAI BA (Fig. 3). Annual aboveground productivity was about 8 Mg·ha^{-1}·year^{-1} (range 4–12 Mg·ha^{-1}·year^{-1}) at Elliot Ranch, more than double the amount produced at Lookout Mountain (~3 Mg·ha^{-1}·year^{-1}, range 1–6 Mg·ha^{-1}·year^{-1}) and Blue Mountains (~2.5 Mg·ha^{-1}·year^{-1}, range 1–4 Mg·ha^{-1}·year^{-1}). Similarly, the average stem volume production was about 15, 6, and 4 m^3·ha^{-1}·year^{-1} at Elliot Ranch, Lookout Mountain, and Blue Mountains, respectively (Figs. 3A–3C).

Table 3. Parameter estimates (model 2) for predicting responses of ponderosa pine growth to residual stand density index (SDI), age, and percentage departure from normal precipitation (PDfN) at three installations of the Ponderosa Pine Level-of-Growing-Stock study (Blue Mountains and Lookout Mountain, Oregon, and Elliot Ranch, California).

Site	β_{0i}	β_{1i}	β_{2i}	β_{3i}	β_{4i}	β_{5i}
PAI QMD						
Blue Mountains	–1.0097*	–0.0018**	0.0117**	0.0424**	–0.0231**	0.0008
Lookout Mountain	–0.8815	–0.0022**	0.0162**	0.0489**	–0.0302**	–0.0005
Elliot Ranch	0.5020**	–0.0017**	0.0058**	0.0837**	–0.1198**	–0.0005
PAI BA						
Blue Mountains	–0.7580	0.0010**	–0.0033	0.0322**	–0.0252**	0.0026
Lookout Mountain	–0.4649	0.0019**	–0.0122**	0.0210	–0.0390*	–0.0003
Elliot Ranch	0.9371**	0.0027**	–0.0145**	–0.0210	–0.0188**	0.0057**
PAI Vol						
Blue Mountains	–11.2002	0.0056	–0.0160	0.3512*	–0.2251*	0.0207
Lookout Mountain	–11.3963	0.0145**	–0.0873*	0.3697*	–0.2618**	–0.0043
Elliot Ranch	–5.7469**	0.0156**	–0.0536*	0.9530**	–1.4520**	0.0737**
PAI AGDW						
Blue Mountains	–6.1711*	0.0036	–0.0107	0.1998*	–0.1311*	0.0131
Lookout Mountain	–7.3150*	0.0074**	–0.0430*	0.2289**	–0.1571**	–0.0026
Elliot Ranch	–0.5403	0.0079**	–0.0261	0.3552**	–0.5969**	0.0342**
Total mortality						
Blue Mountains	0.3959**	0.0063**				
Lookout Mountain	–0.7437	0.0063**				
Elliot Ranch	–0.8197	0.0063**				

Note: PAI, periodic annual increment; QMD, quadratic mean diameter; BA, basal area; Vol, stem volume; AGDW, aboveground dry mass. Significance: *, $P < 0.05$; **, $P < 0.01$.

Table 4. Means, standard deviations (SD), and ranges (minimum–maximum) of periodic annual increment (PAI) of quadratic mean diameter (QMD), basal area (BA), stem volume (Vol), and aboveground dry mass (ABDW) during growth periods (stand ages) at three installations of the Ponderosa Pine Level-of-Growing-Stock study (Blue Mountains and Lookout Mountain, Oregon, and Elliot Ranch, California).

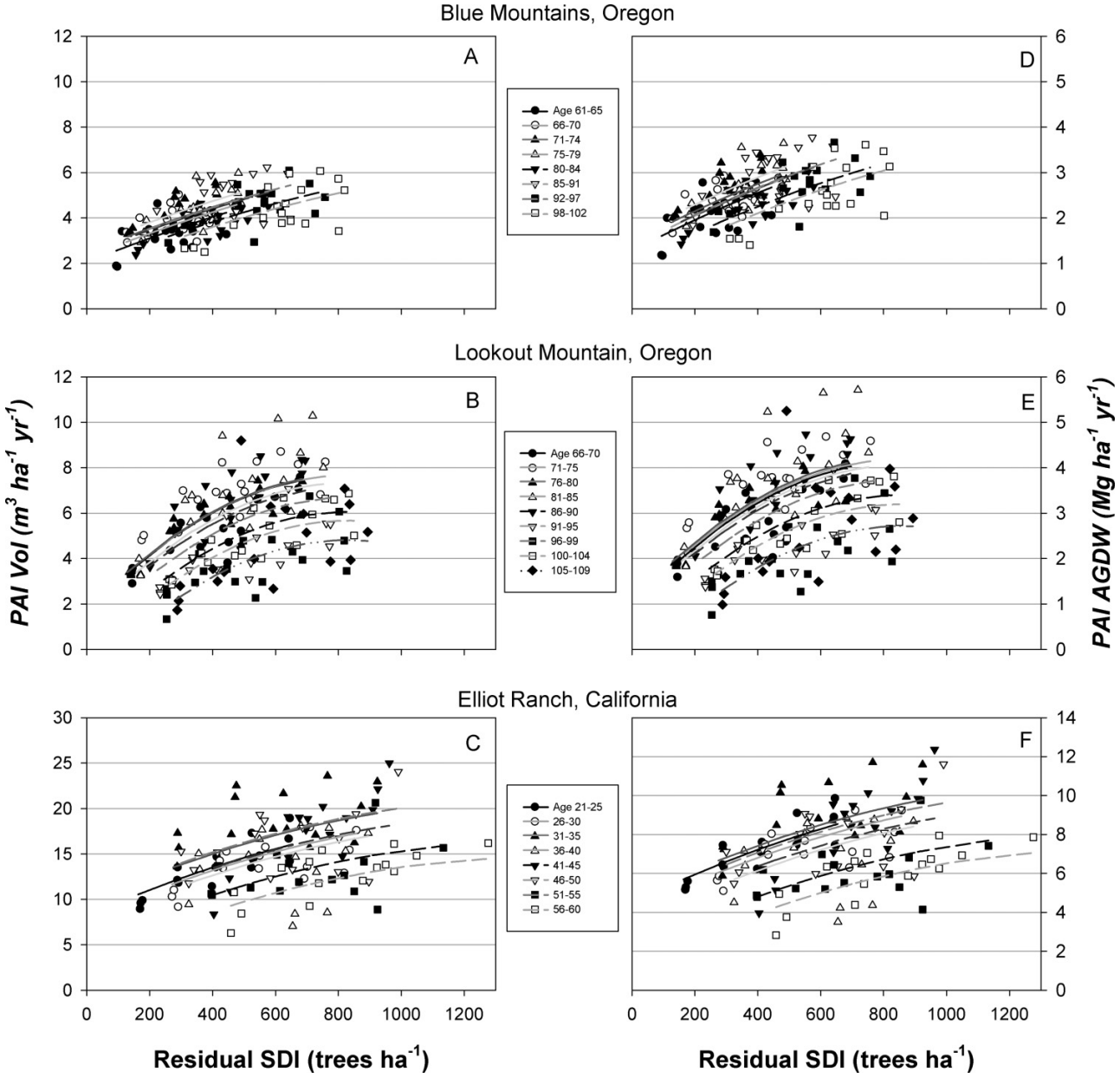
	PAI QMD ($cm \cdot year^{-1}$)			PAI BA ($m^2 \cdot ha^{-1} \cdot year^{-1}$)			PAI Vol ($m^3 \cdot ha^{-1} \cdot year^{-1}$)			PAI AGDW ($Mg \cdot ha^{-1} \cdot year^{-1}$)		
Stand age (years)	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Blue Mountains												
60–65	0.32	0.14	0.17–0.72	0.52	0.12	0.30–0.71	3.27	0.71	1.84–4.63	2.07	0.46	1.16–2.79
66–70	0.34	0.15	0.16–0.66	0.59	0.08	0.43–0.72	3.95	0.57	2.91–5.02	2.43	0.34	1.66–2.92
71–74	0.42	0.17	0.21–0.78	0.62	0.11	0.41–0.82	4.44	0.66	3.29–5.55	2.72	0.40	2.00–3.38
75–79	0.37	0.14	0.19–0.71	0.58	0.12	0.36–0.80	4.42	0.81	2.93–5.98	2.69	0.49	1.82–3.64
80–84	0.34	0.14	0.17–0.64	0.47	0.12	0.27–0.67	3.75	0.73	2.38–4.97	2.26	0.44	1.43–3.04
85–91	0.39	0.18	0.18–0.80	0.57	0.14	0.32–0.79	4.84	0.96	3.11–6.23	2.90	0.58	1.84–3.77
92–97	0.32	0.13	0.14–0.58	0.51	0.12	0.28–0.75	4.58	0.86	2.90–6.09	2.72	0.52	1.69–3.66
98–102	0.27	0.08	0.14–0.39	0.46	0.15	0.20–0.71	4.29	1.12	2.50–6.06	2.54	0.68	1.40–3.61
Lookout Mountain												
65–70	0.39	0.16	0.22–0.74	0.56	0.17	0.29–0.82	5.05	1.42	2.90–7.59	2.71	0.75	1.59–4.09
71–75	0.47	0.19	0.25–0.88	0.72	0.17	0.36–0.96	6.73	1.37	3.80–8.71	3.66	0.72	2.11–4.68
76–80	0.50	0.19	0.26–0.88	0.59	0.16	0.29–0.83	5.82	1.34	3.26–7.53	3.21	0.72	1.82–4.07
81–85	0.51	0.18	0.25–0.89	0.66	0.22	0.28–1.00	6.73	2.08	3.25–10.28	3.73	1.15	1.82–5.71
86–90	0.54	0.15	0.35–0.79	0.59	0.18	0.29–0.86	6.28	1.65	3.62–8.51	3.50	0.90	2.05–4.74
91–95	0.33	0.11	0.18–0.50	0.38	0.12	0.19–0.65	4.17	1.25	2.43–7.08	2.33	0.69	1.38–3.95
96–99	0.28	0.10	0.14–0.49	0.33	0.13	0.10–0.61	3.76	1.36	1.33–6.74	2.11	0.76	0.76–3.77
100–104	0.35	0.11	0.17–0.50	0.43	0.14	0.21–0.64	4.91	1.34	2.84–6.86	2.76	0.74	1.62–3.81
105–109	0.30	0.12	0.15–0.64	0.39	0.17	0.13–0.70	4.58	1.97	1.73–9.20	2.58	1.11	0.99–5.25
Elliot Ranch												
20–25	1.10	0.25	0.78–1.57	1.59	0.37	1.00–2.33	13.37	2.86	8.95–18.92	7.18	1.38	5.16–9.86
26–30	1.12	0.35	0.71–1.87	1.45	0.29	0.95–2.01	13.81	2.48	9.16–17.93	7.26	1.23	5.10–9.25
31–35	1.14	0.36	0.68–1.82	1.58	0.33	0.88–2.12	18.70	3.08	13.60–23.58	9.04	1.68	5.87–11.70
36–40	1.15	0.34	0.57–1.83	1.17	0.25	0.75–1.54	13.80	3.76	7.03–18.09	6.79	1.83	3.51–8.88
41–45	1.06	0.29	0.57–1.58	1.21	0.38	0.50–1.87	17.26	4.38	8.38–25.00	8.43	2.24	3.96–12.37
46–50	1.02	0.32	0.61–1.69	1.14	0.27	0.69–1.81	15.96	3.51	11.76–24.05	7.61	1.70	5.48–11.61
51–55	0.77	0.24	0.45–1.26	0.93	0.22	0.58–1.36	12.86	2.85	8.88–20.63	6.03	1.36	4.14–9.75
56–60	0.53	0.24	0.00–0.93	0.70	0.16	0.41–0.95	12.61	2.88	6.29–16.18	5.96	1.46	2.82–7.95

Mortality response

After fitting the model, we found that Pearson χ^2 was 77.4 and the deviance was 61.2, each with 47 degrees of freedom for their approximately χ^2 distribution, suggesting that the fit is adequate. The likelihood ratio test showed that both SDI ($\chi^2 = 29.63$, $P < 0.001$) and site ($\chi^2 = 12.66$, $P < 0.002$) affected total mortality.

Mortality after thinning occurred on all sites, but mostly on higher density plots (Fig. 4). Low mortality was observed in plots with SDI_{max}

Fig. 3. Periodic annual increment (PAI) of volume (Vol) and aboveground dry mass (ABGW) in relation to residual stand density index (SDI; number of trees per hectare indexed to a quadratic mean diameter of 25.4 cm) and stand age for each measurement period in the Ponderosa Pine Level-of-Growing-Stock study plots installed at Blue Mountains, Lookout Mountain, and Elliot Ranch. Symbols are data directly calculated from inventories and lines are predictions from model 2 (parameter estimates in Table 3). The ranges in SDI covered by each measurement period are indicated by the ranges of the data points and lines, and observed ages are indicated in the legend.



of 500 trees·ha^{-1} or less regardless of site (Fig. 4). Mortality accelerated exponentially with an increase in SDI_{max} after that, including a very high mortality in one plot at the Blue Mountains. Mortality, caused primarily by bark beetles, occurred consistently after SDI_{max} reached about 700 trees·ha^{-1} at BM and 900 trees·ha^{-1} on other sites; numbers represented the maximum SDI that plots reached at Blue Mountains or Lookout Mountain, respectively.

Due to the higher site quality at Elliot Ranch, the stand developed more rapidly and the plots had to be rethinned every five years early in the study. Nonetheless, SDI_{max} at some of Elliot Ranch plots reached as high as 1300 trees·ha^{-1}. Also, bark beetle activity was much more prevalent at Elliot Ranch than at the other sites. As a result, ultimate mortality caused by bark beetles and other factors was considerably higher at Elliot Ranch (Fig. 4).

It appeared that the mortality–SDI function at Blue Mountains differed from the functions at other two sites. A size–density plot (Fig. 5) in a logarithmic scale showed that a limiting SDI of 900 trees·ha^{-1} was lower than what had been observed at Elliot Ranch. It perhaps was adequate at Lookout Mountain. The limiting SDI appeared either to be lower than 900 trees·ha^{-1} or to be not reached on the Blue Mountains. However, a threshold for the zone of imminent bark beetle mortality appeared even lower than the SDI of 568 trees·ha^{-1} proposed by Oliver (1995).

Potential site productivity

Net basal area production, including all live, dead, and thinned trees, was similar among nominal growing stock levels kept at the four highest densities at each site (Fig. 6). Similar trends were also

Fig. 4. The response of plot-level total mortality to maximum stand density index (SDI_{max}) achieved within each plot in the Ponderosa Pine Level-of-Growing-Stock study plots installed at Blue Mountains, Lookout Mountain, and Elliot Ranch. Fitted lines are predicted with parameter estimates in Table 3.

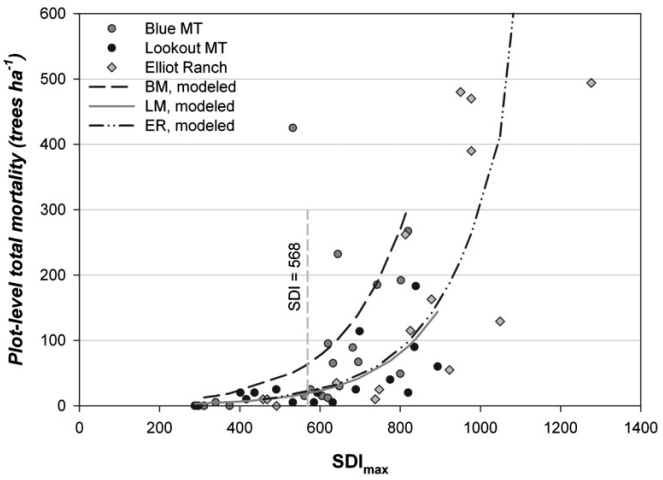
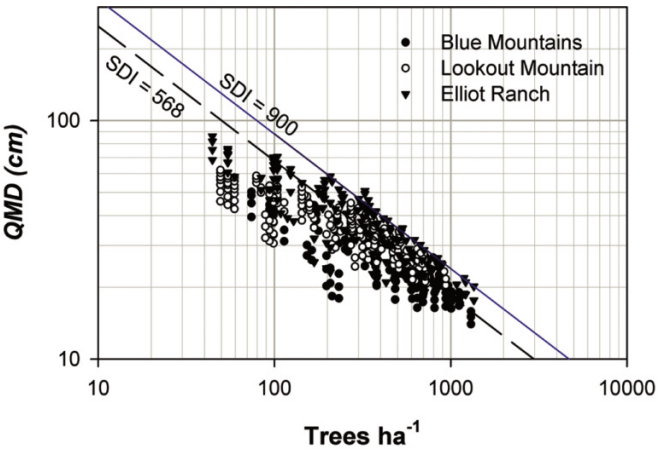


Fig. 5. Size–density plot on logarithmic scales of tree density (trees per hectare) and quadratic mean diameter (QMD) for ponderosa pine trees grown under various stand densities at Blue Mountains, Lookout Mountain, and Elliot Ranch. The two lines represent Reineke's stand density index (SDI) of 900 trees·ha^{-1} (solid line) and 568 trees·ha^{-1} (broken line).



observed, but not shown, for net volume and net aboveground dry mass production. Over all three sites, the variation in net production among different nominal GSLs was smaller than the variation in productivity among sites.

In addition to higher absolute growth rates, Elliot Ranch also showed considerably higher growth efficiency than the other sites (Fig. 7). On average, annually, a stand with initial SDI of 400 trees·ha^{-1} (with BA of 20.3 m^2·ha^{-1}) grew 0.9 m^2 at Blue Mountains, 1.1 m^2 at Lookout Mountain, and 2.1 m^2 at Elliot Ranch. The potential BA productivity converged on a similarly low level across all sites if the stand was allowed to reach a very high density.

Discussion

The Elliot Ranch, Lookout Mountain, and Blue Mountains installations of the PPLOGS study installations are among the oldest replicated and continuously monitored density studies for ponderosa pine in the world. More than 40 years of data confirmed the now widely observed principle that stands managed at lower densities grow trees of larger diameter, a principle that had been previously documented at these sites (Barrett 1983; Ronco et al. 1985; Cochran and Barrett 1995, 1999; Oliver 1997). The magnitude of growth response to stand density was influenced by site quality, because stands on highly productive sites develop much more rapidly than stands on sites of lower quality (Fig. 2). After correcting for the direct effect of thinnings from below on QMD, stands with initial diameter of 25 cm exhibited between 24 cm and 52 cm of diameter increment over a 40-year span at the Elliot Ranch site. In contrast, the 40-year QMD increment on the poorest site (Blue Mountains) reached only 9 to 27 cm. Diameter increment at Lookout Mountain was intermediate between these extremes, ranging between 12 and 27 cm, although tree size was much greater when the study was installed. Individual tree volume and aboveground dry matter should follow the same trends as tree diameter. If the management goal is to produce the large trees characterizing late-seral forests, low-density stands are preferred. Late-seral forests on the eastern slope of the Cascade Range in Oregon and Washington required trees with dbh of 53 cm (Youngblood et al. 2004), and in the Sierra Nevada trees with dbh of 76 cm were required (Smith et al. 1991). Many trees on our lower density plots have grown to these categories. However, restoration of late-seral forests should also consider other characteristics such as tree age, number of cohorts or age classes, spatial pattern, amount of mortality, etc.

At the stand level, growth will parallel individual tree growth with increasing levels of growing stock until the onset of compe-

Fig. 6. Cumulative gross production of basal area (BA) in the various stand density regimes from the Ponderosa Pine Level-of-Growing-Stock study at Blue Mountains, Lookout Mountain, and Elliot Ranch over the last 60 years.

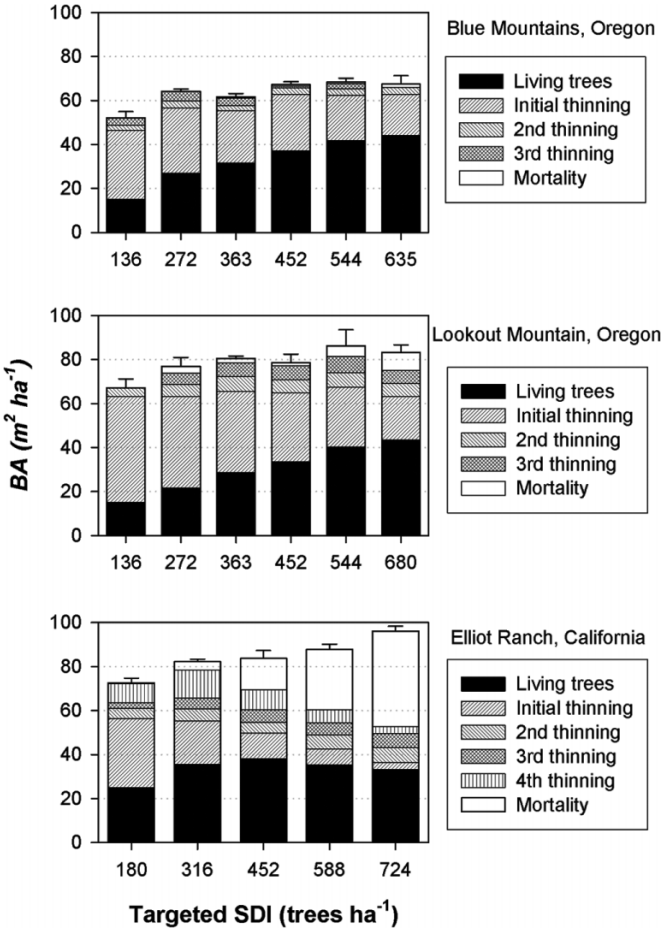
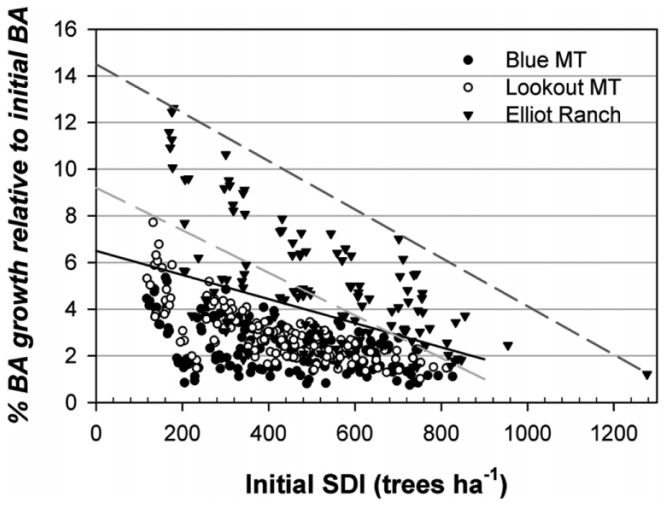


Fig. 7. Annual percentage basal area growth [(PAI BA/initial BA) × 100] in response to residual stand density index (SDI) in the Ponderosa Pine Level-of-Growing-Stock study installed at Blue Mountains, Lookout Mountain, and Elliot Ranch. The lines are subjectively drawn to indicate the potential maximum BA growth (%·year^{-1}) for a given SDI. The equations are as follows: Blue Mountains, $y = 6.5 - 0.00531(SDI)$; Lookout Mountain, $y = 9.2 - 0.00911(SDI)$; and Elliot Ranch, $y = 14.5 - 0.01038(SDI)$.



tition (Langsaeter's zone I; Daniel et al. 1979). Growth of trees and stands continues to increase with increasing stocking after the onset of competition but at a slow rate of increase per unit of growing stock (Langsaeter's zone II) and probably peaks at the stocking that allows leaf area to reach its highest level (Pretzsch 2010). Under a timber management objective, the maximum productive potential of a site is sustained by managing a stand at densities achieving a peak in growth per unit stand area, typically in the upper end of Langsaeter's zone II or in zone III (Daniel et al. 1979). For the three PPLOGS studies, this density range was close to SDI of 700 trees·ha^{-1} (Figs. 2 and 3) (Curtis et al. 1997). However, total BA production did not differ substantially except perhaps for the lowest stand density regimes (Fig. 6). Of management significance is the fact that BA production for the live trees was the highest for plots with SDI around 450 trees·ha^{-1} at Elliot Ranch.

Aboveground net primary productivity (ANPP) is an important dimension for understanding ecosystem structure and function and is fundamental to the process of energy flow through the system. Our ANPP measured by PAI AGDW excluded understory plants but was ~8 Mg·ha^{-1}·year^{-1} (range 4–12 Mg·ha^{-1}·year^{-1}) at Elliot Ranch, a rate that is comparable with the total system ANPP reported for a study site located a few kilometres from the current study (Campbell et al. 2009). At the Oregon sites, the PAI AGDWs of ~2.5 Mg·ha^{-1}·year^{-1} (range 1–4 Mg·ha^{-1}·year^{-1}) at Blue Mountains and 3.0 Mg·ha^{-1}·year^{-1} (range 1–5 Mg·ha^{-1}·year^{-1}) at Lookout Mountain were very similar to the total ecosystem ANPP found at an untreated mixed young and old ponderosa pine forest in the Metolius Basin, about 90 km north of Lookout Mountain (2.8 Mg·ha^{-1}·year^{-1}; Law et al. 1999). These results suggest that ANPP of standing live trees comprises the bulk of total ecosystem ANPP.

Although plots at the lower densities at Elliot Ranch showed slightly lower periodic annual increment of BA, volume, and AGDW (Figs. 2F, 3C, 3F), these plots showed the highest growth per unit of initial BA (Fig. 7). Often, the growth per unit of leaf area is used to measure tree growth efficiency (Waring et al. 1981). Because leaf area was not measured in this study, growth efficiency was defined on the basis of initial basal area for each measurement period to calculate basal area growth percentage (Tappeiner et al. 2007). At SDIs of <600 trees·ha^{-1} (Fig. 7), growth efficiency for BA followed the site index gradient across these installations, with the highest observed at Elliot Ranch and the lowest observed at Blue Mountains. In fact, factors contributing to variation in inherent site productivity included not only soil depth, nutrient level, and water holding capacity, but also length of growing season and precipitation (Table 1). The variation in different PAI estimates among measurement periods closely tracked climatic variation or other stressful events (Tables 2 and 4). At Elliot Ranch, the highest BA growth rate for a given initial SDI occurred at the first growth period from 1970 to 1974 (corresponding to ages 21–25) (Fig. 2F). Growth rate declined gradually as trees aged, although PAIs were similar between second and third periods and among the fourth, fifth, and sixth periods. The lower PAI BA than expected during the fourth and fifth periods (1985–1994) was apparently related to drought conditions during these years (Zhang et al. 2012). Prediction errors were greater for some growth periods than others, as illustrated by observed and predicted PAI BA at the Lookout Mountain installation (Fig. 2E). PAI BA was always underestimated at higher SDI from the model during the earlier periods. During sixth and seventh periods (1991–1999), PAI BA was overestimated by the models, a possible effect of partial defoliation from a Pandora moth (*Coloradia pandora* Blake) outbreak in 1992 and 1994 (Cochran and Barrett 1999; Speer et al. 2001). Although no mortality was attributed to Pandora moth in this study because outbreaks were short and infrequent (Speer et al. 2001), the reduction of growth rate during those growth periods was confounded with stand age.

Pine bark beetles are ubiquitous in the western North America and are currently at epidemic levels that threaten many ponderosa and lodgepole pine forests in Canada and the US (Kurz et al. 2008; Bentz et al. 2010). Western pine beetle (*D. brevicomis*) and occasionally the red turpentine beetle (*D. valens*) attacked trees at Elliot Ranch. Almost all mortality was attributable to mountain pine beetle (*D. ponderosae*) at both Oregon sites, except during the first growing season when mortality was caused either by western pine engraver (*Ips pini*) or by other unidentified factors at the Blue Mountains site (Cochran and Barrett 1995). Mortality rate was much higher at Elliot Ranch than at other sites (Figs. 4 and 6), perhaps because the warm summers and shorter winters on the western side of the Sierra Nevada enhance western pine beetle fecundity by allowing production of three beetle generations per year (Oliver 1995). In contrast, only one generation is usually produced by the mountain pine beetle during the cooler, shorter summers in Oregon (Cochran and Barrett 1995, 1999).

Bark beetle caused mortality was positively related to stand density (Figs. 4 and 5), as has been consistently found in previous studies (Eaton 1941; Startwell and Stevens 1975; Oliver 1995). Although bark beetles follow volatile resins after ponderosa pine trees are cut (Oliver 1995; see Fettig et al. 2007), trees in the lowest density plots (heavily thinned) were rarely killed by bark beetles, regardless of site (Fig. 4). Some heavy mortality that occurred in intermediate densities at the Blue Mountains site was not anticipated during the second (1972–1977) and third (1978–1981) periods (Cochran and Barrett 1995). Although there are numerous stand- and landscape-level factors influencing bark beetle activity and outbreaks, lower mortality rates in the low-density plots suggested that thinning can confer some resistance to bark beetles. In addition, self-thinning in ponderosa pine was apparently mediated by *Dendroctonus* bark beetles, preventing the stands from exceeding an SDI of about 900 trees·ha^{-1} on all three sites (Oliver 1995; Fig. 5). The value of SDI of 568 trees·ha^{-1} proposed by Oliver (1995) as a threshold for the zone of imminent bark beetle mortality was consistent with Lookout Mountain and Elliot Ranch. However, onset of mortality at Blue Mountains appeared lower (Fig. 4). Because we plotted the total mortality against the maximum SDI achieved within each plot, the data points would be

moved to the left if plot average SDI was used. Therefore, our estimates of mortality are more conservative.

Conclusions

Several conclusions can be drawn from the analysis: (1) previous trends in growth responses to initial SDI reported 15 years ago have persisted at three sites of the original six installations PPLOGS study; (2) aboveground biomass productivity showed trends similar to basal area and volume, with highest productivity under higher stand densities that do not experience heavy mortality; (3) site quality affected stand productivity and development rate, but also stand growth efficiency and growth response to stand density and age; (4) *Dendroctonus*-induced mortality can be reduced by thinning ponderosa pine stands to target densities below an SDI of 568 trees·ha^{-1}; (5) reducing stand density to this target should not significantly reduce stand productivity; and (6) the efficacy of maintaining stand densities at levels that provide resistance to bark beetle attack and damage should increase as the proportion of the surrounding landscape is managed similarly.

Acknowledgments

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