Vegetation responses to stand structure and prescribed fire in an interior ponderosa pine ecosystem[1]

Jianwei Zhang, Martin W. Ritchie, and William W. Oliver

Abstract: A large-scale interior ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) study was conducted at the Blacks Mountain Experimental Forest in northeastern California. The primary purpose of the study was to determine the influence of structural diversity on the dynamics of interior pine forests at the landscape scale. High structural diversity (HiD) and low structural diversity (LoD) treatments were created with mechanical thinning on 12 main plots. Each plot was then split in half with one-half treated with prescribed fire. During the 5 year period after the treatments, the LoD treatments showed slightly higher periodic annual increments for basal area (BA) and significantly higher diameter increments than did the HiD treatments, although HiD carried twice as much BA as LoD did immediately after the treatments. Prescribed fire did not affect growth, but killed and (or) weakened some trees. No interaction between treatments was found for any variable. Stand density was reduced from the stands before treatments, but species composition did not change. Old dominant trees still grew and large snags were stable during the 5 year period. Treatments had minor impacts on shrub cover and numbers. These results suggest that ponderosa pine forest can be silviculturally treated to improve stand growth and health without sacrificing understory shrub diversity.

Résumé : Une étude à grande échelle sur le pin ponderosa continental a été réalisée dans la Forêt expérimentale Blacks Mountain située au nord-est de la Californie. Le but principal de l'étude était de déterminer l'influence de la diversité structurale sur la dynamique des pinèdes continentales à l'échelle du paysage. Des traitements de diversité structurale élevée (HiD) et faible (LoD) ont été créés à l'aide d'éclaircies mécanisées dans 12 parcelles principales. Par la suite, chaque parcelle a été divisée en deux et l'une des deux moitiés a reçu un brûlage dirigé. Pendant la période de cinq ans qui a suivi l'application des traitements, les traitements LoD ont produit un accroissement annuel périodique en surface terrière légèrement supérieur et un accroissement en diamètre significativement plus élevé que ceux des traitements HiD, même si la surface terrière des traitements HiD immédiatement après les traitements était deux fois plus grande que celle des traitements LoD. Le brûlage dirigé n'a pas eu d'effet sur la croissance, mais a affaibli ou causé la mort de certains arbres. Aucune interaction entre les traitements n'a été détectée quelle que soit la variable considérée. Par rapport aux conditions avant l'application des traitements, la densité des peuplements a été diminuée mais la composition en espèce n'a pas changé. Les vieux arbres dominants ont continué de croître et le nombre de gros arbres morts sur pied est demeuré stable pendant la période de cinq ans. Le traitement a causé un impact mineur sur le nombre et le couvert d'arbustes. Ces résultats indiquent que les forêts de pin ponderosa peuvent recevoir des traitements sylvicoles pour améliorer la croissance et l'état de santé des peuplements sans sacrifier la diversité des arbustes sous couvert.

[Traduit par la Rédaction]

Introduction

Ponderosa pine (*Pinus ponderosa* Dougl. P. & C. Laws. var. *ponderosa*) forest ecosystems have changed dramatically in structure and composition over the past century in northeastern California (Taylor 2000; Skinner 2005) similar to the findings in other parts of the western United States (Cooper 1960; Agee 1993; Covington and Moore 1994; Allen et al. 2002). In the early years of Euro-American settlement, logging, livestock overgrazing, and wildfire created conditions suitable for tree regeneration. Later, lack of density management and effective fire suppression in both young and old stands created forests dominated by dense saplings and pole-sized trees. The change in conditions favored more shade-tolerant species and led to heavy accumulations of litter and woody fuels (Dolph et al. 1995; Youngblood et al. 2004). In addition, many stands have suffered accelerated mortality from competition and wildfire intensified by drought that threatens the stability of old growth stands (Oliver 2001).

Managing these forests has become a great challenge for forest managers. Current management regimes, including thinning and prescribed fire, are often implemented to reduce fuel loads. A combination of thinning and prescribed fire has proven to be an effective way to mitigate the threat of wildfires (Raymond and Peterson 2006; Ritchie et al. 2007). In addition, thinning increases the growth rate of the

Received 15 May 2007. Accepted 30 November 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 21 April 2008.

J. Zhang,[2] M.W. Ritchie, and W.W. Oliver. Pacific Southwest Research Station, USDA Forest Service, 3644 Avtech Parkway, Redding, CA 96002, USA.

[1]This article is one of a selection of papers from the Special Forum on Ecological Studies in Interior Ponderosa Pine — First Findings from Blacks Mountain Interdisciplinary Research.
[2]Corresponding author (e-mail: jianweizhang@fs.fed.us).

 doi:10.1139/X07-230

remaining trees not only for young ponderosa pine stands (Barrett 1982; Cochran and Barrett 1993; Oliver 1997; Zhang et al. 2006), but also for old dominant trees across the western United States (Fiedler 2000; Latham and Tappeiner 2002; McDowell et al. 2003; Sala et al. 2005; Stov et al. 2005). However, prescribed fire, which reduces the hazardous fuels on the forest floor (Covington and Sacket 1984; Kauffman and Martin 1989), has either directly or indirectly killed both young trees (<20 cm diamter at breast height, DBH) and old dominant trees (Agee 2003; McHugh and Kolb 2003; Kolb et al. 2007). The mechanism of mortality caused by prescribed fire is not well understood, although several possible reasons have been provided (Kolb et al. 2007). Understanding these questions and their interactions, at both stand and landscape scales, can only be obtained through long-term experimentation at a landscape level.

The Blacks Mountain Ecological Research Project, initiated in 1991, is long-term, large-scale, and interdisciplinary in scope (Oliver and Powers 1998; Oliver 2000). This project was designed "to increase our understanding of the effects of forest structural complexity on health and vigor of an interior ponderosa pine ecosystem, quantify the ecosystem's responses to natural and human-induced disturbance, and determine how these ecosystems can be restored and managed" (Oliver 2000). Blacks Mountain Experimental Forest was chosen for this project because of the presence of late-seral structure at a scale needed to meet the requirement of studies at the higher trophic levels such as insects, birds, mammals, and wildlife (Oliver 2000).

In this manuscript, we focus on responses of tree species and understory shrubs to the stand manipulations and prescribed fire during the 5 year period after the treatments were completely installed. Using the results from this long-term study, we intend to address several specific questions: (1) What are the effects of structural diversity and prescribed fire on tree growth and dynamics? (2) Do different species respond differently to these treatments? (3) Are interactions between structural diversity and prescribed fire significant in the short-term in regards to aboveground stand productivity for the individual tree species? (4) How do old dominant trees respond to these treatments? (5) How does regeneration of shrubs respond to structural diversity and prescribed-fire treatments?

Materials and methods

Study area

The study was conducted at Blacks Mountain Experimental Forest (BMEF; Fig. 1), located approximately 35 km northeast of Mount Lassen in northeastern California (40°40′N latitude, 121°10′W longitude). The experimental forest occupies 3715 ha on the Lassen National Forest; the elevational range is between 1700 and 2100 m a.s.l. Soils are in the Taxonomic subgroup Typic Argixerolls, 1–3 m deep over fractured basaltic bedrock with mesic soil temperature regimes at lower elevations. Andic Argixerolls with frigid soil temperature regimes predominate at higher elevations. The climate is characterized by warm, dry summers and cold, wet winters. Annual precipitation is approximately 460 mm and falls primarily as snow from October through May. Mean daily air temperatures usually range from –9 to 29 °C.

The overstory vegetation on the experimental forest is dominated by ponderosa pine with varying amounts of white fir (*Abies concolor* (Gord. & Glend.) Lindl.), incense cedar (*Calocedrus decurrens* (Torr.) Florin), and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.; Oliver 2000). The stands were comprised of at least two age cohorts: an overstory of widely scattered 300- to 500-year-old pines or incense cedars and a dense 50- to 100-year-old understory of pines, white fir, and incense cedar originating after intensive livestock grazing ceased and the onset of wildfire suppression. At the start of the study, an average hectare carried about 2000 trees and seedlings with a basal area of 45 m^2 and a quadratic mean diameter of 28 cm based on the adjacent Research Natural Area (RNA) inventory. These numbers varied somewhat across the entire forest because of a methods-of-cutting study established from 1938 to 1948 (Hallin 1959). About thirty-five 8 ha plots with various cutting prescriptions were distributed across the BMEF and were included in our treatment plots, which tended to increase the variability of stand characteristics. Five common shrub species found throughout the forest are greenleaf manzanita (*Arctostaphylos patula* Greene), prostrate ceanothus (*Ceanothus prostratus* Benth.), snowbrush (*Ceanothus velutinus* Dougl. ex Hook.), antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), and creeping snowberry (*Symphoricarpos mollis* Nutt.).

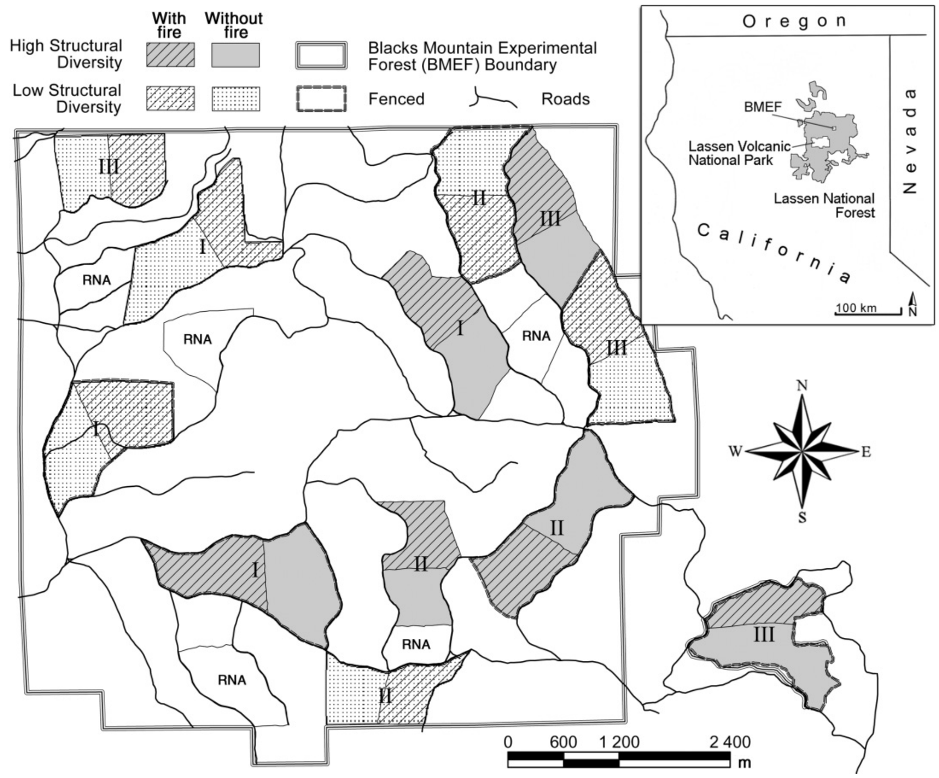
Experimental design

The study uses 1226 ha of the experimental forest and 111 ha of the adjacent national forest. Two by two factorial treatments testing high and low structural diversities, with or without cattle grazing as a main-plot effect were randomly assigned to each of the three blocks (Fig. 1), making a total of 12 main plots for the entire study. Each main plot, which ranged in size from 77 to 144 ha (mean = 111 ha), was split into two subplots; one split plot was randomly assigned a prescribed-fire treatment (Oliver and Powers 1998; Oliver 2000). Main plots were blocked by proportion of species composition along the elevational gradient because white fir and incense cedar become increasingly abundant at the higher elevations in the forest.

The high structural diversity (HiD) treatment was designed to leave all large, old dominant trees (≥300 years old), abundant snags, multiple canopy layers, and many canopy gaps and forest-floor openings (Oliver and Powers 1998; Oliver 2000). The prescription also included a few dense clumps (0.4–0.8 ha) of smaller trees. The low structural diversity (LoD) treatment created stands with a single canopy layer of well-spaced codominant trees by harvesting the large dominant trees, leaving a few snags of pine and incense cedar and few large canopy gaps.

Because of the large plot size, treatment implementation took several years. The three individual blocks, each with four main plots were created in 1996, 1997, and 1998, respectively. Nongrazed plots were fenced in the summer of the following year (1997, 1998, and 1999, respectively). The prescribed fire was planned for the falls of 1997, 1998, and 1999; however, because the burning prescription could not be met in 1998, prescribed fire for those splits thinned

Fig. 1. Geographic location of the Blacks Mountain Experimental Forest and layout of the Blacks Mountain Ecological Research Project in northeastern California. RNA refers to Research Natural Area. I, II, and III are block numbers.



in 1997 and 1998 was delayed to the fall of 1999 and 2000, respectively. The debris around existing snags was raked prior to the application of prescribed fire.

Vegetation sampling

Throughout each of the experimental units (subplots), permanent plots keyed to a 100 m grid oriented from north to south and from east to west were installed. All measurements were referenced to these grid points. With the grid point as a center, three nested circular plots sampled the trees and snags by species depending on their size as follows:

- Large trees and snags (>29.2 cm DBH) were sampled on a 0.08 ha (16.0 m radius) plot;
- Living and dead pole-size trees (9.1–29.2 cm DBH) were sampled on a 0.02 ha (8.0 m radius) plot; and
- Living seedlings and saplings (between 0.3 and 1.4 m in height or <9.1 cm DBH) were sampled on a 0.004 ha (3.6 m radius) plot.

All trees and snags ≥9.1 cm DBH were tagged within each of the respective sampling plots. Height was measured with an Impulse laser hypsometer (Laser Technology, Inc., Englewood, Colorado) to the nearest 0.3 m, and DBH was measured with a D-tape to the nearest 0.25 cm for all large trees. For pole-size trees, DBH was measured for all trees and height was subsampled. Heights of seedlings and saplings were not measured. In addition, tree and snag conditions were evaluated (Dunning 1928; Keen 1943; Ferrell 1980). For this analysis, we consider trees and snags ≥76.2 cm DBH to represent the old dominant trees.

A pretreatment inventory was conducted in 1994, with a 25% grid point sampling intensity and a slightly different sampling scheme. The purpose of the pretreatment inventory was to collect the baseline data to designate the block and unit layout. Therefore, DBH was only measured on pole-size trees within a 0.004 ha plot and large trees within 0.08 ha plot at selected grid points. The post-treatment inventories were more intensive with 50% of the grid points systematically sampled. The first post-treatment inventory was in the year immediately following the prescribed fire application (1998, 2000, and 2001), 2–3 years after thinning. The second post-treatment inventory was conducted 5 years later in 2003, 2005, and 2006, respectively.

Understory shrubs were sampled in the post-treatment measurements using a line-intercept method on a 100 m transect (Mueller-Dombois and Ellenberg 1974). Each transect is centered on the grid point and oriented randomly ±45° from true north. Six steel pins were installed along each transect at ~14 m intervals to ensure the transect location would be found for subsequent inventories. Beginning at the southern end, each shrub crown was measured for average height and start and stop distance were recorded along the transect for estimating shrub cover.

Data analysis

After treatment installation, an interdisciplinary team of scientists concluded that our grazing treatment had not been effective because grazing intensity was not controlled, being largely a function of proximity to water. Moreover, the current data also showed that there was no significant grazing effect in any of the measured variables. Therefore, the grazing treatment will not be considered in the analysis, effectively doubling the replications within each block. Additionally, in September of 2004, a wildfire burned into one of the main plots (Ritchie et al. 2007) causing enough damage to warrant its exclusion from the post-treatment data set.

Several variables were derived from the understory shrub measurements: (1) species richness and diversity determined from the total number of individual plants counted by species; (2) shrub cover as a percentage of measured intercept length for each shrub species divided by total transect length; and (3) relative species dominance measured by the total intercept length for the given species divided by the total intercept length for all species.

Stand basal area (BA), quadratic mean diameter (QMD), trees per hectare, and height were calculated based on data at each selected grid point. Periodic annual increments (PAIs) for BA, QMD, and heights were calculated based on those trees that lived through the 5 year period. Because seedling and samplings were not tagged, they were excluded from the PAI calculations. The number of shrub species, shrub cover, and relative dominance were also calculated from the grid-point data. Then, means of all variables were calculated within each of the 22 subplots (experimental units). We compared the treatment differences using analysis of variance with the following statistical model for each period:

$$Y_{ijkl} = \mu + B_j + D_i + e(a)_{ijl} + F_k + DF_{ik} + e(b)_{ijkl}$$

where Y_{ijk} is a stand-level dependent variable from the ith (1, 2) structural diversity (D) and jth (1, 2, 3) block (B), kth (1, 2) prescribed-fire treatment (F), and lth (1, 2) grazing treatment. The $e(a)$ is the main-plot error term, DF is the interaction between structural diversity and prescribed fire, and $e(b)$ is the error term for subplot effect. Both error terms are assumed normally distributed and independent from each other. All analyses were performed with SAS Proc GLM with $\alpha = 0.05$ as a critical value of significance.

Results

Overall stand characteristics

Before treatments were installed, the average stand BA and QMD of large and pole-size trees across the proposed experimental units (subplots) were 32.4 ± 1.5 (SE) m^2·ha^{-1} and 36.7 ± 0.7 (SE) cm, respectively (Table 1). There were about 871± 58 (SE) large and pole-size trees per hectare composed of 36% white fir, 7% incense cedar, and 57% ponderosa and Jeffrey pines throughout these subplots.

After the thinning and prescribed-fire treatments, the structural diversity effect became highly significant in BA, QMD, trees per hectare, and height for all trees regardless of species, including seedlings and saplings, based on data collected immediately after the treatments (Table 2). However, neither prescribed-fire effect nor interactions between structural diversity and prescribed fire were significant ($P >$ 0.11) for these variables. The average values of LoD and HiD treatments were 10 versus 25 m^2·ha^{-1} for BA, 26 versus 34 cm for QMD, 282 versus 513 trees·ha^{-1} for number of trees, and 13 versus 16 m for height, respectively (Table 1). Because treatments were installed in different years among blocks, the block effects for post-treatment measurements would have been confounded with years and, therefore, were not tested.

Based on measurements 5 years after the treatments were completed, the structural diversity effect was significant in all variables (Table 2). The prescribed-fire effect was also significant for QMD and trees per hectare (Table 2). Differences were mainly related to delayed mortality caused by prescribed fire (Table 1). No significant interaction was found in any variable between structural diversity and prescribed fire. The average values of LoD and HiD treatments were 11 versus 25 m^2·ha^{-1} for BA, 28 versus 34 cm for QMD, 258 versus 487 trees·ha^{-1} for number of trees, and 13 versus 17 m for height, respectively (Table 1). Pooled across structural diversity levels, average QMD and trees per hectare were 30 cm and 452 trees·ha^{-1} for treatments without prescribed fire and 33 cm and 293 trees·ha^{-1} for treatments with prescribed fire, respectively.

Stand periodic annual increment

The difference in the PAIs of the QMDs between structural diversities was significant (Table 2). Trees at the LoD treatment grew significantly more in QMD (0.65 cm·year^{-1}) than did trees in the HiD treatment (0.33 cm·year^{-1}; Fig. 2). The effect of structural diversity was not significant for both PAI BA and PAI height, although PAI BA was 0.38 m^2·ha^{-1}·year^{-1} at the LoD treatment and 0.34 m^2·ha^{-1}·year^{-1} at HiD treatment. Neither PAI BA, PAI QMD, nor PAI height was significantly different between prescribed-fire treatments and no interactions between structural diversity and prescribed fire were significant for any response variable.

Species responses

Composition of the four primary species differed among the three blocks as we indicated in the Materials and methods. We grouped ponderosa pine and Jeffrey pine into a pine category. Immediately after the treatments were installed, the proportion of white fir, incense cedar, and pines became 38%, 9%, and 53%, respectively, in the LoD without prescribed fire; 29%, 11%, and 61%, respectively, in the LoD with prescribed fire; 30%, 9%, and 61%, respectively, in the HiD without prescribed fire; and 42%, 9%, and 49%, respectively, in the HiD with prescribed fire (Table 1). During the 5 year period, net BA change was positive for all treatments except pine on HiD with fire (Fig. 3A). In general, more trees died in the prescribed-fire subplots than trees in the subplots without prescribed fire (Fig. 3B), which slightly changed species composition. Basal area growth of living trees offset the loss of tree numbers to yield a net positive BA increment in the LoD treatment with prescribed fire.

For the large and pole-size trees living through the period, we found that the trend of DBH increment during the 5 year period in the LoD treatment was: white fir > incense cedar > pines (Fig. 3C). In the HiD treatment, white fir grew the most in DBH, whereas incense cedar and pines were similar.

Responses of tree size-classes

Regardless of structural diversity and prescribed fire, the number of pole-size trees decreased, while large trees increased (Fig. 4). Except on the LoD without prescribed fire, the number of seedlings and saplings also decreased. The

Table 1. Average basal area (BA), quadratic mean diameter (QMD), and trees per hectare for seedlings and saplings, pole-size trees, and large trees, and height for pole-size and large trees of white fir (*Abies concolor*, ABCO), incense cedar (*Calocedrus decurrens*, CADE), ponderosa pine (*Pinus ponderosa*, PIPO), and Jeffrey pine (*Pinus jeffreyi*, PIJE) for low structural diversity (LoD) and high structural diversity (HiD) stand treatments, with (F) and without (NoF) prescribed fire at the Blacks Mountain Ecological Project measured before (pretreatment), immediately, and 5 years after the treatments were installed.

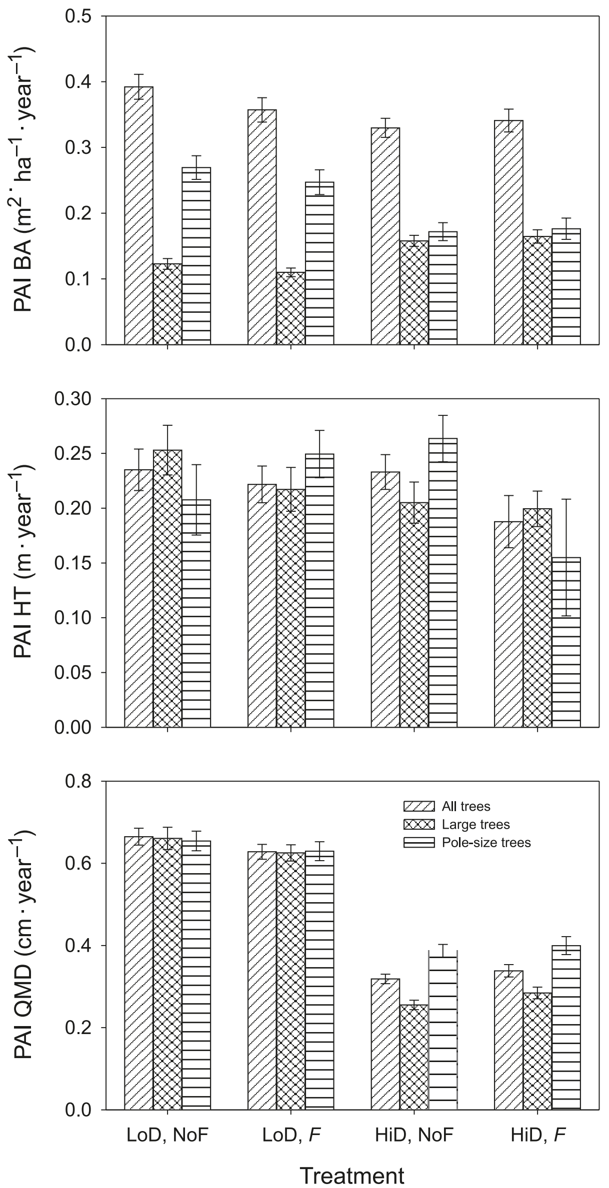
		Pretreatment				Immediately after the treatments				Five years after the treatments			
		LoD		HiD		LoD		HiD		LoD		HiD	
Variable	Species	NoF	F	NoF	F	NoF	F	NoF	F	NoF	F	NoF	F
BA ($m^2 \cdot ha^{-1}$)	ABCO	10.3	8.1	5.3	10.6	2.5	2.5	4.1	5.6	3.3	2.6	4.4	5.6
	CADE	4.1	2.6	2.7	1.9	0.9	0.9	2.1	2.0	1.1	1.0	2.5	2.1
	PIPO/PIJE	19.7	19.1	22.4	22.9	5.7	6.4	18.0	17.6	6.6	6.8	18.8	16.2
	Total	34.1	29.8	30.5	35.4	9.1	9.8	24.2	25.2	11.1	10.5	25.8	23.8
QMD (cm)	ABCO	30.2	31.2	31.3	31.6	23.9	25.0	27.7	28.4	28.1	30.1	28.0	30.0
	CADE	48.1	42.2	51.6	33.3	26.8	25.2	37.5	38.3	27.5	29.1	36.2	38.7
	PIPO/PIJE	37.9	39.5	44.0	38.0	25.5	26.1	36.8	39.6	26.7	29.8	37.3	41.0
	Overall	33.8	36.4	40.8	35.3	25.8	27.0	32.7	34.9	26.8	29.8	32.7	35.6
Trees·ha^{-1}	ABCO	360	311	183	396	107	80	155	214	102	50	172	163
	CADE	78	49	37	65	27	30	47	44	39	23	81	34
	PIPO/PIJE	535	476	461	534	151	170	320	245	175	126	335	187
	Total	972	838	681	994	285	280	522	503	316	199	588	384
Height (m)	ABCO					12.9	11.9	15.4	14.7	14.3	13.3	15.5	15.2
	CADE					12.5	10.0	17.9	17.2	12.8	11.1	16.4	14.4
	PIPO/PIJE					14.2	13.0	19.3	19.5	13.8	14.0	18.8	19.1
	Overall					12.8	12.2	16.6	16.1	13.3	13.4	16.6	16.3

Note: Seedlings, saplings, and height for all trees were not measured at the pretreatment measurement.

Table 2. Source of variation, degrees of freedom (df), mean squares (MS), probability values for net basal area (BA), quadratic mean diameter (QMD), trees per hectare, and height for all trees in the Blacks Mountain Ecological Research Project immediately after the treatments and 5 years after the treatments, as well as periodic annual increments (PAIs) for BA, QMD, and height only for trees living through the 5 year period.

		BA ($m^2 \cdot ha^{-1}$)		QMD (cm)		Trees ha^{-1}			Height (m)	
Source of variation	df	MS	Pr > *F*	MS	Pr > *F*	MS	Pr > *F*	df	MS	Pr > *F*
Immediately after the treatments										
Block	2	598.99		2.28		1 755 587		2	40.03	
Diversity (*D*)	1	27 109.95	0.001	7290.12	0.001	6 807 050	0.003	1	1231.85	0.009
Error (*a*)	7	71.47		153.25		356 848		4	54.19	
Prescribed fire (*F*)	1	81.70	0.525	518.30	0.114	75 522	0.638	1	1.51	0.767
D × *F*	1	0.64	0.955	29.80	0.684	6 398	0.890	1	3.61	0.648
Error (*b*)	9	186.96		169.05		317 812		6	15.68	
Five years after the treatments										
Block	2	633.54		1.99		2 060 069		2	4.58	
Diversity (*D*)	1	23 940.18	0.001	4775.58	0.001	7 463 223	0.006	1	1259.31	0.001
Error (*a*)	7	84.33		136.06		498 286		7	26.84	
Prescribed fire (*F*)	1	238.27	0.236	1458.63	0.030	4 102 391	0.017	1	0.79	0.871
D × *F*	1	86.96	0.462	0.24	0.974	345 315	0.418	1	1.72	0.811
Error (*b*)	9	147.48		220.13		478 329		9	28.37	
Five year PAI										
Block	2	0.95		0.96				2	0.78	
Diversity (*D*)	1	0.39	0.168	13.05	0.001			1	0.12	0.173
Error (*a*)	7	0.16		0.11				4	0.05	
Prescribed fire (*F*)	1	0.01	0.631	0.00	0.933			1	0.01	0.576
D × *F*	1	0.05	0.312	0.10	0.294			1	0.00	0.731
Error (*b*)	9	0.04		0.08				6	0.03	

Fig. 2. Average (μ ± 1 SE) periodic annual increments (PAIs) for basal area (BA), height, and quadratic mean diameter (QMD) for the various treatments calculated from trees that lived through the 5 years of observation on the Blacks Mountain Ecological Research Project. Large trees, >29.2 cm diameter at breast height (DBH); pole-size trees, 9.1–29.2 cm DBH. LoD, low structural diversity; NoF, without prescribed fire; *F*, with prescribed fire; and HiD, high structural diversity.

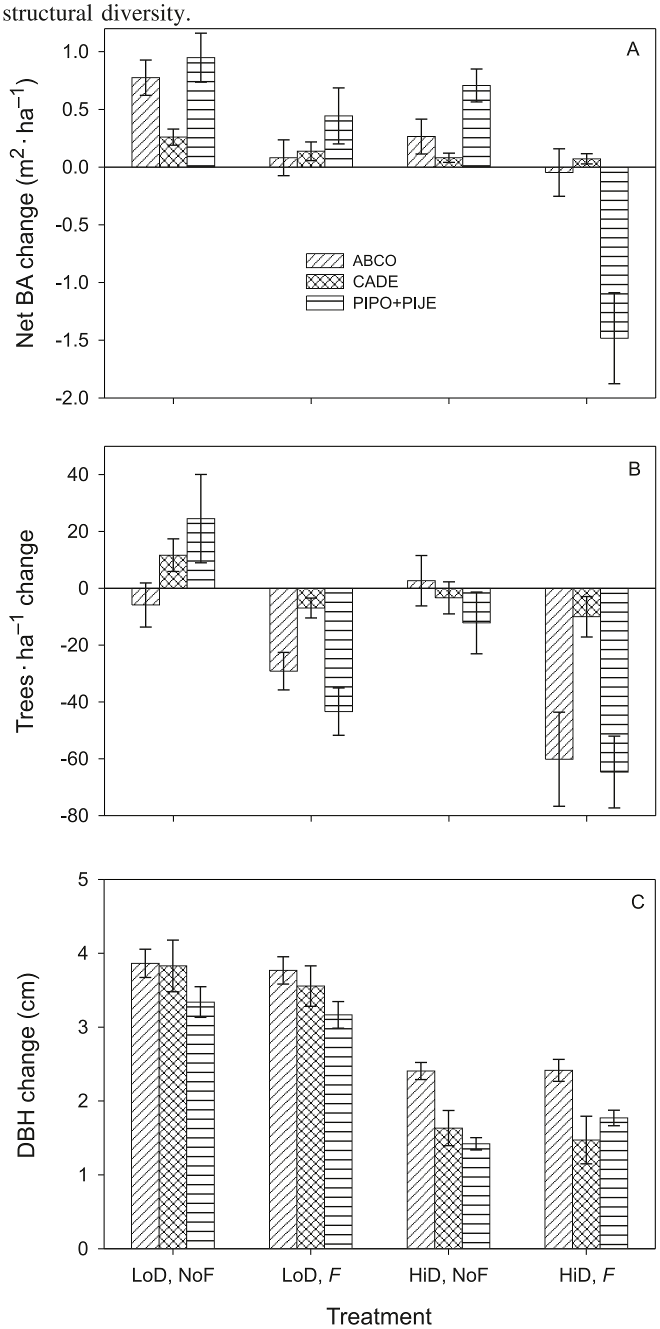


loss of pole-size trees might suggest some grew into the large tree category.

In terms of the 5 year increment, pole-size trees showed higher PAI BA in the LoD treatments compared with the HiD treatment (Fig. 2), whereas large trees showed the opposite pattern. Both large trees and pole-size trees show higher diameter growth (PAI QMD) in LoD treatment plots than in HiD treatment plots. No trends could be generated for PAI height.

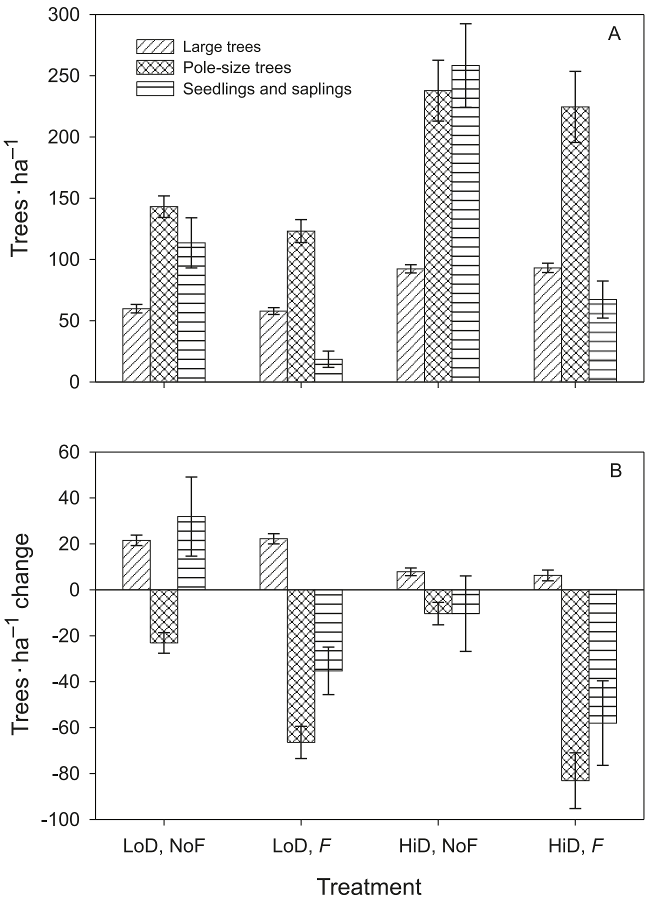
Before treatments were installed, there were about 8 old dominant trees·ha^{-1} (DBH > 76 cm) and 4 large snags·ha^{-1}

Fig. 3. Average changes (μ ± 1 SE) in net basal area (A), trees per hectare (B), and diameter at breast height (DBH) (C) for different species for the first 5 years after treatments were applied in the Blacks Mountain Ecological Research Project. ABCO, white fir (*Abies concolor*); CADE, incense cedar (*Calocedrus decurrens*); PIPO, ponderosa pine (*Pinus ponderosa*); and PIJE, Jeffrey pine (*Pinus jeffreyi*). BA, basal area; LoD, low structural diversity; NoF, without prescribed fire; *F*, with prescribed fire; and HiD, high structural diversity.



(DBH > 76 cm) in these stands. After treatment, LoD plots did not carry any old dominant tree component and averaged 1 large snag·ha^{-1}, whereas HiD plots kept the entire old dominant tree component and approximately 2 large snags·ha^{-1}. Five years later, these numbers did not change significantly. Old dominant trees grew about 0.6 cm in

Fig. 4. Trees per hectare for three tree size-classes (large trees, >29.2 cm diameter at breast height (DBH); pole-size trees, 9.1–29.2 cm DBH; and seedlings and saplings, <9.1 cm DBH) after 5 years post-treatment (A) and changes in trees per hectare (B) during the 5 years in the different treatments in the Blacks Mountain Ecological Research Project. LoD, low structural diversity; NoF, without prescribed fire; *F*, with prescribed fire; and HiD, high structural diversity.



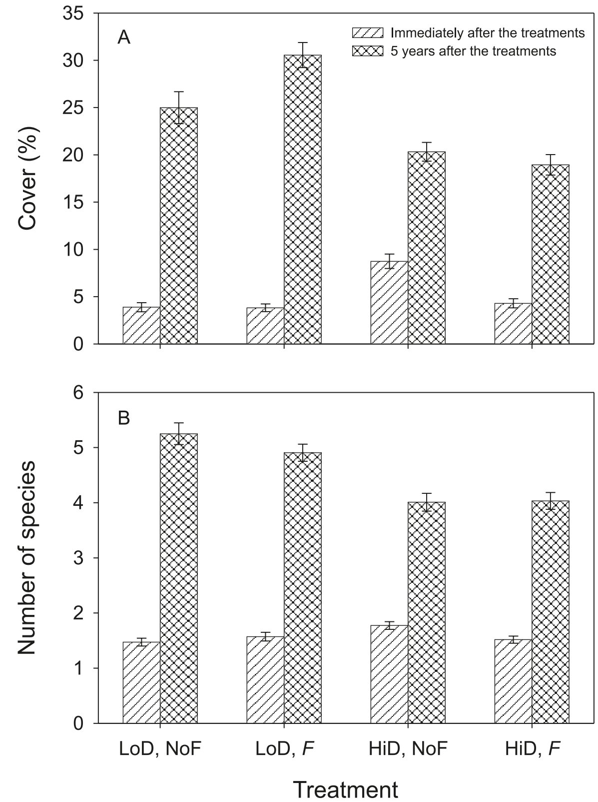
DBH in the HiD plots with or without prescribed fire over the 5 year measurement period.

Shrub characteristics

The inventory conducted immediately after treatment did not show any significant differences in shrub cover and number of species between structural diversities ($F < 1.73$ and $P > 0.23$). However, the prescribed-fire effect was significant for shrub cover ($F = 5.38$ and $P = 0.046$), but not in the number of species ($F = 2.94$ and $P = 0.12$). No interactions between these factors were significant ($F < 2.06$ and $P > 0.18$).

In the inventory conducted 5 years after treatments were applied, none of the treatment effects and their interactions were significant for shrub cover ($F < 5.03$ and $P > 0.05$) or for the number of species ($F < 1.23$ and $P > 0.29$). However, mean shrub cover increased from about 5% at the immediately post-treatment inventory to 20% 5 years later (Fig. 5). Shrub-cover increment over the 5 year measurement period was significantly higher on LoD units than on HiD units ($F = 5.97$ and $P = 0.04$) and on the treatments with prescribed fire than on treatments without prescribed fire ($F = 10.03$ and $P = 0.01$). In contrast, there was no significant structural diversity or prescribed-fire effect ($P > 0.14$) on change of the number of species.

Fig. 5. Average shrub cover (%) and number of species (±1 SE) found in the treatments at the Blacks Mountain Ecological Research Project immediately and 5 years after the treatments. LoD, low structural diversity; NoF, without prescribed fire; *F*, with prescribed fire; and HiD, high structural diversity.

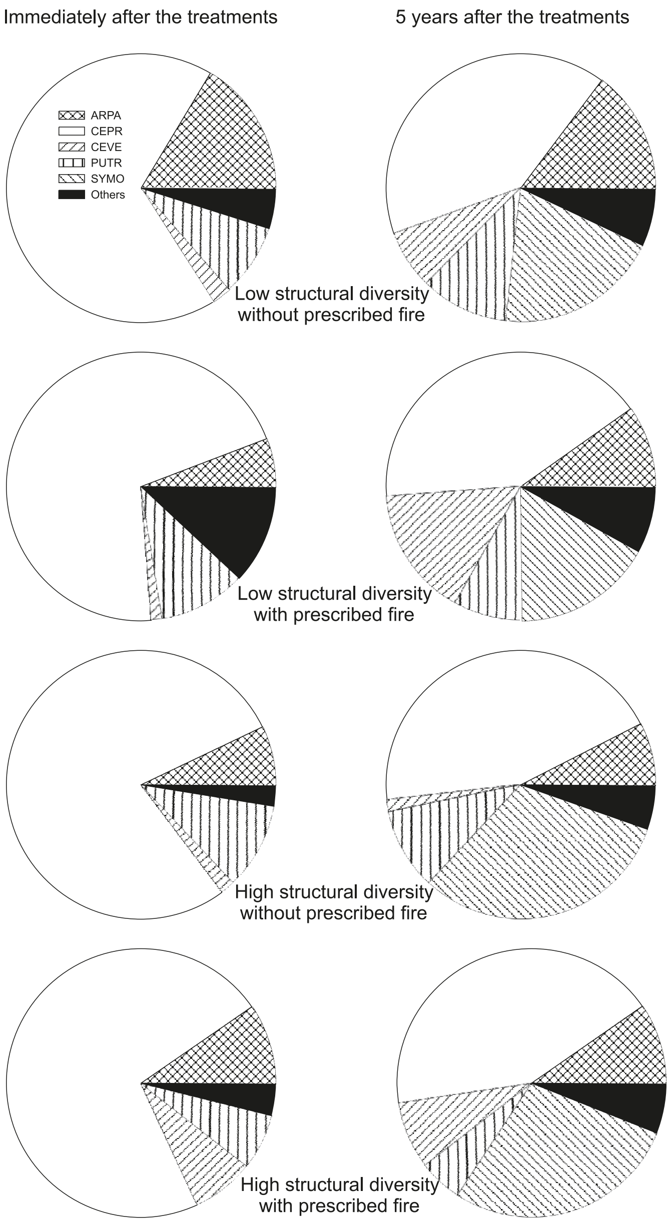


A summary of the relative dominance for the five most common shrubs indicated a decrease in prostrate ceanothus, the most disturbance-resistant species, and an increase in creeping snowberry during the 5 year period (Fig. 6). Antelope bitterbrush did not change substantially across the entire study.

Discussion

To address our proposed questions, we found that (1) the PAI for QMD was significantly greater in LoD than in HiD treatments (PAIs in Table 2 and Fig. 2). In addition, the effect of structural diversity varied significantly for average stand BA, QMD, trees per hectare, and height after treatments were applied and 5 years later. By removing small trees, prescribed fire reduced tree density and increased QMD. (2) Except for the HiD treatment with prescribed fire, BA net growth was positive during the 5 year period; the magnitude followed the proportion of the total number of trees for each species (Fig. 3). However, the trend in DBH increment by species was white fir > incense cedar > ponderosa and Jeffrey pine. (3) No interaction between structural diversity and prescribed fire was found for any stand characteristics (Table 2). (4) Both old dominant trees

Fig. 6. Individual shrub species responses to the treatments based on relative dominance at the Blacks Mountain Ecological Research Project measured immediately and 5 years after the treatments. ARPA, greenleaf manzanita (*Arctostaphylos patula*); CEPR, prostrate ceanothus (*Ceanothus prostratus*); CEVE, snowbrush (*Ceanothus velutinus*); PUTR, antelope bitterbrush (*Purshia tridentata*); and SYMO, creeping snowberry (*Symphoricarpos mollis*).



and large snags were relatively stable across treatments. Old dominant trees (DBH ≥ 76.2 cm) were still growing in diameter. (5) Understory shrub species richness was not affected by structural diversity (Fig. 5). However, coverage increment was significantly higher in the LoD than in the HiD, and with prescribed fire than without prescribed fire. During the 5 year period, prostrate ceanothus decreased in relative dominance because of the significant increase of creeping snowberry (Fig. 6).

Trees in low structural diversity stands showed significantly higher stem growth than did trees in high structural stands during the 5 year period of observation (Table 2 and Fig. 2). At the stand level, a similar trend was found for net BA increment (Fig. 3A). Periodic annual increment for BA of LoD trees was 12% higher than that of HiD trees (Fig. 2), although the effect was not significant (Table 2). In addition, pole-size trees had higher PAI BA than did the large trees (Fig. 2). These trends should not be surprising because growth rate and health of residual trees usually will be improved after being released from an overstory as was done in this study (Daniel et al. 1979; Tappeiner et al. 2007).

Surprisingly, PAI BA was not significantly higher in the HiD treatments than it was in the LoD treatments, considering that the site potential was probably not fully realized in the LoD treatments. At an average of 9.4 $m^2 \cdot ha^{-1}$ of BA after treatment, the LoD treatment would seem to be in stage II of Langsaeter's growth curve (sensu Daniel et al. 1979, p. 318), whereas the HiD treatment at 26.4 $m^2 \cdot ha^{-1}$ of BA would be at or near stage III. If an optimum leave-stand density for maximum BA growth is 25.2 $m^2 \cdot ha^{-1}$ on site qualities similar to BMEF (Oliver 1972, 1979; Oliver and Edminster 1988), the HiD treatments should have produced significantly more BA annually than the LoD treatments. The results from the current study showed otherwise (Fig. 2). The answer can be found in the much lower PAI QMD of the old dominant trees in the HiD treatment and the fact that this component represented 24% of the BA of the HiD treatment. Old dominant trees were only growing 0.6 cm during the 5 years after treatment, whereas the smaller younger pole-size trees in the LoD treatment were growing 3.3 cm. These old dominant trees have sparser foliage, lower leaf area, lower photosynthetic capacity, higher respiration proportional to their gross primary production, and a higher carbon allocation to the roots compared with the smaller and younger trees (Helms 1964; Daniel et al. 1979; Smith et al. 1996; Ryan et al. 2004). Therefore, converting old-growth stands to younger, fast-growing stands would increase stem production (Hallin 1959), although total net primary productivity may not vary (Spurr and Barnes 1980; Kaye et al. 2005).

Timber production may not be the primary goal in managing today's forests. Rather, the development and maintenance of late-seral forest values have become paramount, especially on public lands. Yet, many of these forests are threatened by wildfires, pest outbreaks, and drought. These threats are exacerbated by past harvesting practice and fire exclusion for most of the last century (Covington and Moore 1994; Allen et al. 2002). Restoration of late seral attributes can mitigate these threats. Results from the HiD treatment suggest that we have enhanced late seral attributes in these stands relative to the untreated stands. They carry many fewer trees and less basal area (Table 1). The large snags were relatively stable across treatments and the old dominant trees were still growing in diameter. The prescribed fire did not cause any mortality for the old dominant trees (≥76.2 cm DBH) as suggested by some (see review of Kolb et al. 2007) or any damage to the large snags, although there was some mortality among trees <76.2 cm DBH. It should be noted that raking duff layer away from individual snags prior to burning contributed to snag retention.

Mortality from prescribed fire must be considered because the conditions of these stands can only be maintained with repeated thinning and (or) prescribed fire. Although observed mortality was delayed, many trees apparently alive after prescribed fire, died during the next 5 years. Mortality assessments should consider secondary (mainly bark beetle; Fettig et al. 2008) as well as primary (fire) mortality after prescribed fire to obtain accurate estimates (McHugh and Kolb 2003). Fettig et al. (2008) found that bark beetle colonies in 2.6% of the trees in the prescribed fire split compared with only 0.4% in the unburned split, regardless of structural diversity. Therefore, managers must consider the possible bark beetle damage when treating these stands with prescribed fire. However, trees found surviving 5 years after prescribed fire grew as much as trees without fire (Fig. 2), suggesting that low intensity surface fires might not affect tree growth, at least over the short term (Stephenson et al. 1991; Brown and Swetnam 1994; Busse et al. 2000; Ritchie and Harcksen 2005).

Response of shrubs suggests the need for future treatments to maintain an open understory (Fig. 5). Shrub cover increased in all treatments during the 5 year period and returned to the 21% found in untreated stands in adjacent RNAs (Blacks Mountain Ecological Research Project, unpublished data). The average number of species across plots is over twice as great in treated stands (Fig. 5) than in untreated stands, which averaged only two species (unpublished data), indicating shrub diversity was not adversely affected. We found that prostrate ceanothus lost its dominance during the 5 years after treatment, mainly because of increasing dominance of creeping snowberry, a flammable species. Coverage of antelope bitterbrush, the only valuable forage species among the common shrubs measured in the study, was relatively stable across the entire study during the 5 year period (Fig. 6).

Restoration of natural ecosystems attempts to mimic the forest conditions prior to Euro-American settlement, which are described as open parklike stands able to survive frequent surface fires (Covington and Moore 1994; Allen et al. 2002). However, we are often lacking quantitative measures of those conditions. By using the stand inventory data for large and pole-size trees at the BMEF in 1934, Ritchie et al. (2008) found that stand density in our current HiD treatment (~330 trees·ha^{-1}) was still higher than the stand density (~240 trees·ha^{-1}) in 1934. The proportion of white fir is higher and pine species lower in the current HiD stands (~31% and 61%, respectively) than in 1934 (~7% and 85%, respectively). The LoD treatment is not comparable because it was not intended to mimic the old-growth stands.

Throughout the range of ponderosa pine, risk of severe, stand-replacing fire and bark-beetle outbreaks have led to increased interest in restoring late seral attributes to these systems. The stand structures considered in this study are representative of two contrasting management priorities. The LoD stand is consistent with a timber production emphasis, yielding a higher rate of growth at the individual tree and stand levels. The HiD stand is consistent with an emphasis on maintenance of a range of tree sizes that may be more consistent with historic conditions prior to Euro-American settlement. This increase in structural diversity comes at a cost in terms of tree productivity. This cost may be offset by other amenities such as wildlife habitat or visual resources. With either type of stand structure, use of prescribed fire may be beneficial in maintaining the health and vigor of these stands in the long term. However, its application may reduce the occurrence of snags and woody debris; both are key components of wildlife habitat.

Acknowledgements

This long-term project could not have succeeded without so many dedicated people who designed, installed, and maintained the study. We thank them all. Particularly, we want to give our appreciation to Kathleen Harcksen and Bob Carlson, who oversaw the study installation, and to Todd Hamilton, Nicholas Vaughn, Brian Wing, and John Anstead, who oversaw collection and management of the data for this manuscript. The comments from Sylvia Mori, Brian Wing, Robert Powers, and John Tappeiner for improving the manuscript are greatly appreciated. Use of trade names in this paper does not constitute endorsement by the USDA Forest Service.

References

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Agee, J.K. 2003. Monitoring postfire tree mortality in mixed-conifer forests of Crater Lake, Oregon, USA. Nat. Areas J. **23**: 114–120.

Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., and Klingel, J.T. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecol. Appl. **12**: 1418–1433. doi:10.1890/1051-0761(2002)012[1418:EROSPP]2.0.CO;2.

Barrett, J.W. 1982. Twenty-year growth of ponderosa pine thinned to five spacings in central Oregon. Portland, Oregon. Pacific Northwest Forest and Range Station. Res. Paper PNW-301.

Brown, P.M., and Swetnam, T.W. 1994. A cross-dated fire history from coast redwood near Redwood National Park, California. Can. J. For. Res. **24**: 21–31. doi:10.1139/x94-138.

Busse, M.D., Simon, S.A., and Riegel, G.M. 2000. Tree growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. For. Sci. **46**: 258–268.

Cochran, P.H., and Barrett, J.W. 1993. Long-term response of planted ponderosa pine to thinning on Oregon's Blue Mountains. West. J. Appl. For. **8**: 126–132.

Cooper, C.F. 1960. Changes in vegetation, structure and growth of southwestern pine forests since white settlement. Ecology, **42**: 493–499. doi:10.2307/1932235.

Covington, W.W., and Moore, M.M. 1994. Southwestern ponderosa forest structure and resource conditions: changes since Euro-American settlement. J. For. **92**: 39–47.

Covington, W.W., and Sacket, S.S. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. For. Sci. **30**: 183–192.

Daniel, T.W., Helms, J.A., and Baker, F.S. 1979. Principles of silviculture. 2nd ed. McGraw-Hill Book Company.

Dolph, K.L., Mori, S.R., and Oliver, W.W. 1995. Long-term response of old-growth stands to varying levels of partial cutting in the eastside pine type. West. J. Appl. For. **10**: 101–108.

Dunning, D. 1928. A tree classification for selection forests of the Sierra Nevada. J. Agric. Res. **36**: 755–771.

Ferrell, G.T. 1980. Risk-rating systems for mature red fir and white fir in northern California. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, Calif. Gen. Tech. Rep. PSW-39.

Fettig, C.J., Borys, R.R., McKelvey, S.R., and Dabney, C.P. 2008.

Blacks Mountain Experimental Forest: bark beetle responses to differences in forest structure and the application of prescribed fire in interior ponderosa pine. Can. J. For. Res. **38**. This issue.

Fiedler, C.E. 2000. Restoration treatments promote growth and reduce mortality of old-growth ponderosa pine (Montana). Ecol. Rest. **18**: 117–118.

Hallin, W.E. 1959. The application of unit area control in the management of ponderosa – Jeffrey pine at Blacks Mountain Experimental Forest. USDA For. Serv. Tech. Bull. No. 1191.

Helms, J.A. 1964. Apparent photosynthesis of Douglas-fir in relation to silvicultural treatment. For. Sci. **10**: 432–442.

Kauffman, J.B., and Martin, R.E. 1989. Fire behavior, fuel consumption and forest-floor changes following prescribed understory fires in Sierra Nevada mixed conifer forests. Can. J. For. Res. **19**: 455–462. doi:10.1139/x89-071.

Kaye, J.P., Hart, S.C., Fule, P.Z., Covington, W.W., Moore, M.M., and Kaye, M.W. 2005. Initial carbon, nitrogen, and phosphorus fluxes following ponderosa pine restoration treatments. Ecol. Appl. **15**: 1581–1593. doi:10.1890/04-0868.

Keen, F.P. 1943. Ponderosa pine tree classes redefined. J. For. **41**: 249–253.

Kolb, T.E., Agee, J.K., Fule, P.Z., McDowell, N.G., Pearson, K., Sala, A., and Waring, R.H. 2007. Perpetuating old ponderosa pine. For. Ecol. Manage. **249**: 141–157. doi:10.1016/j.foreco.2007.06.002.

Latham, P., and Tappeiner, J. 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. Tree Physiol. **22**: 137–146. PMID:11830410.

McDowell, N.G., Brooks, J.R., Fitzgerald, S.A., and Bond, B.J. 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. Plant Cell Environ. **26**: 631–644. doi:10.1046/j.1365-3040.2003.00999.x.

McHugh, C.W., and Kolb, T.E. 2003. Ponderosa pine mortality following fire in northern Arizona. Int. J. Wildland Fire, **12**: 7–22. doi:10.1071/WF02054.

Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

Oliver, W.W. 1972. Growth after thinning ponderosa and Jeffrey pine pole stands in northeastern California. USDA For. Serv. Res. Pap. PSW-85.

Oliver, W.W. 1979. Fifteen-year growth patterns after thinning a ponderosa – Jeffrey pine plantation in northeastern California. USDA For. Serv. Res. Pap. PSW-141.

Oliver, W.W. 1997. Twenty-five-year growth and mortality of planted ponderosa pine repeatedly thinned to different stand densities in northern California. West. J. Appl. For. **12**: 122–130.

Oliver, W.W. 2000. Ecological research at the Blacks Mountain Experimental Forest in northeastern California. Pacific Southwest Research Station, Albany, Calif. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-179.

Oliver, W.W. 2001. Can we create and sustain late successional attributes in interior ponderosa pine stands? Large-scale ecological research studies in northeastern California. *In* Proceedings of Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship, Flagstaff, Ariz., 25–27 April 2000. *Compiled by* R.K. Vance, C.B. Edminster, W.W. Covington, and J.A. Blake. Rocky Mountain Research Station, Ogden, Utah. Proceedings RWRS-P-22. pp. 99–103.

Oliver, W.W., and Edminster, C.B. 1988. Growth of ponderosa pine thinned to different stocking levels in the western United States. *In* Proceedings of Future Forests of the Mountain West: a Stand Culture Symposium, Missoula, Montana, 29 September – 3 October 1986. *Compiled by* W.C. Schmidt. USDA For. Serv. Gen. Tech. Rep. INT-243. pp. 153–159.

Oliver, W.W., and Powers, R.F. 1998. Blacks Mountain, California: interdisciplinary field research in ponderosa pine. J. For. **96**: 4–9.

Raymond, C.L., and Peterson, D.L. 2005. Fuel treatments alter the effects of wildfire in a mixed-evergreen forest, Oregon, USA. Can. J. For. Res. **35**: 2981–2995. doi:10.1139/x05-206.

Ritchie, M.W., and Harcksen, K.A. 2005. Accelerating development of late-successional features in second-growth pine stands of the Goosenest Adaptive Management Area. *In* Proceedings of the Symposium on Ponderosa Pine: Issues, Trends, and Management, Klamath Falls, Oreg., 18–21 October 2004. *Compiled by* M.W. Ritchie, D.A. Maguire, and A. Youngblood. Pacific Southwest Research Station, Albany, Calif. Gen. Tech. Rep. PSW-GTR-198. pp. 81–93.

Ritchie, M.W., Skinner, C.N., and Hamilton, T.A. 2007. Probability of wildfire-induced tree mortality in an interior pine forest: effects of thinning and prescribed fire. For. Ecol. Manage. **247**: 200–208. doi:10.1016/j.foreco.2007.04.044.

Ritchie, M.W., Wing, B.M., and Hamilton, T.A. 2008. Stability of the large tree component in treated and untreated late-seral interior ponderosa pine stands. Can. J. For. Res. **38**. This issue.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., and Senock, R.S. 2004. An experimental test of the causes of forest growth decline with stand age. Ecol. Monogr. **74**: 393–414. doi:10.1890/03-4037.

Sala, A., Peters, G.D., McIntyre, L.R., and Harrington, M.G. 2005. Physiological responses of ponderosa pine in western Montana to thinning, prescribed burning, and burning season. Tree Physiol. **25**: 339–348. PMID:15631982.

Skinner, C.N. 2005. Reintroducing fire into the Blacks Mountain Research Natural Area: effects on fire hazard. *In* Proceedings of the Symposium on Ponderosa Pine: Issues, Trends, and Management, Klamath Falls, Oreg., 18–21 October 2004. *Compiled by* M.W. Ritchie, D.A. Maguire, and A. Youngblood. Pacific Southwest Research Station, Albany, Calif. Gen. Tech. Rep. PSW-GTR-198. pp. 245–257.

Smith, D.M., Larson, B.C., Kelty, M.J., and Ashton, P.M.S. 1996. The practice of silviculture: applied forest ecology. John Wiley & Sons, Inc., New York.

Spurr, S.H., and Barnes, B.V. 1980. Forest ecology. 3rd ed. John Wiley & Sons, New York.

Stephenson, N.L., Parsons, D.J., and Swetnam, T.W. 1991. Restoring fire to the sequoia – mixed conifer forest: Should intense fire play a role? *In* High Intensity Fire in Wildlands: Management Challenges and Options. Proceedings of the 17th Tall Timbers Fire Ecology Conference, Tallahasee, Florida, 18–21 May 1989. pp. 321–337.

Stov, K.R., Kolb, T.E., and Wallin, K.F. 2005. Difference in radial growth response to restoration thinning and burning treatments between young and old ponderosa pine in Arizona. West. J. Appl. For. **20**: 36–43.

Tappeiner, J.C., II, Maguire, D.A., and Harrington, T.B. 2007. Silviculture and ecology of western US forests. Oregon State University Press, Corvallis, Oreg.

Taylor, A.H. 2000. Fire regimes and forest changes along a montane forest gradient, Lassen Volcanic National Park, south Cascade Mountains, USA. J. Biogeogr. **27**: 87–104. doi:10.1046/j.1365-2699.2000.00353.x.

Youngblood, A., Timothy, M., and Kent, C. 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. For. Ecol. Manage. **199**: 191–217. doi:10.1016/j.foreco.2004.05.056.

Zhang, J.W., Oliver, W.W., and Busse, M.D. 2006. Growth and development of ponderosa pine on sites of contrasting productivities: relative importance of stand density and shrub competition effects. Can. J. For. Res. **36**: 2426–2438. doi:10.1139/X06-078.