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Response of old-growth conifers to reduction in stand density in western Oregon forests

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Summary The positive growth response of healthy young trees to density reduction is well known. In contrast, large old trees are usually thought to be intrinsically limited in their ability to respond to increased growing space; therefore, density reduction is seldom used in stands of old-growth trees. We tested the null hypothesis that old-growth trees are incapable of responding with increased growth following density reduction. The diameter growth response of 271 Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) and sugar pine (*Pinus lambertiana* Dougl.) trees ranging in age from 158 to 650 years was examined 20 to 50 years after density reduction. Density reduction involved either light thinning with removal of less vigorous trees, or shelterwood treatments in which overstory trees were not removed. Ratios of basal area growth after treatment to basal area growth before treatment, and several other measures of growth, all indicated that the old trees sometimes benefited and were not harmed by density reduction. Growth increased by 10% or more for 68% of the trees in treated stands, and nearly 30% of trees increased growth by over 50%. This growth response persisted for at least 20 years. During this 20-year period, only three trees in treated stands (1.5%) exhibited a rapid decrease in growth, whereas growth decreased in 64% of trees in untreated stands. The length of time before a growth response to density reduction occurred varied from 5 to 25 years, with the greatest growth response often occurring 20 to 25 years after treatment. These results have important implications both for the basic biology of aging in woody plants as well as for silvicultural practices in forests with old-growth trees.

Keywords: basal area growth, density reduction, Pinus lambertiana, Pinus ponderosa, Pseudotsuga menziesii, southern Cascades, thinning, tree vigor.

Introduction

Old-growth trees are an important resource ecologically, economically and aesthetically. In the Pacific Northwest, the importance of maintaining large, old-growth trees in stands for the structural diversity and unique habitats they provide has frequently been emphasized (Habeck 1988, Hunter 1990, Franklin and Spies 1991, Marcot 1997). Old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) and sugar pine (*Pinus lambertiana* Dougl.) in the southern Cascades are often greater than 60 m tall with crowns extending over 50% of their height. Bole diameters at breast height (dbh; 1.37 m) are well over a meter with thick furrowed bark that allows the trees to withstand periodic low-intensity fires. Trees of this size may be 300 years old or more and many may be at risk as a result of damage from intense wildfires, drought and attacks by insects or pathogens.

Since fire suppression began in the early 1900s, both the numbers of trees and the basal area in the understory of many old-growth stands have increased (Parsons and DeBendetti 1979, McNeil and Zobel 1980), potentially making them more susceptible to stand-replacing fires. Prior to 1900, fire was much more common in mid- to low-elevation old-growth forests than it is today (Agee 1990). Low-intensity fires reduced both the density of understory trees and accordingly, the potential for carrying fire into old-growth tree crowns (Thomas and Agee 1986). Current high densities of understory trees may also contribute to water stress in large old-growth trees that could make them susceptible to insect-related mortality (Dolph et al. 1995), especially during periods of drought (Mitchell et al. 1983, Cochran 1998). Because these threats are related to increasing stand densities, thinning old-growth stands may reduce the threat of stand-replacing fires and increase resource availability to large old-growth trees, which in turn may prolong their lives by reducing the effects of competition. It is usually assumed that large old-growth trees are unable to respond to increased resource availability following thinning; however, this assumption has not been tested in very old trees. The assumption that old-growth trees are intrinsically limited may be partially because most studies of old-growth forests have focused on volume growth of entire stands rather than the growth of individual trees. Currently, there is no information about the magnitude of the growth response or the proportions of trees that might be expected to increase in growth following thinning of an old-growth forest. However, growing space available to individual trees in stands is an important factor governing tree and stand vigor (Cochran et al. 1994). Although old-growth trees might not show growth responses to thinning similar to those of young trees, even a small increase in growth or stabilization of a formerly decreasing growth rate might indicate an improvement in tree vigor and increased resistance to insects and pathogens, which may prolong the life of the trees. Even if growth is unaffected by density reduction, thinning might be considered to reduce fire hazard in stands with old trees.

Our primary objective was to test the null hypothesis that individual, old-growth trees do not respond to density reduction treatments. We also attempted to describe the length of the sustained growth response (if any), the period of time that passed until a response occurred, and differences between trees that did and did not significantly increase in growth. We did not attempt to characterize the response of stands. A secondary objective was to determine whether current attributes such as crown length and fullness (Ferrell 1983), as well as the current density around individual trees, could be used to assess how old-growth trees might respond to thinning.

Materials and methods

Study sites

Many old-growth stands in the western United States were partially cut in the past 50 or more years. For instance, trees that were most susceptible to mortality from insects and other causes were removed (Salman and Bongberg 1942, Keen 1943, Wickman and Eaton 1962), leaving those trees thought to be less susceptible (Dunning 1928, Ferrell 1983). Where regeneration harvests occurred, large old-growth trees were sometimes left to provide shelter for the regenerating stand or as a seed source for natural regeneration. Thus, today there are many stands of old-growth trees that have received some level of thinning treatment, and they encompass a range of densities, sizes, ages and crown characteristics.

We investigated the diameter growth of 271 old-growth Douglas-fir, ponderosa pine and sugar pine trees in 13 treated and four untreated stands in western Oregon (Table 1). Eight of the treated stands had been partially cut. Five stands had received regeneration harvests with overstory trees retained. Most of the stands were in the southern Cascades of southwestern Oregon. However, we also included one stand in the Siskiyou Mountains (Woodpecker Springs) and two stands in the central Coast Range (Bottomline 1 and 2), to compare the growth responses of trees in areas with site quality differences. These stands represent the extremes of site conditions, ranging from hot and dry to sites with abundant moisture and moderate temperatures.

We selected stands by querying the USDI Bureau of Land Management (BLM) silviculture database for stands with known treatment dates and with a cohort of trees at least 200 years old. All of the treated stands were tractor-logged at least 20 years ago (Table 1 provides specific details). Comparable untreated stands within 2 km of treated stands were selected as controls. We included all comparable untreated stands that we could locate. Elevations of the stands selected in southwest Oregon ranged from 1400 to 1600 m. The elevation of the two stands in the Coast Range was about 213 m.

To evaluate possible interactions between thinning intensity and growth response, we assigned a density class (L = low density, M = medium density) to all treated stands. All of the stands receiving regeneration harvests, including most of the ponderosa pine stands, were classified as L. Current basal area in these stands ranges from 4 to 18 m^2 ha^{-1} with 4 to 15 trees ha^{-1} ≥ 76 cm dbh. The remaining treated stands, including both of the sugar pine stands, were classified as M. Basal area in these stands ranges from 28 to 58 m^2 ha^{-1} with 12 to 38 trees ha^{-1} ≥ 76 cm dbh. The basal area in untreated stands ranges from 61 to 104 m^2 ha^{-1} with 24 to 60 trees ha^{-1} ≥ 76 cm. A variety of treatments occurred in the Douglas-fir stands. Estimated ages of the study trees ranged from 158 to 650 years (Table 1).

Field methods

At each site, 12 or more healthy trees with a dbh of at least 76 cm were randomly selected. Trees in the control stands were comparable with those in the treated stands and were unlikely to have been removed had the control stands been treated. We recorded the species, height, dbh and height to the base of the live crown (the lowest whorl with at least two branches). We accounted for gaps and irregularities in the crowns by measuring percent raggedness (Ferrell 1983). This measure was then combined with the traditional crown ratio measurement to provide an estimate of crown fullness (CR2), where CR2 = (Crown length(1 – %Raggedness/100)/Height) 100. Radial growth was measured from increment cores extracted from the uphill side of trees. The cores included equal periods of time before and after density reduction treatments. Sapwood (the moist portion of the core) was marked for Douglas-fir trees at the time the core was extracted. In the laboratory, the cores were mounted in holders, sanded, and the year of treatment marked by counting back from the current ring the number of years indicated by the BLM harvest records. We then measured radial growth in 5-year increments before and after treatment, using magnification when needed, and calculated basal area growth for each of these time intervals. In untreated stands, increment cores were obtained for equivalent lengths of time. Because the study trees were too large to obtain ages accurately from increment cores, ages were estimated at each site by counting rings on nearby tree stumps that matched the range of tree diameters that we measured.

To account for local stocking differences and the effect of local competition around each study tree, we recorded the diameters of all trees ≥ 25 cm dbh on 0.04-ha circular plots around each study tree. Previous studies of the relationship of stand structure to tree growth indicate that vertical relationships among tree crowns also significantly affect the growth of individual trees (Biging and Dobbertin 1995, Latham et al.

Table 1. Description of old-growth study trees in treated and untreated stands. Current stand densities appear following the tree data. Abbreviations: OGT = old-growth trees; *H* = tree height; *D* = trunk diameter; BA = tree basal area ($m^2\ ha^{-1}$); DF = Douglas-fir; PP = ponderosa pine; and SP = sugar pine.

Site	Years after treatment	Age range of OGT	No. and species of OGT	*H* (m)	*D* range (cm)	*H*/*D* ratio	Crown ratio 2 (%)	No. live trees ha^{-1} ≥ 25 cm	No. live trees ha^{-1} ≥ 76 cm	BA of live trees ≥ 25 cm	Cut trees ha^{-1} ≥ 25 cm dbh	
											No.	BA
Treated stands: low density												
Conde Creek 3	25	158–221	15 (DF)	45	72–126	46	25–51	15	8	7	82	41
Divide Lakes 1	30	180–250	15 (14PP/1SP)	42	78–110	44	32–60	22	4	9	235	57
Divide Lakes 2	30	203–242	15 (PP)	40	76–114	43	34–56	60	12	17	152	51
Woodpecker	20	202–280	15 (PP)	47	72–138	46	16–57	45	15	18	82	43
Bottomline 1	50	~250	13 (DF)	61	94–184	43	35–64	2	–	4	–	–
Treated stands: medium density												
Shell Peak 1	30	290–390	14 (12DF/2PP)	50	90–180	38	50–83	45	12	28	92	37
Conde Creek 2	35	330–380	14 (13DF/1PP)	48	76–161	45	33–76	98	28	29	95	44
Beaver Creek	30	166–317	22 (1DF/1PP/20SP)	45	78–180	44	14–67	120	34	36	20	13
Shell Peak 2	35	180–360	15 (DF)	54	96–188	39	21–73	122	28	40	86	38
Howard Prairie	30	194–512	15 (10DF/4PP/1SP)	49	86–138	47	17–55	175	28	48	12	10
Moon Prairie 1	35	~400	13 (DF)	50	94–243	31	59–82	38	28	51	55	26
Yew Springs	35	277–515	15 (SP)	44	86–144	39	20–53	262	25	52	38	16
Keno Pine	30	187–650	15 (8DF/7PP)	48	82–161	46	14–57	258	38	58	85	22
Untreated stands												
Jenny Creek	35	238–640	30 (11DF/19SP)	48	76–164	40	18–66	225	24	61	5	3
Hoxie Creek	30	162–377	15 (PP)	48	78–144	50	16–49	350	38	65	4	2
Moon Prairie 2	35	~350	15 (12DF/3PP)	56	108–179	38	17–60	178	60	104	2	1
Bottomline 2	35	~280	15 (DF)	62	104–280	45	14–42	–	–	77	–	–

1998). Therefore, we recorded the vertical positions of the crowns of other trees on the 0.04-ha plots relative to the crown of the study tree in three positions identified by Latham et al. (1998): overlapping the upper 60% of the study tree's crown (POS1); overlapping the lower 40% of the crown (POS2); and below the crown (POS3). The diameters of all stumps ≥ 25 cm were measured at stump height.

Stand density (trees ha^{-1} and basal area ha^{-1}) and species composition were characterized for each site based on four to five randomly placed 0.1-ha circular plots in which we recorded species and diameters of all trees at least 1.37 m tall and the diameters of all stumps.

Growth characteristics

Growth was quantified for each tree based on three primary indices: mean basal area growth, from 5-year increment measurements, for the interval between stand treatment and growth measurement (BAGA); mean basal area growth for an equal number of years before treatment (BAGB); and the ratio BAGA/BAGB. We also calculated mean growth for the most recent 10 years since treatment. This measure and the percentage of trees (for all sites and species combined) in cumulative growth ratio classes ranging from ≤ 1.0 to ≥ 2.0 by 5-year time periods after treatment were used to indicate the longevity of the treatment response.

Time period used to assess growth response

In most cases, the period used to analyze growth was 30–35 years before and after the treatment year, but in some of the more recently cut stands a shorter period (20–25 years) was used (Table 1). We used relatively long time periods for these comparisons because we had previously observed that it might take several years after a thinning treatment for a response to become noticeable. Because there were not enough untreated stands for paired comparisons, we determined growth in the untreated stands over the time period occurring in the majority of the treated stands to which they were being compared.

Relationships between basal area growth and other tree and stand characteristics

Sapwood area was calculated for Douglas-fir as the difference between heartwood area and total basal area at breast height and used as an estimate of growth potential or tree vigor (Waring et al. 1982, O'Hara and Valappil 1995). We related the following measures to BAGA: CR2, height/diameter ratios (Williams et al. 1996), current basal area and basal area removed (stand measures), and local competition (basal areas of live trees in the three crown positions relative to the study tree on the 0.04-ha plots). Basal areas of dead and cut trees were also calculated on the 0.04-ha plots.

Statistical tests

To test the null hypothesis that there was no effect of density reduction on basal area growth, we performed a one-way analysis of variance (ANOVA) with the GLM procedure of the SYSTAT 8.0 software package (Wilkinson 1998) followed by

Fisher's least significant difference (LSD) multiple comparison tests and two-sample separate variance *t*-tests. For all statistical tests, $\alpha = 0.05$.

Statistical tests were performed hierarchically starting with comparisons of BAGA in the two density classes of the treated stands and the control stands, with all sites and species combined (ANOVA). We then performed *t*-tests to compare BAGA and BAGB for each species in treated and untreated stands with all densities combined. Then, we tested for significant differences between BAGA and BAGB at individual sites (*t*-tests), and compared BAGA and the growth ratios (BAGA/BAGB) among all of the sites (ANOVA). Finally, we used *t*-tests to compare BAGA and BAGB for each of the 271 trees. We could not find enough stands of different densities for ponderosa pine and sugar pine to test for possible species × density interactions in the growth response. Individual trees were assigned to one of three growth change classes (I = increasers, D = decreasers and NC = no significant change in growth) based on the results of the *t*-tests. We then tested differences in growth, tree and plot characteristics for trees in the two largest growth response groups in treated (I and NC) and untreated (D and NC) stands for all species combined. There were not enough I trees in untreated stands or D trees in treated stands to test.

We used univariate and multiple linear regression to examine the relationships between estimates of mean basal area growth after treatment (mean BAGA) and estimates of residual basal area and basal area removed. We also used regression to examine the relationships between BAGA and the basal area removed, the total live basal area, and the basal area of live trees in Positions 1, 2 and 3 on the 0.04-ha plots around each study tree. Finally, BAGA was examined in relation to crown ratios of the study trees. We tested differences between mean basal area growth for the last 10 years in treated and untreated stands by ANCOVA with sapwood area as the covariate to determine if growth responses to density reduction were long-lasting and if sapwood area was related to the response.

Results

Tree characteristics

Crown fullness (CR2) in treated stands averaged 55% (± 2% SE), whereas it averaged 39 ± 1.4% in the untreated stands. Height/diameter (*H*/*D*) ratios were consistently low with means ranging from 31 to 47 in treated stands and 38 to 50 in untreated stands (Table 1). Density immediately around the study trees varied with current mean basal area ranging from 1.25 to 7 $m^2\ ha^{-1}$ in the shelterwood treatments (L treatments) and from 17.25 to 56 $m^2\ ha^{-1}$ in the medium residual density treatments (M treatments).

Growth responses—comparisons of mean responses by density, species and site

For all species combined, BAGA was significantly greater for trees in stands with low and medium residual densities than for trees in the untreated stands. However, there was no significant difference in growth between trees in L and M stands (Table 2). When results for all treated stands were combined by species, BAGA was significantly greater than BAGB for Douglas-fir and ponderosa pine but not for sugar pine (Table 3). For populations of trees within stands, BAGA was significantly greater than BAGB in three of four ponderosa pine stands and three of eight Douglas-fir stands (indicated by an asterisk in Table 4). There were no significant differences between BAGA and BAGB in the control stands.

For ponderosa pine trees, BAGA was significantly greater for trees in treated stands than in control stands ($F = 8.555$, $P = 0.0001$) irrespective of density class (Table 4). There was no significant difference in BAGA between treatment and control stands for sugar pine trees. Only three Douglas-fir stands had BAGA that was significantly greater than BAGA for trees in control stands ($F = 3.563$, $P = 0.0001$); all three of these stands had moderate residual densities (Moon Prairie 1, Keno Pine-DF, Shell Peak 2).

Growth of individual trees before and after treatment

Student's *t*-tests comparing BAGA to BAGB for all 271 trees showed that most trees in treated stands had significantly greater growth or no change in growth following the treatment year; in contrast, most trees in the control stands exhibited decreased growth over the same time period (Table 5). For all species combined, BAGA was significantly greater than BAGB for 38% of the trees in treated stands. Basal area growth after treatment (BAGA) significantly decreased for 4% of the trees and was not significantly different from BAGB for 58% of the trees. Significant increases in BAGA occurred for 47 and 38% of trees in L and M stands, respectively. In L stands, BAGA did not decrease relative to BAGB for any trees. In control stands, however, 17 to 47% of the trees of all species continued to decrease growth slowly compared with trees in the treated stands. When we examined differences in BAGA and BAGB between trees that increased growth and trees whose growth did not change, we found that trees with no significant change in growth following treatment had been growing more rapidly before treatment than trees that had significant increases in growth following density reduction. That is, BAGA (0.034 m^2) for I trees was significantly greater ($P = 0.0001$) than BAGA (0.026 m^2) for NC trees in treated stands, whereas

Table 2. Mean basal area growth after the treatment year (BAGA; m^2 (5 years)$^{-1}$) for trees in low and medium density categories compared with trees in untreated stands (ANOVA followed by LSD multiple comparison tests). Standard errors are in parentheses following the means. The duration of mean period varied between 20 and 35 years. All species are combined in these groups.

Treatment	BAGA	*P*-value with untreated	*P*-value between treatments
Low density	0.028 (0.002)	< 0.007	0.469
Medium density	0.029 (0.001)	< 0.007	
Untreated	0.022 (0.002)		

Table 3. Mean basal area growth (m^2 (5 years)$^{-1}$) before (BAGB) and after (BAGA) treatment for all trees in treated stands by species. Standard errors are in parentheses following the means.

Species	BAGB	BAGA	*P*-value
Douglas-fir	0.026 (0.001)	0.033 (0.001)	< 0.001
Ponderosa pine	0.015 (0.001)	0.027 (0.002)	< 0.001
Sugar pine	0.023 (0.002)	0.025 (0.002)	0.430

BAGB for I trees (0.018 m^2) was significantly less (P = 0.0001) than BAGB for NC trees (0.024 m^2).

Relationship of BAGA to tree characteristics and local density

We found that BAGA was significantly correlated with live crown ratios and with total basal area on 0.04-ha plots around each study tree on only 50% of the sites ($\alpha = 0.1$). These variables explained a maximum of 25% of the variation in BAGA when trees at all treated sites were grouped by species, and a maximum of 51% of the variation at individual sites. However, basal area around the few trees whose growth decreased was 1.45 times greater than basal area around trees whose growth increased or remained unchanged. Compared with the standard measure of crown ratio, crown ratios that accounted for gaps and irregularities in the crown were more strongly related to the measured growth characteristics.

Growth ratios

When data for all species were combined, mean basal area growth ratios (BAGA/BAGB) for trees in treated stands were significantly greater than growth ratios for trees in untreated controls (P = 0.04). The same was true for comparisons of BAGA/BAGB for each species relative to its appropriate control (Figure 1), especially for ponderosa pine and Douglas-fir ($P \le 0.0001$). Mean BAGA/BAGB for trees in treated stands ranged from 1.63 to 2.55 for ponderosa pine, 1.12 to 1.14 for sugar pine and 1.04 to 3.49 for Douglas-fir (Table 4.).

In treated stands, 68% of the trees had growth ratios > 1.0, indicating an increase in growth in response to density reduction (Figure 2A). Of these, nearly 30% had growth ratios ≥ 1.5 (Figure 2B). This pattern was reversed in the control stands where 64% of the trees had growth ratios < 1.0 and 36% had growth ratios > 1.0. Moreover, 35% of trees determined to have no significant change in growth following density reduction had growth ratios ≥ 1.2 (Figure 3).

The variation in growth ratio for individual trees both within and among species is shown in Figure 1. Growth ratios for ponderosa pine in treated stands ranged from 0.77 to more than 4.0; growth ratios of trees in the untreated ponderosa pine

Table 4. Mean 5-year basal area growth (m^2 (5 years)$^{-1}$) after treatment (BAGA) and mean growth ratio (BAGA/BAGB). Standard errors are in parentheses. Means followed by the same letter are not significantly different as determined by ANOVA followed by Fisher's LSD multiple comparison tests. An asterisk indicates that growth after treatment (BAGA) was significantly different from growth before treatment (BAGB) for that tree population (Student's *t*-tests). For all tests, $\alpha = 0.05$. Abbreviations: T = density reduction treatment; U = untreated (control); L = low density; and M = moderate density.

Site	Treatment	No. of trees	Mean BAGA	Mean BAGA/BAGB
Douglas-fir (n = 137)				
Bottomline 1	T (L)	13	0.023 (0.003) e*	3.49 (0.27) a
Moon Prairie 1	T (M)	13	0.042 (0.004) a*	1.66 (0.27) b
Keno Pine-DF	T (M)	8	0.040 (0.004) ab	1.34 (0.35) bc
Shell Peak 2	T (M)	15	0.040 (0.003) ab*	1.31 (0.25) bc
Howard Pr.-DF	T (M)	10	0.023 (0.004) cde	1.19 (0.31) bc
Conde Creek 3	T (L)	15	0.033 (0.003) bc	1.18 (0.25) bc
Shell Peak 1	T (M)	12	0.032 (0.004) bcd	1.14 (0.28) bc
Conde Creek 2	T (M)	13	0.025 (0.004) de	1.04 (0.27) bc
Moon Prairie 2	U	12	0.023 (0.004) de	1.08 (0.28) bc
Jenny Creek-DF	U	11	0.028 (0.004) cde	0.91 (0.30) c
Bottomline 2	U	15	0.029 (0.003) cde	0.78 (0.25) c
Ponderosa pine (n = 66)				
Woodpecker	T (L)	15	0.028 (0.003) a*	2.55 (0.21) a
Divide Lakes 1	T (L)	14	0.025 (0.003) a*	1.71 (0.22) b
Keno Pine-PP	T (M)	7	0.020 (0.004) a	1.68 (0.31) b
Divide Lakes 2	T (L)	15	0.030 (0.003) a*	1.63 (0.21) b
Hoxie Creek	U	15	0.009 (0.003) b	0.99 (0.21) c
Sugar pine (n = 54)				
Yew Springs	T (M)	15	0.025 (0.003) a	1.14 (0.08) a
Beaver Creek	T (M)	20	0.024 (0.002) a	1.12 (0.07) a
Jenny Creek-SP	U	19	0.025 (0.002) a	0.92 (0.07) b

Table 5. Proportion (%) of trees with a significant change (α = 0.05) in BAGA compared with BAGB based on *t*-tests of individual trees. Abbreviations: T = density reduction treatment; U = untreated (control); L = low density; and M = moderate density.

Species	Treatment	Proportion of trees with	
		Increased growth (%)	Decreased growth (%)
Douglas-fir			
Bottomline 1	T (L)	77	0
Moon Prairie 1	T (M)	46	0
Keno Pine-DF	T (M)	63	0
Shell Peak 2	T (M)	47	7
Howard Pr.-DF	T (M)	20	0
Conde Creek 3	T (L)	33	0
Shell Peak 1	T (M)	25	8
Conde Creek 2	T (M)	15	23
Moon Prairie 2	U	17	17
Jenny Creek-DF	U	0	36
Bottomline 2	U	0	47
Ponderosa pine			
Woodpecker	T (L)	53	0
Divide Lakes 1	T (L)	43	0
Keno Pine-PP	T (M)	57	0
Divide Lakes 2	T (L)	33	0
Hoxie Creek	U	0	27
Sugar pine			
Yew Springs	T (M)	40	13
Beaver Creek	T (M)	25	5
Jenny Creek-SP	U	0	26

stand were much less, ranging from 0.38 to 1.45. Only 8% of the ponderosa pine trees in treated stands had growth ratios < 1.0, whereas 53% of the trees in the control stand had growth ratios < 1.0. The range of variation in the growth response of sugar pine trees was less than for the other two species. However, the range of variation in harvest treatments in sugar pine stands was also narrow, confounding direct comparisons among species. The mean growth ratio of sugar pine trees in the treated stands was significantly greater than in the untreated stand (Figure 1).

Longevity of growth response

Generally, growth tended to increase after density reduction, although there was considerable variation in the lag between density reduction and growth response (Figure 4). Some trees responded within the first 5-year period after thinning, whereas other trees did not respond until later (Table 6). For example, 34.5% of trees had growth ratios ≥ 1.3 during the first 5-year period after thinning. The proportion increased to 42.2, 50.8 and 56.2% in the three succeeding 5-year growth periods. In general, the greatest increase in growth occurred 20 years after thinning for all growth ratio classes ≥ 1.2 (Table 6). Mean basal area growth for the most recent 10 years was also significantly greater for trees in treated stands compared with trees in untreated stands (*t*-test: $P = 0.013$).

It appears that longevity of response may be associated with differences in sapwood area. Twenty to 35 years after thinning, there was no significant difference in sapwood area at breast height between trees in treated and control Douglas-fir stands

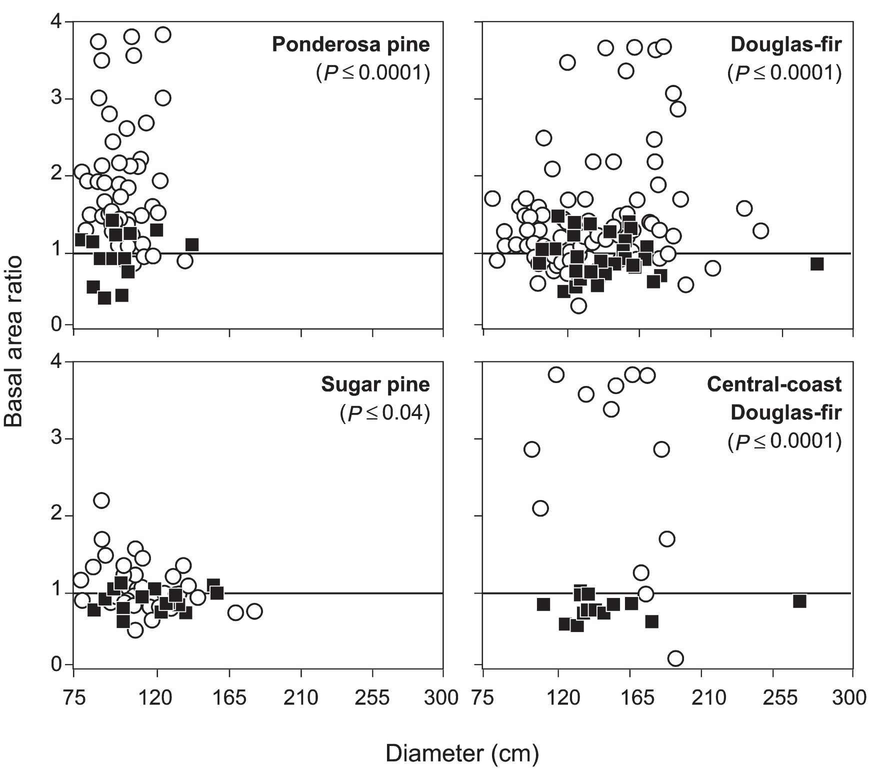

Figure 1. Ratio of basal area growth (mean 5-year basal area growth after treatment/mean 5-year basal area growth for an equivalent period before treatment) by tree diameter for all trees. Horizontal line indicates a ratio of one, i.e, no difference in, post- to pre-treatment growth (○ = trees in treated stands, ■ = trees in untreated stands). Three trees from the coastal Douglas-fir site and two ponderosa pine trees with ratios ≥ 8.0 are not shown. The *P*-values indicate significant differences in mean growth ratios of trees for treated and untreated stands.

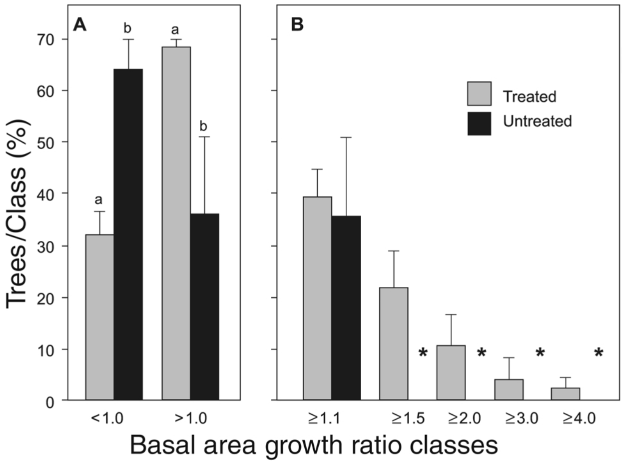

Figure 2. Percentage of trees in treated stands (n = 196) by basal area growth ratio classes for all sites combined. Ratios are the mean 5-year basal area growth after treatment divided by the growth before treatment. Figure 2A includes all trees and compares the percentage of trees that decreased growth (< 1.0) to those that increased growth (> 1.0). The difference in proportions of treated and untreated trees in each class is significantly different ($P \le 0.05$). Figure 2B shows the percent of trees that increased growth by growth ratio class. Vertical lines represent standard errors. An asterisk indicates no observations.

(t-test: P = 0.833). However, when the difference between BAGA for the most recent 10 years in treated and control stands was tested by ANCOVA with sapwood area as the covariate, the adjusted means were significantly different (P = 0.019) and sapwood area covaried significantly ($P < 0.001$).

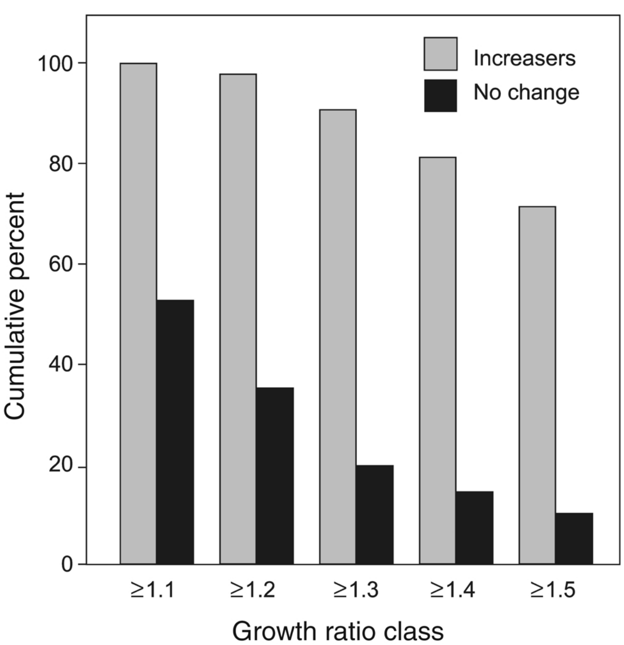

Figure 3. Cumulative percentage of trees by growth ratio classes (BAGA/BAGB) for trees with significantly greater (α = 0 .05) BAGA (Increasers, n = 75) and trees with no significant increase in BAGA (No change trees, n = 113). Growth ratios of all species in the treated stands are combined.

Discussion

Douglas-fir, ponderosa pine and sugar pine trees in old-growth stands can respond to density reduction by increasing their basal area growth rates. Both absolute growth rates and ratios between growth before and after treatment were generally greater in treated stands than in control stands. Although increases in absolute basal area growth were relatively small in most treated stands, growth was improved for a large percentage of trees after thinning. Even in stands where the mean values of BAGA and BAGB were not significantly different, BAGA was significantly greater than BAGB for 15 to 63% of the trees. Moreover, both measures of response longevity (the proportions of trees in cumulative growth ratio classes in 5-year time intervals since thinning and basal area growth for the most recent 10 years) indicated that increased growth after thinning was long lasting.

When evaluating the response of an old-growth stand to treatments such as thinning, it is important to consider both the proportion of the trees that show the response as well as the magnitude of the mean growth response. The comparisons of mean BAGA to mean BAGB within stands are conservative estimates of response to density reduction. For example, many trees that did not show significant increases in growth following density reduction maintained the high growth rates exhibited prior to treatment. In another example, at Conde Creek 3 BAGA was not significantly different from BAGB, yet growth increased significantly in 33% of individual trees (determined by t-tests). The mean growth ratio in the stand was 1.18, indicating an 18% average increase in growth. The comparison of BAGA to BAGB for each tree was also a conservative measure of growth response because of the nature of the test. Growth in the 5-year periods after thinning was more variable than growth before thinning. Although we used separate variance t-tests to account for differences in growth variation before and after thinning, approximately 8% more trees would have been classed in a significant change category if a distribution free non-parametric test were used. No differences in classification occurred when paired t-tests were used.

By examining growth response in several ways, we have increased our understanding of how growth varies among individual trees and among stands. For example, there was no difference in growth after the treatment year between the treated and untreated Bottomline stands, but the comparison of growth ratios for these stands shows that large and opposite growth trends are occurring even though both stands are currently growing at similar rates (Figure 4).

Marshall et al. (1992) reported that basal area growth following thinning increased from 5.4 to 7.5 times in the dominant trees in 30- to 40-year-old Douglas-fir. Although these values are greater than the mean values for our trees (Table 4), 13 of the old-growth study trees increased basal area growth by three to 11 times following density reduction. Other studies have also indicated the potential of old-growth trees to respond

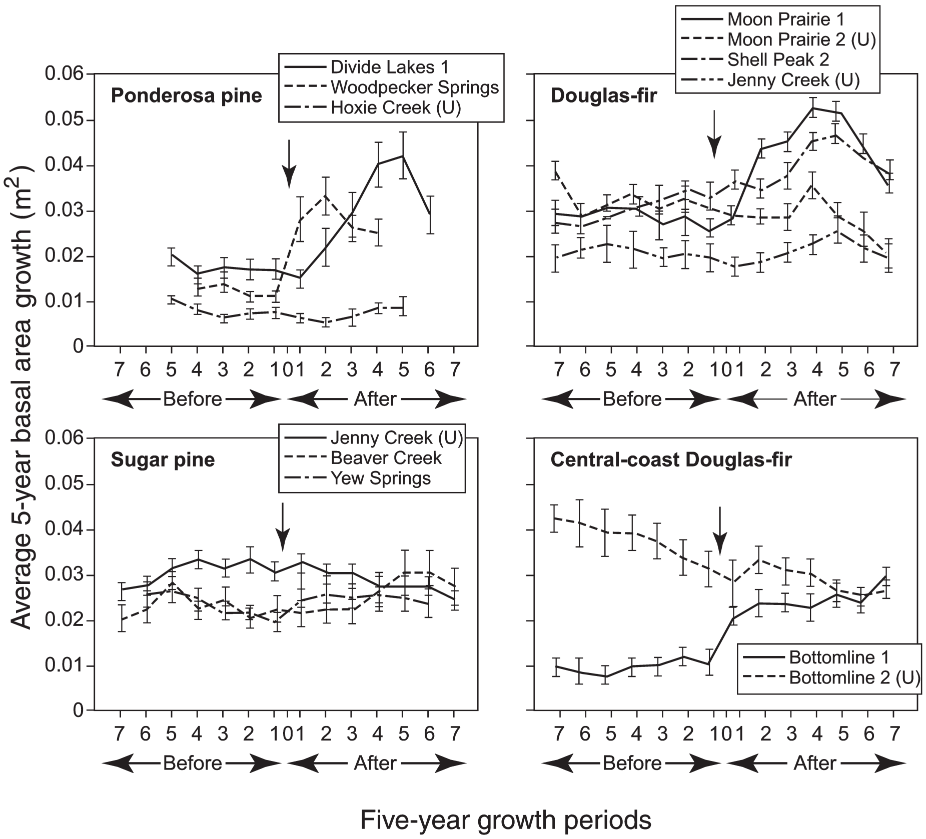

Figure 4. Mean basal area growth by 5-year growth periods before and after treatment for each species on representative sites in southwest Oregon and central Oregon. Vertical lines represent standard errors. Vertical arrows indicate time of treatment. Abbreviation: U = untreated stand.

to density reduction, but the tree ages in those studies were generally much less than in our study. Youngblood (1991), in a study of 175-year-old white spruce in Alaska, found that there was a 16.5% increase in basal area in an untreated stand and a 26.8% increase in a shelterwood stand over a 14-year period. Similarly, Williamson (1982) and Williamson and Price (1971) found that 100- and 150-year-old Douglas-fir increased their diameter growth from 8 to 14 times in lightly and heavily thinned stands, respectively, and Newton and Cole (1987) document long-term response to thinning of Douglas-fir stands 110 to 140 years of age. The mean basal area after thinning in Williamson and Price's (1971) study was over 45 m^2 ha^{-1}, about the midpoint of the densities in our medium density class (28 to 52 m^2 ha^{-1}).

We found that old trees may be subject to competitive stress in dense stands despite their dominant positions and that a high proportion of trees retain the ability to respond to density reduction. However, there may be intrinsic growth limitations in these old trees in addition to other factors that affect their growth. For example, we found no difference in BAGA between trees in L- and M-density stands. Furthermore, stand density around individual study trees in addition to their crown ratios explained a maximum of 51% of the variation in BAGA. Therefore, there were site or tree characteristics or both that we did not measure that affected BAGA. Density reduction may reduce the influence of these other factors on old-growth trees.

We conclude that it may be possible to increase the vigor of old trees by reducing stand density. The increases in basal area were considerable for many trees, often exceeding 1.3 times the rate of pre-treatment growth (Figures 1 and 2). These increases lasted for 20 to 30 years (Figure 4) and were even

Table 6. The proportion (%) of trees in each cumulative growth ratio category for consecutive 5-year periods following density reduction. All species and sites in treated stands are combined. Data are shown for the first four periods (20 years); n = 185 trees.

Five-year period	Proportion of trees in each growth ratio category (%)						
	≤ 1.0	≥ 1.1	≥ 1.2	≥ 1.3	≥ 1.4	≥ 1.5	≥ 2.0
5	48.1	51.9	38.4	34.5	30.3	25.4	10.3
10	36.8	63.2	51.4	42.2	36.2	30.8	15.7
15	32.4	67.6	57.8	50.8	41.6	36.8	15.1
20	34.1	65.9	58.9	56.2	54.1	45.9	26.5

maintained during extended droughts in the 1970s and 1980s. Moreover, ANCOVA indicated that sapwood area was strongly related to BAGA for Douglas-fir trees 20–30 years after density reduction. Sapwood area has been related to tree vigor and resistance to insects in lodgepole pine (Mitchell et al. 1983).

Our results imply that ponderosa pine may increase growth after density reduction more than Douglas-fir or sugar pine and that sugar pine responds the least (Figures 1 and 4). However, we could not locate enough sites with similar ranges of density reduction and time elapsed since treatment for each species to compare the effects of density reduction among species. In particular, we had no sites with sugar pine at low residual densities and only one ponderosa pine site at medium residual density.

The variability in basal area growth in both treated and untreated stands has implications for the interpretation of xylem growth patterns in old-growth trees. Although growth rates were relatively constant for the untreated Douglas-fir trees over 200 years old in southwest Oregon stands (cf. Poage 2001), there were periodic growth increases and declines (Figure 4). However, the changes were neither as great nor as long lasting as the increases measured in treated stands after density reduction. These fluctuations may have been caused by variations in weather (Graumlich 1987), or changes in density caused by low-intensity fire (Wetzel and Fonda 2000), windthrow, or the production of cones and seed cone crops (Tappeiner 1969). Sustained increases in growth may reflect long-term changes in stand density.

Management implications

Cutting trees to reduce density in old-growth stands or to modify the amount and distribution of fuels can be beneficial to residual large old-growth trees. Reduction of stand density around individual trees with full crowns is likely to increase the basal area growth of a high proportion of the trees for several decades. We conclude that about 68% of old trees may experience an increase in growth; however, this will likely vary among species. Based on our most conservative measure of growth, only 5–23% of trees in sugar pine or Douglas-fir stands significantly decreased growth following density reduction and no ponderosa pine trees did. Moreover, the decrease in growth observed in response to the density reduction was not a sharp decrease, but rather a continuation of the slower growth of these trees. The growth of trees late in ontogeny is typically characterized by a decline in ring width associated with size and age.

We note that our study trees were the largest and had probably been the most vigorous in the stands. They had long live crowns, low height/diameter ratios and generally appeared to be healthy. After density reduction, trees whose growth significantly increased also had less competition from other trees on the 0.04-ha plots immediately around them than trees that did not significantly increase growth. We noted little mortality from windthrow or other causes on the study sites, except for suppression and insect-related mortality in the untreated ponderosa pine stand at Hoxie Creek, and there was no apparent logging damage to tree boles or crowns. Trees on windy sites or those with small crowns and large height/diameter ratios might respond less positively to density reduction than our study trees.

We conclude that the old-growth trees in our study are able to respond positively to a wide range of density reduction treatments. Even small reductions in density improved growth and, presumably, vigor. Although there were significant differences in growth between trees in treated and untreated stands, there was no significant difference in growth between the low and medium residual density categories. Thus, vigor of the trees can be improved without intensive density reduction.

Note

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