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TECHNICAL ARTICLE

Radial and stand-level thinning treatments: 15-year growth response of legacy ponderosa and Jeffrey pine trees

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Restoration efforts to improve vigor of large, old trees and decrease risk to high-intensity wildland fire and drought-mediated insect mortality often include reductions in stand density. We examined 15-year growth response of old ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*) trees in northeastern California, U.S.A. to two levels of thinning treatments compared to an untreated (control) area. Density reductions involved radial thinning (thinning 9.1 m around individual trees) and stand thinning. Annual tree growth in the stand thinning increased immediately following treatment and was sustained over the 15 years. In contrast, radial thinning did not increase growth, but slowed decline compared to control trees. Available soil moisture was higher in the stand thinning than the control for 5 years post-treatment and likely extended seasonal tree growth. Our results show that large, old trees can respond to restoration thinning treatments, but that the level of thinning impacts this response. Stand thinning must be sufficiently intensive to improve old tree growth and health, in part due to increasing available soil moisture. Importantly, focusing stand density reductions around the immediate neighborhood of legacy trees was insufficient to elicit a growth response, calling into question treatments attempting to increase vigor of legacy trees while still maintaining closed canopies in dry, coniferous forest types. Although radial thinning did not affect tree growth rates, this treatment may still achieve other resource objectives not studied here, such as protecting wildlife habitat, reducing the risk of severe fire injury, and decreasing susceptibility to bark beetle attacks.

Key words: forest restoration, old-growth, *Pinus jeffreyi*, *Pinus ponderosa*, release, thinning intensity

Implications for Practice

- Old ponderosa and Jeffrey pine trees are capable of increased growth rates after thinning. Removing trees 9.1 m around legacy trees (i.e. radial thinning) is insufficient to increase growth, but stand-level thinning can have beneficial effects for up to 15 years post-treatment.
- Radial thinning can stabilize growth trends in old trees, whereas untreated old trees will likely decline in vigor without intervention.
- Attempts to increase vigor of legacy trees while still maintaining closed canopies in dry, coniferous forest types by reducing stand density only around the immediate neighborhood of legacy trees will likely be unsuccessful if the radius is not greater than 9.1 m.

Introduction

Large, old trees, often referred to as legacy trees, serve a foundational role in old-growth forests, but are becoming increasingly rare in many areas (Lindenmayer et al. 2012). These trees are significantly older and larger and provide a range of ecosystem services, such as structural diversity, wildlife habitat, forest biodiversity, and carbon sequestration (Lindenmayer et al. 2014). In addition, they allow insight into past disturbance, climate, and land use over time scales lasting hundreds to thousands of years (Dearing et al. 2006). There is a growing concern that large, old trees in western North America are in jeopardy of disappearing due to a variety of factors, including wildfire, insects, and climatic stress (Spies et al. 2006; Bennett et al. 2015). Over the past 150 years, these forests have experienced dramatic changes in strand structure and vegetation type as a result of fire suppression, logging, and livestock grazing (Syphard et al. 2007). These changes have altered disturbance regimes and led to shifts in species compositions and increased forest density in many areas, which has reduced the productivity and health of large older trees (Kolb et al. 2007).

Prior to Euro-American settlement, frequent, low-intensity fire maintained open, multiaged stands in dry ponderosa pine

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(*Pinus ponderosa* Lawson & C. Lawson) and Jeffery pine (*P. jeffreyi* Balf.) forests (Kolb et al. 2007; Hood 2010). Restoration treatments in fire-dependent, old-growth forests often involve thinning and prescribed burning to reduce stand density and remove shade-tolerant species that have established with fire exclusion (Kolb et al. 2007; Fulé et al. 2012). Treatment goals include increasing the likelihood of old tree survival and improving tree health and vigor, as reducing competition through thinning and other silvicultural activities can increase resistance to high-severity fire (Fulé et al. 2012) and insect attack (Fettig et al. 2014) and help ameliorate the effects of drought (Sohn et al. 2016). However, most studies include responses of younger trees and do not specifically test if forest restoration treatments can improve old tree growth and vigor.

Most studies show that restoration treatments do not harm old trees and usually have beneficial effects, though response timing varies (see Kolb et al. 2007 for study summaries; Gray et al. 2012; Erickson & Waring 2014; York et al. 2015). Latham and Tappeiner (2002) reported radial growth increases following thinning in old Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), ponderosa pine, and sugar pine (*Pinus lambertiana* Douglas) from 5 to 25 years, with the greatest growth 20 to 25 years post-treatment. In contrast, old ponderosa pine in Arizona (Feeney et al. 1998; Kolb et al. 2007; Erickson & Waring 2014), Montana (Fajardo et al. 2007), and Oregon (McDowell et al. 2003) increased radial growth within 1–4 years of density reduction treatments. Although Skov et al. (2005) found no change in radial growth of pre-settlement ponderosa pine following thinning, responses were only tracked for 3 years. Sixteen-year response to variable density reduction treatments in old-growth Douglas-fir-dominated forests were less consistent, but generally showed positive effects of growth with decreasing competition (Gray et al. 2012). Increases in growth have been attributed to increased water and nutrient availability that increases net photosynthetic rate and stomatal conductance (McDowell et al. 2003; Kolb et al. 2007). Studies that examined thinning intensities in old-growth forests, showed growth increased with greater reductions in stand density (Latham & Tappeiner 2002; Gray et al. 2012; York et al. 2015).

We examined 15-year growth effects of two density reduction treatments in comparison to untreated areas (control) in old ponderosa pine (*P. ponderosa* var. *ponderosa* C. Lawson) and Jeffrey pine. Treatments included thinning within 9.1 m of individual trees (radial thinning) and stand thinning. Radial thinning is a relatively new treatment designed to reduce mortality and improve vigor of old trees while complying with regulatory and social constraints that limit more extensive stand-level thinning. We predicted that both radial and stand thinning would have a positive effect on radial growth and improve vigor, with stand thinning having a greater effect than radial thinning. Knowledge of thinning effects on old trees is important to evaluate alternative restoration strategies to promote old-growth characteristics and resilience in fire-dependent forests.

Methods

Site and Treatment Description

The 133 ha study area is located on the Eagle Lake Ranger District, Lassen National Forest in northeastern California (40.751°N, 121.066°W). Average elevation is 1,700 m (±122 m). Climate is semiarid with 450-mm mean annual precipitation falling from October to May, roughly half as snow. Air temperatures range from −9 to 29°C. Soils are basalt derived and classified as Typic Argixeroll with a mesic soil regime.

The study area consists of an open overstory of mature ponderosa and Jeffrey pine with an extremely dense midstory of white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.). *Arctostaphylos patula* Greene and *Ceanothus velutinus* Douglas ex Hook. are the dominant shrubs. The majority of the white fir establishment has occurred since the last fire, circa 1876 (Cluck unpublished data; Taylor 1989). One of two thinning treatments, radial thinning (completed in 1998) and stand thinning (completed in 2000), were applied to two stands (Fig. S1, Supporting Information). Two adjacent, untreated forest stands with comparable structure containing old pines with 85% white fir and average basal area of 35.5 m^2/ha served as controls. The radial thinning treatment was designed to preserve Northern Goshawk (*Accipiter gentilis*) habitat, maintain old trees through increased health and vigor, and reduce ladder fuels around old trees. Radial thinning removed all trees less than 25.4 cm diameter at breast height (dbh), regardless of species, only within 9.1 m of selected trees, with no thinning outside of this radius. Stand thinning was designed to imitate pre-settlement conditions, maintain old trees through increased health and vigor, and reduce ladder fuels to limit crown fire hazard. Stand thinning retained all pine species greater than 15.2 cm dbh (1.37 m aboveground) and removed all white fir less than 58.4 cm dbh in the stand. This resulted in the removal of 93% of existing white fir stems, reducing average basal area 37.3–18.4 m^2/ha. Sample legacy trees greater than 61 cm dbh were selected in 1999–2001 after thinning treatments were implemented, with 50 ponderosa and Jeffrey pine selected per treatment. All 150 trees were within approximately 1.3 km of each other on a west aspect.

Data Collection

We monitored trees annually for tree status (alive or dead) from 2000 to 2015. We considered trees with no green needles dead and recorded probable cause of death based on signs of insect attack. In 2007 and 2008, we recorded dwarf mistletoe rating (DMR; Hawksworth 1977), Keen (1936) vigor class, and live crown ratio for each tree. DMR is a six-class rating system of increasing severity of dwarf mistletoe infection, with zero being uninfected and six being heavily infected throughout the crown. The Keen vigor class is a four-letter rating system of bark beetle susceptibility, where A is least susceptible and D is most susceptible. In 2015, we measured dbh, bark thickness, and estimated two metrics of basal area (i.e. cross-sectional area of living trees per hectare; m^2/ha) as a measure of neighborhood competition. We measured basal area 9.1 m from each sample tree in the cardinal directions using an angle gauge to calculate mean neighborhood basal area per tree. We also estimated local neighborhood competition by measuring basal area 1.5 m from the north side of each tree (hereafter "local basal area"). In fall 2015, we extracted two, opposing 5-mm wide cores from each tree approximately 1.4 m aboveground using a manual increment borer to obtain a cross section of wood containing annual rings from 2015 to the tree pith. We were unable to collect cores from 3 live trees due to rot and 10 trees that died.

We prepared cores using standard techniques (mounted and sanded until cellular structure was visible through a binocular microscope), and scanned cores using an Epson platform scanner at 2400 dpi. We assigned the calendar year to each tree ring (i.e. crossdated) and measured ring widths to the nearest 0.001 mm using CooRecorder v7.8 (Cybis Elekronik & Data AB, Saltsjöbaden, Sweden). We calculated average ring width measurements per tree. Tree age could not be determined for 19 trees due to cores that did not reach the pith. For these trees, we used the oldest dated ring as a conservative estimate of tree age. For tree radial growth, we calculated basal area increment ([BAI]; cross-sectional area of secondary xylem produced per year) from ring widths and the tree diameter inside bark using dplR package v. 1.6.0 in R v. 3.0.1 (Bunn 2008). We were able to crossdate 108 ponderosa pine and 24 Jeffrey pine trees of the 137 cored trees (series intercorrelation = 0.55; mean sensitivity = 0.25). The five undated trees were excluded from further analysis. To determine long-term trends in growth, we calculated growth ratio of each tree by dividing post-treatment 15-year mean annual BAI by pre-treatment 15-year mean annual BAI. Trees with growth ratio greater than 1 showed increasing growth following treatment and less than 1 showed decreased growth.

Soil moisture was measured using permanently established Irrometer WATERMARK granular matrix sensors (Irrometer Company, Inc., Riverside, CA, U.S.A.). Five sensors were installed at 15 cm in depth in the fall of 2001 in the stand thinning and untreated control on the southwest facing side of five randomly selected legacy trees with similar aspect and slope position. Soil moisture tension measurements were recorded approximately every 2 weeks from April to October from 2002 through 2006.

Data Analysis

We used general linear mixed models to compare treatment differences in tree age, dbh, species, live crown ratio, neighborhood and local basal area, and mean 15-year BAI before and after thinning. We tested treatment differences in post-treatment BAI within and among DMR and Keen classes using Kruskal–Wallis nonparametric tests with Dunn's tests for post hoc multiple comparisons due to non-normally distributed data. Small sample sizes precluded statistical comparisons of BAI for DMR greater than 0 or Keen classes C and D.

We used analysis of covariance to test treatment effects on radial growth response in two ways: BAI and growth ratio. The model of BAI used annual BAI as the response variable and independent, fixed-effect variables were treatment, time (before or after treatment), treatment × time, tree age, species, neighborhood basal area, local basal area, and the interactions of treatment × time × tree age, treatment × time × neighborhood basal area, and treatment × time × local basal area. We used individual trees as the experimental unit, and therefore specified treatment × time as the group and individual tree as the subject in the random statement to account for interdependence of annual BAI measurements within a single tree and a gamma distribution to stabilize residuals. The growth ratio model independent variables were treatment, neighborhood basal area, tree age, and the interactions of basal area × treatment and tree age × treatment, with a lognormal distribution. Pairwise differences were determined using Tukey's post hoc test ($\alpha = 0.05$). Statistical analysis was performed using the GLIMMIX procedure in SAS 9.4 (SAS Institute, Cary, NC, U.S.A.).

Results

A total of 10 of the 150 trees died during the 15 years of post-treatment monitoring: four in the control, five in the radial thinning, and one in the stand thinning. One tree in the control was struck by lightning and was subsequently attacked and killed by western pine beetle (*Dendroctonus brevicomis* LeConte). The remaining nine trees were also killed by western pine beetle or Jeffrey pine beetle (*Dendroctonus jeffreyi* Hopk.). The low mortality rate prevented the statistical analysis of treatment effects on mortality.

Pre-treatment, sample trees were comparable in size and age, but growth rates were higher in the control compared to the radial thinning (Table 1; $F_{2,84.99} = 4.46$, $p = 0.0143$). Tree age and dbh did not differ between treatments (Table 1; age: $F_{2,72.47} = 2.22$, $p = 0.1155$; dbh: $F_{2,85.25} = 1.42$, $p = 0.2469$). Post-treatment neighborhood basal area was lowest in the stand thinning unit, followed by the radial thinning, and highest in the control trees (Table 1; $F_{2,81.28} = 11.60$, $p < 0.0001$). Local neighborhood basal area was similar between the trees in radial thinning and stand thinning trees and lower than the control trees (Table 1; $F_{2,84.09} = 8.06$, $p = 0.0006$). There was no statistical difference in live crown ratio across treatments (Table 1; $F_{2,73.91} = 2.57$, $p < 0.0835$).

Only stand thinning impacted mean radial BAI ($F_{2,83.92} = 35.91$, $p < 0.0001$), and the response occurred within 1 year of treatment and was sustained over the entire 15-year post-treatment monitoring period (Tables 1 & S1; Fig. 1). In contrast, radial thinning had no effect on BAI and tracked closely with the control trees (Table 1; Fig. 1). Radial growth fluctuated with climate in all treatments, though the stand thinning dampened the effect of extreme drought years on radial growth compared to the control and radial thinning treatments (Fig. 1).

In addition to the stand thinning treatment effect, radial growth response was influenced by pre-treatment BAI (treatment × time: $F_{2,232} = 4.22$, $p = 0.0158$), tree age ($F_{1,342} = 57.31$, $p = 0.0001$), and neighborhood basal area ($F_{1,335} = 7.21$, $p = 0.0076$), whereas species ($F_{1,306} = 0.14$, $p = 0.7072$) and

Table 1. Mean (±SE) values of tree characteristics and competition (i.e. basal area) by treatment. BAI, basal area increment. Different letters within rows denote significantly different treatment means and * denotes significantly different BAI between pre- and post-treatment ($\alpha = 0.05$).

	Control	*Radial Thinning*	*Stand Thinning*
No. ponderosa pine	41	30	37
No. Jeffrey pine	4	11	9
Total no. trees	45	41	46
Pre-treatment BAI (mm^2/year)	927.7 (78.2)[a]	654.7 (53.4)[b]	743.9 (59.0)[ab*]
Post-treatment BAI (mm^2/year)	873.6 (82.2)[a]	855.0 (62.7)[a]	1,849.5 (126.9)[b*]
Tree age (years)	294 (12)[a]	335 (15)[a]	317 (13)[a]
dbh (cm)	80.1 (1.7)[a]	80.3 (1.6)[a]	83.8 (1.8)[a]
Live crown ratio	55 (2)[a]	56 (2)[a]	61 (2)[a]
Post-treatment neighborhood basal area (m^2/ha)	30.3 (1.3)[a]	26.3 (0.7)[b]	22.4 (1.0)[c]
Post-treatment local basal area (m^2/ha)	28.6 (1.8)[a]	20.9 (1.0)[b]	22.0 (1.1)[b]

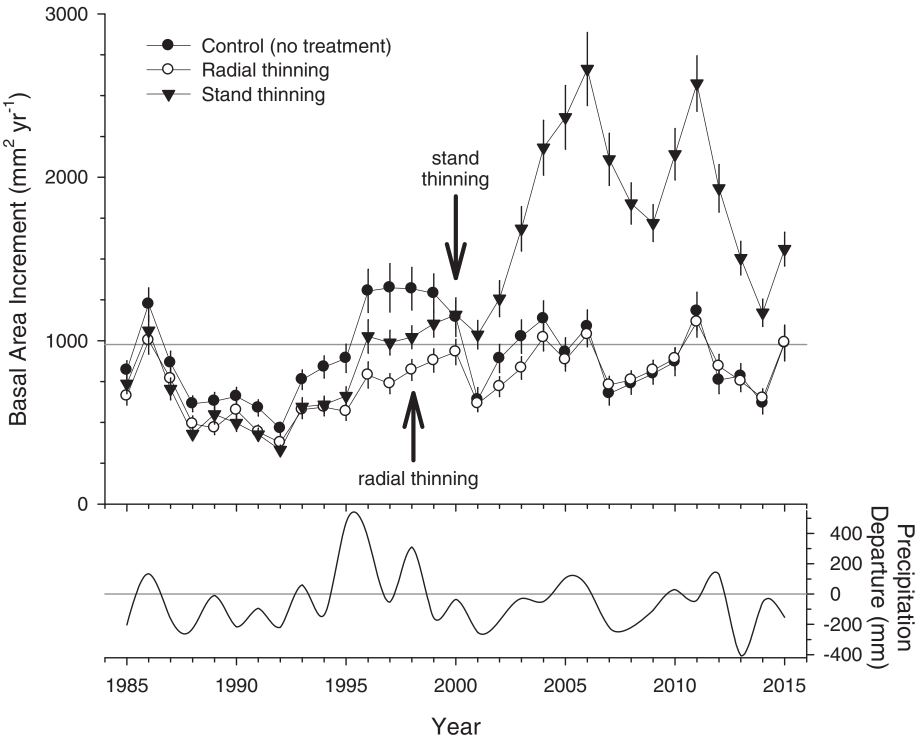

Figure 1. Upper panel: annual mean (±SE) BAI from 1985 to 2015 by treatment. Arrow shows timing of radial and stand thinning treatments. Gray line denotes mean BAI across all treatments and all years. Lower panel: annual departure from 30-year normal precipitation (1981–2010) obtained for the site location (PRISM; 800-m resolution; http://www.prism.oregonstate.edu).

local neighborhood basal area ($F_{1,313} = 0.09$, $p = 0.7705$) did not affect post-treatment BAI (Table S1). Trees with slower growth rates prior to treatment and older trees had a dampened response to stand thinning (Fig. 2A & 2B). Trees with less competition after treatment, as reflected by post-treatment neighborhood basal area, had increased radial growth (Fig. 2C).

Growth ratio was higher in both the stand thinning (1.31; CI 1.30–1.33) and radial thinning (2.29; CI 2.27–2.32) treatments compared to the control ($F_{2,123} = 11.53$, $p < 0.0001$), with stand thinning higher than the radial thinning (Table S1; Fig. 3). Mean growth ratio in the control was 0.97 (CI 0.96–0.98), indicating legacy tree growth was declining in untreated units. As with the BAI model, there was a significant treatment × neighborhood basal area effect, indicating trees with less competition had higher growth ratios. Tree age did not affect growth ratio. Growth ratio patterns were most consistent in the stand thinning, with 45 of 46 trees (98%) having a ratio of greater than 1, compared to 31 of 41 trees (76%) in the radial thinning, and 17 of 45 trees (38%) in the control.

Stand thinning improved the growth of trees uninfected by mistletoe ($\chi^2_{(2, n=115)} = 34.7$, $p < 0.0001$; Fig. S2) and trees with higher infection levels generally had lower post-treatment BAI. There were no treatment differences in BAI for trees with Keen class = A, whereas trees with Keen class = B in the stand thinning had higher post-treatment BAI than the

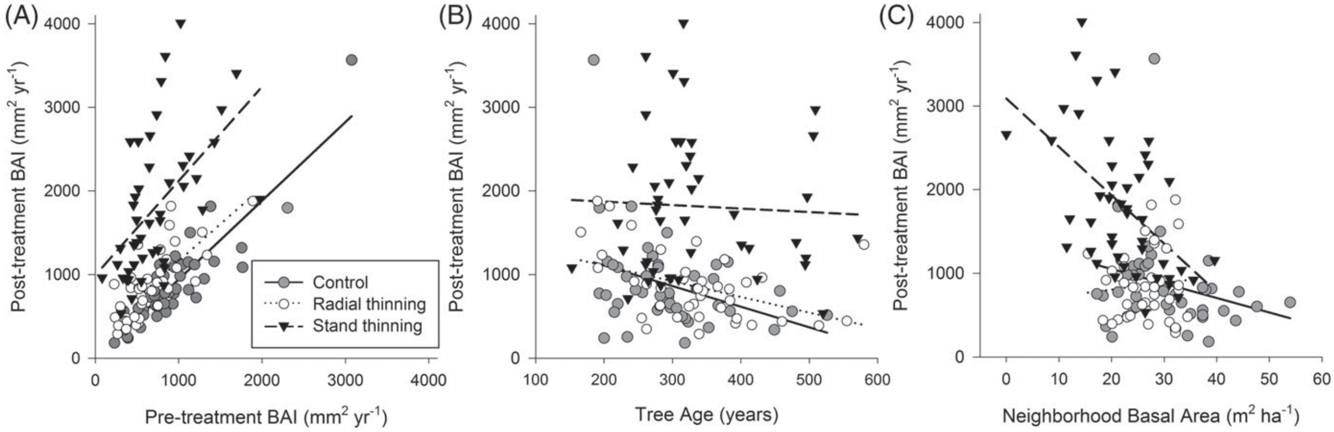

Figure 2. Individual tree 15-year post-treatment annual average BAI compared to: (A) 15-year pre-treatment annual average BAI, (B) tree age, and (C) neighborhood basal area of the trees within 9.1 m of tree. Lines are simple linear regression lines by treatment. See Table S1 for full model of radial growth response effects.

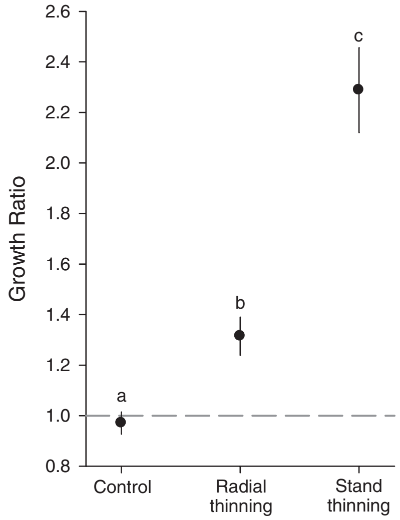

Figure 3. Mean (±SE) growth ratio by treatment. Growth ratio greater than 1 indicates higher 15-year mean annual growth post-treatment compared to the 15 years pre-treatment, less than 1 indicates lower growth, and growth ratio = 1 (dashed line) is no change. Different letters denote significantly different treatment means ($\alpha = 0.05$).

radial thinning and control B class trees ($\chi^2_{(5,\, n = 123)} = 64.6$, $p < 0.0001$; Fig. S3).

Two-to-five years following treatment, soil moisture was higher in the stand thinning compared to the control (Fig. S4). Although this difference declined over time, soil moisture was generally higher for longer in the growing season for the first 5 years after thinning.

Discussion

Although there is a concern that old trees have little-to-no ability to respond to environmental changes and management could even cause unintended harm (Kolb et al. 2007), our results show shade-intolerant old trees can respond to density-reduction treatments. Stand thinning caused an immediate, sustained increase in BAI compared to radial thinning and unthinned stands in large, old ponderosa and Jeffrey pines. Although tree age was negatively related to tree growth, neighborhood basal area had a much stronger effect as shown by both significant main and interaction effects and steeper slopes for basal area compared to tree age. These results are consistent with other studies showing centuries-old conifers can respond to changes in resource availability (Latham & Tappeiner 2002; Kolb et al. 2007; Erickson & Waring 2014; York et al. 2015), but differ somewhat in the timing of response. For example, greater than 200-year-old ponderosa pine in Arizona (Erickson & Waring 2014) and Oregon (McDowell et al. 2003) did not increase radial growth until 3 years following stand-level density reduction treatments, whereas we found trees responded to stand thinning within 1 year of treatment.

The stand thinning seemed to mitigate the effects of the extreme drought conditions that occurred the year after treatment, such that growth reductions were much less than the control and radial thinning trees. Soil moisture differences likely drove the increase in radial growth, as water availability was almost 40 days longer than in the control 2 years post-treatment. By 2 years post-treatment, stand thinning growth rates increased above pre-treatment levels and continued until the severe drought of 2014. Although growth declines in the stand thinning were greater during the 2013–2015 exceptional drought, trees in the stand thinning continued to have higher growth rates than the control and radial thinning trees, supporting the conclusions of Kolb et al. (2007) that trees in thinned stands have higher resilience to drought compared to trees in unthinned stands.

Consistent with other studies, we show tree vigor affects growth response to treatment, with the greatest increases occurring in healthy-appearing, vigorous, mistletoe-free trees (e.g. Keen class A and DMR <2). Keen class was not an informative predictor of mortality in old-growth unburned forests in

Oregon, but was useful for identifying trees most likely to survive fire and respond to density-reduction treatments (Swezy & Agee 1991). Numerous studies have shown dwarf mistletoe reduces tree growth and lifespan (Geils & Hawksworth 2002).

Somewhat surprisingly, radial thinning did not increase BAI, though growth ratio was higher than the control. The radial thinning removed all stems less than 25.4 cm dbh within approximately the width of the tree crowns, which was most trees and average local basal area in the immediate vicinity of legacy trees was the same between the radial thinning and stand thinning. Therefore, though leaving larger trees in the radially thinned zone could certainly negatively affect growth, this did not seem to be the case in our study. We posit that the lack of observed response in BAI seems to be due to the small zone of radial thinning around the legacy trees, especially considering the size of the legacy trees. Although no other studies report the effects of radial thinning on old tree growth responses, studies of thinning intensity (Latham & Tappeiner 2002; Gray et al. 2012; York et al. 2015) suggest that removing trees can improve old tree growth, but must be done for a larger area around legacy trees than the treatment tested here.

Although radial thinning did not increase tree growth, it did lessen growth decline and this type of treatment may provide other benefits to legacy trees, such as reductions in wildfire severity, drought mitigation, and risk of bark beetle attack. Large, old trees are typically the most fire resistant and creating heterogeneous canopy conditions can reduce the risk of active crown fire (Agee & Skinner 2005; Fulé et al. 2012), thus increasing the probability of survival of highly desirable legacy trees in the event of a wildfire. Thinning can also reduce drought-induced tree mortality (Bradford & Bell 2017). Radial thinning may also create microsite conditions unfavorable to bark beetle aggregation, making successful attacks more difficult (Fettig et al. 2014).

Reconstructions of historical tree spatial patterns show fire-prone forests were patchy, with openings, single large trees, and clumps of large trees (Larson & Churchill 2012). Our results suggest that density-reduction restoration treatments in fire-prone, old-growth forests should decrease tree density around legacy trees to an area larger than the crown diameter to spur growth rates. Thinning gradients from low to high removal around old trees within a stand could mimic historical patterns of spatial heterogeneity, while also reducing the risk of losing hard-to-replace legacy trees to drought and disturbance. Our results, consistent with the past research (Kolb et al. 2007; Erickson & Waring 2014; York et al. 2015), show that thinning does not negatively impact old trees and in fact, can improve tree growth. In contrast, conditions in many untreated, long-unburned fire-dependent forests are conducive to high-severity wildfire and drought-mediated bark beetle outbreaks that will almost certainly cause high levels of tree mortality should these disturbances occur (Hood 2010; Fulé et al. 2012; Fettig et al. 2014). Restoration of old-growth, frequent fire-dependent forests is not always plausible, and benefits to legacy trees must be carefully weighed against potentially detrimental effects, such as potential mortality, high costs, invasive weeds, soil compaction, and undesirably high post-treatment regeneration (Kolb et al. 2007; Naficy et al. 2010; Roccaforte et al. 2015). However, where warranted, proactive restoration efforts in fire-dependent, old-growth forests could buffer risk of disturbance and severe drought events to help maintain these highly valuable legacy trees on the landscape.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Models of treatment effects and covariates on mean annual BAI 15 years before and after treatment and growth ratio.
Figure S1. Example of tree with radial thinning and stand-level thinning.
Figure S2. Fifteen-year post-treatment annual average BAI by Hawksworth DMR and treatment.
Figure S3. Fifteen-year post-treatment annual average BAI by Keen Vigor Class and treatment.
Figure S4. Soil moisture tension from 2002 to 2006 in the control and stand thinning unit by Julian day.

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Supplemental Information

Table S1**.** Models of treatment effects (control, radial thinning, stand thinning) and covariates on mean annual basal area increment (BAI) 15 years before and after treatment (time) and growth ratio. *df* = degrees of freedom.

Effect	*df*	*F*-value	*P*-value
Basal area increment model			
Treatment	2	1.6	0.2031
Time	1	0.58	0.4487
Treatment × Time	2	4.22	0.0158
Species	1	0.14	0.7072
Tree age	1	57.31	<0.0001
Neighborhood basal area	1	7.21	0.0076
Local basal area	1	0.09	0.7705
Treatment × Time × Tree age	5	1.17	0.3235
Treatment × Time × Neighborhood basal area	5	2.42	0.0381
Treatment × Time × Local basal area	5	1.01	0.4143
Growth ratio model			
Treatment	2	11.53	<0.0001
Neighborhood basal area	1	2.53	0.1146
Tree age	1	2.34	0.1288
Treatment × Neighborhood basal area	2	3.91	0.0227
Treatment × Tree age	2	0.59	0.5546

Figure S1. Example of tree with radial thinning (upper photo) and the stand-level thinning (lower photo).

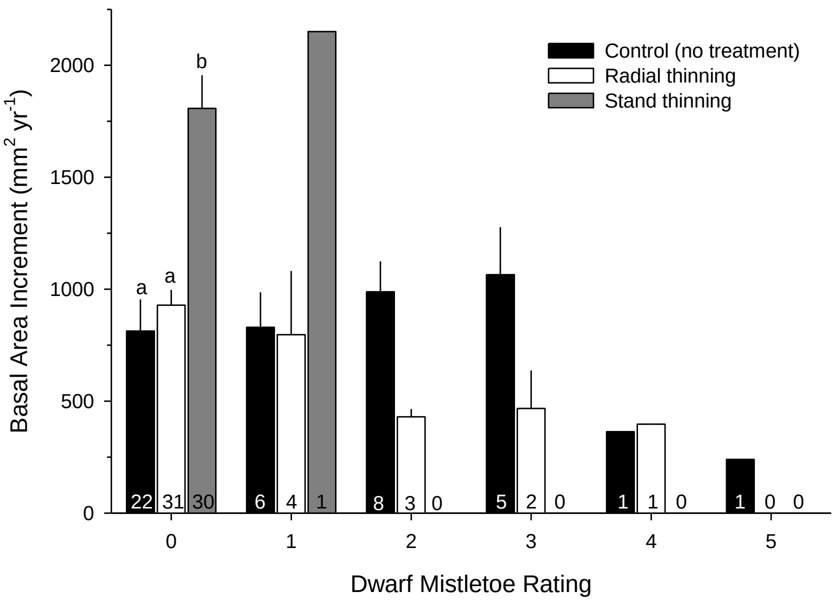

Figure S2. 15-year post-treatment annual average (+SE) basal area increment (BAI) by Hawksworth dwarf mistletoe rating (DMR) and treatment. Numbers inside bars are sample sizes. Different letters for DMR = 0 denotes significantly different treatment means (α = 0.05). Small sample sizes precluded statistical comparisons of BAI for DMR > 0.

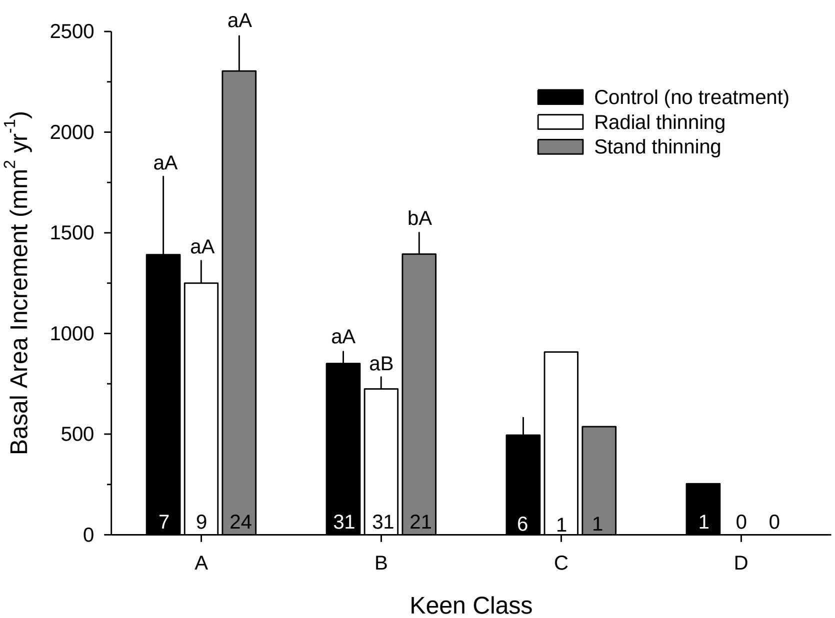

Figure S3. 15-year post-treatment annual average (+SE) basal area increment (BAI) by Keen Vigor Class and treatment. Numbers inside bars are sample sizes. Different lowercase letters denote significantly different treatment means within a class and uppercase letters denote differences between classes by treatment (α = 0.05). Small sample sizes precluded statistical comparisons for Keen class C and D.

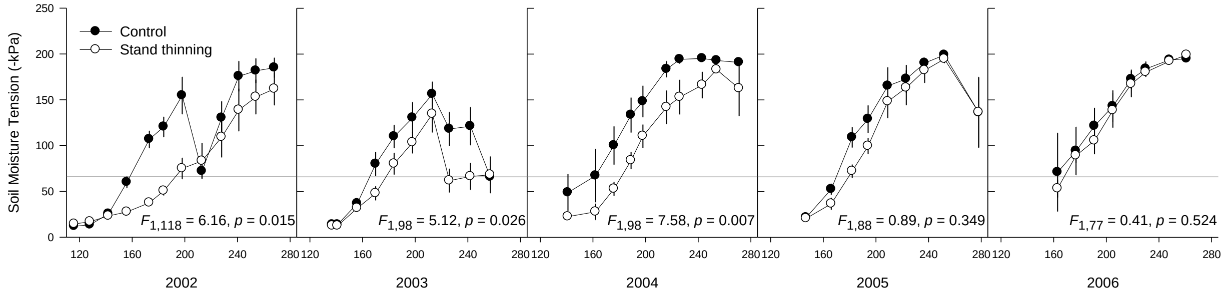

Figure S4. Mean (±SE) soil moisture tension from 2002 – 2006 in the control (no treatment) and stand thinning unit by Julian day. Thinning occurred in 2000. Higher values indicate drier soil conditions. Grey line indicates 66 –kPa, the benchmark soil moisture value where plant growth becomes limiting.