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Restoration Treatments Improve Overstory Tree Resistance Attributes and Growth in a Ponderosa Pine/Douglas-Fir Forest

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Abstract: *Research Highlights:* This study provides much needed insight into the development of resistance to disturbance and growth dynamics of overstory trees in response to restoration-based fuel reduction, and will be useful to scientists and managers attempting to better grasp the relative merits of restoration treatment types. *Background and Objectives:* Restoration-based fuel reduction treatments are common in dry, fire-prone forests of the western United States. The primary objective of such treatments is to immediately reduce a stand's crown fire hazard. However, the impact of these treatments on residual trees is relevant to assess their longevity and resistance to future disturbances. In this study, we evaluate the effects of restoration on retained overstory ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees in western Montana, where treatments were experimentally implemented 13 years prior as part of the national Fire and Fire Surrogate study. *Materials and Methods:* We examined tree attributes in response to the following replicated treatments: thin-only, burn-only, thin + burn, and a no-action control. We analyzed three different tree attributes that confer resistance to common disturbances: height-to-diameter ratio (resistance to wind), bark thickness (resistance to surface fire), and growth efficiency (resistance to bark beetles). *Results:* Our models suggest that thinning (with or without burning) alters tree attributes relative to the control in a manner that may increase tree resistance to wind and snow breakage, surface fire, and biotic agents such as bark beetles. Further analysis of annual growth of ponderosa pine and Douglas-fir varied by treatment type: thinning-based restoration (thin-only and thin + burn) increased diameter growth for both species, crown length and width in ponderosa pine, and crown length in Douglas-fir relative to unthinned treatments. Burning (burn-only and thin + burn) did not significantly affect tree growth relative to unburned treatments. *Conclusions:* While low-severity prescribed burning treatments are often used for restoration and have various ecosystem benefits, this study demonstrates that thinning (alone or in addition to burning) produces more measureable, beneficial results to overstory tree disturbance resistance metrics and growth.

Keywords: fire and fire surrogate study; frequent-fire forests; height-to-diameter ratio; bark thickness; growth efficiency; treatment effectiveness

1. Introduction

Restoration and fuel reduction treatments in dry forests are acutely concerned with large tree longevity [1]. This is intimately tied with more traditional management objectives, but is focused on morphological attributes that enable trees to survive disturbance [2]. Since a persistent overstory is necessary for diverse management objectives (e.g., productivity and carbon storage [3–5], wildlife habitat [6,7], and timber products that offset costs of future treatment [8,9]), retained overstory trees must be resistant to natural disturbance agents. Common disturbance agents that trees face in dry forests include surface fire, wind and snow loads, and insect attack (e.g., [10,11]). Understanding how treatments imbue resistance to these disturbance agents and promote longevity should help managers better attain targets and meet restoration objectives.

Many of today's dry, temperate forests are susceptible to high-severity crown fire due to management history and changing climate [12–15]. One common means of mitigating this hazard is with restoration-based fuel reduction, whereby land managers remove excess live and dead forest fuels while retaining fire-resistant trees via thinning and/or prescribed burning [1,9]. Those treatments are typically evaluated by assessing fire behavior in subsequent wildfire or fire modeling. How fuel treatments affect other management objectives not directly related to crown fire resistance remains unclear, especially multiple-use management objectives that depend on the retained overstory. Retained trees scale up to comprise the residual stand, and, therefore, impacts on retained trees have direct implications for the entire suite of management objectives, even where the immediate management need was to reduce fuel load and contiguity.

One of the most transcendent goals in management objectives is overstory longevity and persistence even through future disturbances. As such, disturbance resistance is a highly prized characteristic of individual trees. Given three common disturbance agents such as surface fire, heavy wind or snow loads, and tree-killing insects, tree attributes such as bark thickness, height-to-diameter ratio, and growth efficiency, respectively, are measureable characteristics that improve resistance to those disturbances. Thick bark is advantageous in fire-prone forests because it insulates the cambium during surface fires, increasing tree survival [16,17]. Conifer height-to-diameter ratios have a strong negative relationship with snow and wind damage incidence [18,19]. Growth efficiency, here defined as wood growth per tree leaf area, quantifies tree vigor [20] and theoretically reflects tree capacity to withstand bark-beetle attack. However, it is unclear how restoration treatment, which immediately alters forest structure and subsequent vegetation dynamics [21], impacts these attributes in the years following.

Part and parcel with tree longevity and resistance attributes are basic morphological attributes that are more even elementary to forest management, namely stem and crown dimensions. Past studies on restoration-based fuel reduction treatments document differences from pre-treatment to immediate post-treatment stand structure (e.g., [22,23]), but mostly omit individual-level tree responses over time (but see [24,25]). Furthermore, much of forest health, crown fire hazard, and ecosystem function is tied to tree crown attributes [4,26,27], but crowns are more often predicted with forest growth simulators than directly measured. Restoration treatments preferentially retain or remove trees based on stem and crown attributes, and the post-treatment forest environment may continue to impact development of these basic structures in unforeseen ways. Whatever the mechanism causing overstory tree change, treatment effects on individual responses over time will form the basis of future stand structure and subsequent silvicultural options but have not been adequately quantified [28].

The primary research goal of this study is to test enduring effects of restorative fuel reduction strategies on overstory tree attributes and growth in a dry ponderosa pine/Douglas-fir forest in the inland Northwest, USA. We pose and answer two questions to achieve this goal. First, what effects do thinning and/or burning restoration treatments have on tree attributes that have implications for resistance to future disturbance (i.e., bark thickness, height-to-diameter ratio, and growth efficiency)? Second, what effects do these treatments have on stem and crown growth? We postulated that a period of 13 years after treatment was a sufficient time for treatment differences to be expressed. We hypothesize that thinning and burning will have differing results on tree attribute dynamics because low-severity burning causes more physical tree damage than thinning and does not remove as much overstory competition. We expect that this study will guide researchers, modelers, and managers to better understand the broad-ranging impacts of fuel treatments on tree-level attributes important to achieving diverse management objectives. The results of this study can be used to improve individual tree growth estimates based on treatment history and press us to further define restoration treatment effectiveness.

2. Materials and Methods

2.1. Study Site

This study was conducted at the University of Montana's Lubrecht Experimental Forest (LEF; 46°53′ N, 113°26′ W), an 11,300 ha forest in western Montana's Blackfoot River drainage of the Garnet Range. Study sites range in elevation from 1230 to 1388 m ASL, and are comprised *of Pseudotsuga menziesii/Vaccinium caespitosum* and *Pseudotsuga menziesii/Spiraea betulifolia* habitat types [29]. This forest is generally composed of second-growth ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco), and western larch (*Larix occidentalis* Nutt.) regenerated from heavy cutting in the early 20th century. Soils are fine or clayey-skeletal, mixed, Typic Eutroboralfs and loamy-skeletal, mixed, frigid, Udic Ustochrepts [30].

Climate in this study area is maritime–continental. Annual precipitation is approximately 460 mm [31], nearly half of which falls as snow. Mean temperatures range from −6 °C in December and January to 17 °C in July and August. Average plant growing season is between 60 and 90 days. Grissino-Mayer et al. [32] identified that the historic fire frequency at LEF prior to the 20th century ranged from 2 to 14 years, with a mean composite fire return interval of 7 years.

The LEF was part of the Fire and Fire Surrogate (FFS) Study, a multidisciplinary research project that aimed to quantify the short-term effects of restorative fuel reduction treatments in frequent-fire forests across the US. The FFS Study provides a framework to examine fuel treatment effects on tree growth as it has a balanced experimental design and was specifically created to test for differences among treatments [33]. As a nationally implemented network, researchers have used the FFS Study to answer a wide gamut of short-term ecological response questions (see [34]). At LEF, treatments were implemented on 8% to 24% slopes in each of three blocks using a randomized factorial design: two levels of thinning (not thinned and thinned) by two levels of prescribed burning (not burned and burned), for a total of four treatment levels (no-action control, thin-only, burn-only, thin + burn). Prescription severity was intended to maintain 80% overstory tree survival given a wildfire in 80th percentile weather conditions. Stands were cut in 2001 and burned in 2002, creating twelve 9 ha experimental units. The cutting prescription was a combined low thinning and improvement cut to a residual 11.5 m^2 ha^{-1} of basal area, favoring ponderosa pine and western larch over Douglas-fir. Prescribed fire treatments were low-severity spring burns, with windspeeds less than 13 km h^{-1} and flame lengths typically less than 0.6 m, but ranging up to 2.7 m in slash piles. Stand conditions have been documented to assess treatment effects on fire hazard and overall vegetation dynamics from 4 to 14 years [21,24,35].

Although LEF's FFS study is a randomized complete block design, bark-beetle-induced tree mortality has complicated the assessment of longer-term treatment effects. Beetle populations (primarily *Dendroctonus ponderosae* Hopkins) rose to outbreak levels in Montana between 2006 and 2012. Beetle mortality was highest in control and burn-only units [25], leading to similar live ponderosa pine basal area in all treatments. Since Hood et al. [25] found a treatment effect on beetle-induced tree mortality (i.e., greater mortality in the unthinned units: control and burn-only) and stands are more similar now than in the pre-outbreak years, statistical differences between treatments found in this study will either be due to a combination of treatment and subsequent beetle kill or will be due to a muted treatment effect. We mitigate this confounding element by examining treatment effects while simultaneously accounting for local beetle-outbreak impacts.

2.2. Field Methods

We sampled trees on permanently monumented plots in the FFS Study. We measured previously tagged mature trees in 2014 using 0.04 ha circular plots, measuring a subset of trees from the center of each of the study's rectangular modified-Whittaker plots [35,36]. These were 10 randomly selected plot locations from 36 systematically located grid points within each treatment unit, making for a total of 120 revisited points. For each mature tree (diameter at breast height [dbh; 1.37 m] greater than 10 cm), we recorded species, dbh, total height, height to the base of live crown, and crown width. Height to the base of live crown was the estimated average branch height of the compacted lower limit of the crown [37]. Crown width was the projected horizontal distance between live crown edges as visualized by GRS densitometers (Geographic Resource Solutions; Arcata, CA); two measurements were made per tree at right angles. We used a historical dataset from these same plots dating back to 2001 (residual trees) and 2005 (residual trees plus ingrowth). The 2001 data comprised the same measurements as our 2014 dataset; however, crown width was not measured in 2005. Live stand structure metrics are presented in Table 1 and Figure 1.

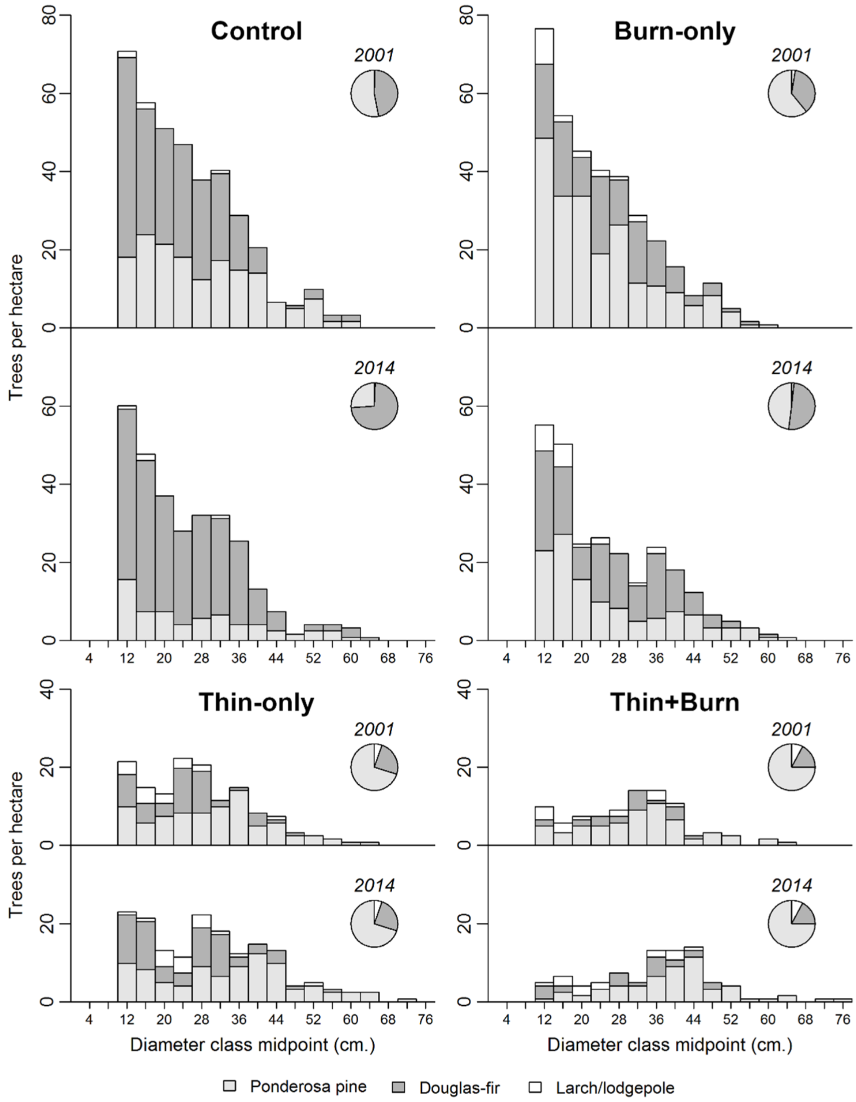


Figure 1. 2001 and 2014 diameter distributions by treatment, year, and species. Stacked bars show stem density by 4-cm classes (blocks pooled). Inset pie charts represent proportional basal area by species. Understory trees (less than 10 cm dbh) are not shown.

Table 1. Stand summary statistics for Lubrecht's Fire and Fire Surrogate Study across measurement years. Data presented are aggregated means of experimental units and 1 standard error. Note that the 2001 date is post-harvest but pre-burn, and that insect outbreak occurred between the 2005 and 2014 measurements. We considered 1111 the maximum Stand Density Index [38] in these ponderosa pine stands, per [39].

Attribute	Treatment	2001	2005	2014
Density (trees ha^{-1})	Control	379 (41)	373 (43)	323 (60)
	Burn-only	347 (12)	322 (17)	291 (43)
	Thin-only	143 (15)	143 (15)	184 (22)
	Thin + Burn	89 (14)	86 (12)	99 (13)
Basal area (m^2 ha^{-1})	Control	22.6 (4.6)	23.5 (4.8)	18.0 (5.1)
	Burn-only	19.3 (1.8)	19.3 (1.1)	17.6 (2.9)
	Thin-only	10.0 (0.3)	11.1 (0.3)	14.9 (0.2)
	Thin + Burn	7.6 (1.0)	8.0 (1.1)	11.0 (0.8)
Quadratic mean diameter (cm)	Control	27.2 (1.0)	27.9 (1.6)	26.1 (1.3)
	Burn-only	26.5 (1.6)	27.7 (1.3)	27.9 (2.1)
	Thin-only	30.0 (1.7)	31.7 (1.8)	32.5 (2.0)
	Thin + Burn	33.2 (1.6)	34.6 (1.6)	38.1 (2.4)
Stand Density Index (metric units)	Control	431 (80)	443 (82)	348 (92)
	Burn-only	373 (29)	368 (15)	335 (49)
	Thin-only	185 (6)	201 (7)	267 (8.8)
	Thin + Burn	135 (17)	140 (19)	186 (14)

In 2015, we measured bark thickness and collected tree cores using an increment borer for each of the tagged trees. Trees were cored along two perpendicular axes at breast height. Live sapwood boundaries were located and marked on the cores, then taken back to the lab to measure sapwood length.

2.3. Statistical Analysis

We considered all live tagged trees in plots when calculating stand summary statistics and diameter distributions. Since we were interested in overstory tree response, subsequent calculations and analyses were performed using data only from trees initially present and greater than 25 cm (10 inches) dbh in 2001 and surviving through 2014.

We created two response variable suites each for ponderosa pine with initial dbh ≥ 25 cm (161 trees) and Douglas-fir ≥ 25 cm dbh (167 trees). Western larch was not included in this analysis because of poor representation across experimental blocks. These included tree resistance attributes (bark thickness, height-to-diameter ratio, and growth efficiency in 2015) to answer our first research question, and annualized growth dimensions (periodic annual growth in dbh, height, crown length, and crown width from 2001 to 2014) to answer the second (i.e., a suite of seven responses per species).

Height-to-diameter ratio was calculated as height in meters divided by dbh in meters. Growth efficiency was defined as annualized mass of wood grown per unit leaf area (g m^{-2} yr^{-1}), sensu [40,41]. We used two-parameter volume equations [42] to calculate periodic annual growth over the 13-year period, then converted it to mass assuming a constant wood density of 400 g m^{-3} (as in [40]). Sapwood length was converted to cross-sectional area at breast height (less heartwood area), which we then used to estimate tree leaf area using local species-specific regressions [43,44].

We used linear mixed-effects models as the primary statistical engine to test our research questions, which were focused on treatment effect detection in resistance attributes and annualized growth responses. In these models, we included continuous variables to remove statistical noise and isolate treatment effects (i.e., dead basal area on the measured plot in 2014 as a surrogate for beetle outbreak severity; 2001 dbh to account for tree size in the annual dbh growth model; 2001 height for the height model; etc.), not necessarily to improve predictive capacity or make extended inference on non-treatment terms. These covariates were specified for inclusion *a priori* to mitigate the effects of beetle outbreak severity and tree size on responses, so their first-order terms were not subject to removal in the model selection routine. We used AIC for model selection when checking for interaction between tree covariates and treatment, but AIC was always lower for the simpler, non-interactive models. Models were fit in R [45] with the lme function [46]. The same model form is used for each of the response variables tested:

$$y_{ijklm} = \mu + \alpha_i \times \beta_j + \gamma_k + \varepsilon_{ijk} + \varphi_{ijkl} + \rho_{ijkl} + \tau_{ijklm} + \omega_{ijklm} \quad (1)$$

where y is the tree response variable of interest, μ is the grand mean, α is the thinning effect (levels i: 1 = not thinned, 2 = thinned), β is the burning effect (levels j: 1 = not burned, 2 = burned), γ is the block effect (levels k:1–3), ε is the error term by which treatment is evaluated, φ is the dead basal area on the measured plot in 2014 (a surrogate for beetle-kill severity), ρ is the plot effect (levels l:1–120), τ is a measured tree covariate to account for size in 2001 (for tree m), and ω is the tree error term. This model structure reflects the factorial experimental design inherent to this study. That is, defined treatment factor terms reflect two thinning levels crossed by two burning levels, plus their interaction. Therefore, the "thinning" treatment factor refers to a combined effect of "thinned" experimental units (thin-only and thin + burn) in contrast to the combined "unthinned" units (control and burn-only). "Burning" likewise contrasts the combined "burned" units (burn-only and thin + burn) against the "unburned" (control and thin-only). The interacting "thinning × burning" term will only be significant when effect is different than the combined "thinning" and "burning" factor terms; hence, non-significance does not necessarily mean no difference between thin + burn and control experimental units. We use this treatment factor language to discuss statistical significance, and refer to the appropriate experimental or treatment units when needed. This model form was applied to all 14 response variables, but n varied by response from 84 to 204 (mean: 171).

Model residuals were visually inspected for normality. Residuals from some of the height-based responses demonstrated slight departures from normality (long distributional tails) but could not be ameliorated by transformation; we note that model standard errors are therefore approximate. Overall model fit was evaluated with marginal and conditional R^2 values [47]. Marginal R^2 is here defined as the proportion of variance explained by the fixed effects (μ, α, β, φ, and τ) to all variance components in the model; conditional R^2 is the proportion of the summed fixed and random components (all except ω) to all variance components in the model. We used an α of 0.10 to interpret statistical significance of p-values, judging $0.10 < p \leq 0.05$ as marginal evidence and $p < 0.05$ as strong evidence of a statistical effect.

3. Results

The FFS treatments at LEF had substantial impacts on forest structure and composition (Figure 1; Table 1), as characterized by past studies [21,24,25,35,48]. Broadly summarized, the burn-only treatment had little evident effect on overstory trees and composition, as evidenced by the high residual densities of small diameter trees. The thin-only treatment resulted in low tree density, higher quadratic mean diameter, and greater proportional dominance by ponderosa pine than Douglas-fir, especially in the larger diameter classes. Prescribed fire in the combination thin + burn treatment resulted in even lower overstory density and higher ponderosa pine dominance than the thin-only and burn-only treatments. Assuming a maximum Stand Density Index (SDI, [38]) of 1111 [39], the average thin-only stand was 16.7% of maximum SDI in 2001 and reached 24.0% as of 2014; thin + burn stands began at 12.2% and grew to 16.7% of maximum SDI. In contrast, SDI in unthinned stands was between 30% and 40% of maximum SDI throughout the entire measurement period.

3.1. Treatment Effects on Disturbance Resistance Attributes

Disturbance resistance attributes varied by tree diameter (Tables 2 and 3) and treatment had differential effects on ponderosa pine and Douglas-fir attributes. Of the three resistance attributes, model fit was best for the height-to-diameter model in both species. Furthermore, initial tree size (dbh) had a significant effect on all attributes in both species.

Table 2. Average tree resistance attributes by treatment. Mean and 1 standard error shown.

Species	Attribute	Treatment	All Size Classes	Only dbh > 25 cm
Pinus ponderosa	Bark thickness (cm)	Control	1.68 (0.07)	2.89 (0.14)
		Burn-only	1.87 (0.14)	2.86 (0.08)
		Thin-only	1.99 (0.09)	2.76 (0.20)
		Thin + Burn	2.34 (0.2)	2.80 (0.30)
	Height-to-diameter (m m^{-1})	Control	67.5 (3.7)	58.8 (6.0)
		Burn-only	67.3 (1.2)	53.5 (1.8)
		Thin-only	56.5 (2.7)	52.8 (1.9)
		Thin + Burn	57.2 (1.7)	55.0 (1.3)
	Growth efficiency (g m^{-2} yr^{-1})	Control	60 (87)	125 (14)
		Burn-only	123 (23)	118 (8)
		Thin-only	178 (3)	171 (5)
		Thin + Burn	180 (19)	173 (21)
Pseudotsuga menziesii	Bark thickness (cm)	Control	1.64 (0.04)	2.00 (0.04)
		Burn-only	1.71 (0.19)	2.19 (0.23)
		Thin-only	1.38 (0.22)	1.69 (0.24)
		Thin + Burn	2.24 (0.27)	2.58 (0.29)
	Height-to-diameter (m m^{-1})	Control	64.9 (1.2)	59.5 (2.3)
		Burn-only	61.9 (3.2)	55.8 (0.9)
		Thin-only	59.1 (0.6)	53.7 (0.8)
		Thin + Burn	55.3 (2.5)	49.9 (4.5)
	Growth efficiency (g m^{-2} yr^{-1})	Control	137 (19)	191 (36)
		Burn-only	145 (17)	175 (11)
		Thin-only	126 (21)	163 (18)
		Thin + Burn	205 (7)	245 (9)

Table 3. Linear mixed-effects model coefficients for individual tree (DBH > 25 cm) disturbance resistance metrics (height-to-diameter, bark thickness, and growth efficiency). "(Intercept)" coefficient refers to the Control treatment. Note that the "Thinned" factor refers to Thin-only and Thin + Burn treatment units, while the "Burned" factor refers to Burn-only and Thin + Burn treatment units.

		Bark Thickness (cm)		Height:dbh (m m^{-1})		Growth Efficiency (g m^{-2} yr^{-1})	
Species	**Coefficient**	**Estimate**	***p* Value**	**Estimate**	***p* Value**	**Estimate**	***p* Value**
Pinus ponderosa	(Intercept)	1.738	<0.001	78.746	<0.001	166.845	<0.001
	Outbreak severity	0.062	0.056	0.577	0.115	4.807	0.093
	Initial dbh	0.063	<0.001	-4.030	<0.001	-9.068	0.001
	Thinned	−0.118	0.691	−1.177	0.621	54.629	0.015
	Burned	−0.066	0.821	−3.083	0.217	−10.560	0.533
	Thinned×Burned	0.134	0.743	1.819	0.573	1.486	0.948
	Marginal R^2	0.20		0.52		0.41	
	Conditional R^2	0.54		0.69		0.48	
Pseudotsuga menziesii	(Intercept)	0.587	0.020	84.260	<0.001	73.469	0.017
	Outbreak severity	0.000	0.974	−0.015	0.943	7.439	0.001
	Initial dbh	0.093	<0.001	−5.753	<0.001	16.503	<0.001
	Thinned	−0.170	0.572	−9.488	0.074	12.535	0.650
	Burned	0.132	0.560	−2.624	0.440	1.427	0.945
	Thinned × Burned	0.583	0.199	6.855	0.274	47.888	0.258
	Marginal R^2	0.35		0.52		0.24	
	Conditional R^2	0.50		0.77		0.31	

We found no direct evidence of a treatment effect on bark thickness in either ponderosa pine or Douglas-fir (Table 3), though there was strong evidence of a positive effect of tree size on bark thickness in both species, and ponderosa pine bark thickness increased with local beetle-outbreak severity.

There was some evidence that thinning reduced height-to-diameter ratio in Douglas-fir, but not ponderosa pine (Table 3), while burning had no effect on either species. Thinning was associated with 15% to 32% lower height-to-diameter ratios than the unthinned treatment as tree size increased from small (25 cm) to large (61 cm) initial tree dbh.

Thinning significantly improved growth efficiency in ponderosa pine, but not Douglas-fir (Table 3); burning had no effect on either. In ponderosa pine, our model showed growth efficiency was 42%

greater for small diameter trees (25 cm) and 73% greater for large trees (66 cm) in thinned versus unthinned treatments. Whereas tree size improved treatment effect on growth efficiency, there was marginal evidence that beetle outbreak severity dampened treatment effect: holding tree size constant at 35 cm, gains in growth efficiency due to thinning reduced from 46% to 28% as severity increased from 0 to 3.9 m^2 basal area lost.

We observed no effect of treatment interaction in any of the attributes (Table 3).

3.2. Treatment Effects on Growth

Treatment influenced ponderosa pine and Douglas-fir stem growth over the course of the study (Figures 2 and 3; Table 4). Our suite of models showed that thinning (thin-only and thin + burn treatments) positively influenced dbh growth over unthinned treatments in both ponderosa pine and Douglas-fir. More specifically, ponderosa pine dbh growth was twice as great in thinned treatments (model prediction: 0.50 cm yr^{-1}) than unthinned treatments (model prediction: 0.24 cm yr^{-1}) regardless of initial tree size, which was not a significant covariate. Initial tree size was significant for the Douglas-fir dbh model, and, given the initial data range of 25 cm to 61 cm dbh, our models predict dbh growth to be 0.45 cm yr^{-1} and 0.56 cm yr^{-1}, respectively, in thinned treatments, but 0.25 cm yr^{-1} and 0.36 cm yr^{-1} in the unthinned treatment. Thus, Douglas-fir dbh growth was improved by thinning, but the effect (relative to unthinned) decreased with tree size from 78% greater growth in the smallest trees to only 56% more growth in the largest trees. Likewise, thinning caused 73% greater dbh growth on plots that had no beetle-caused mortality (for median dbh, 32 cm), but only 47% greater growth on plots that had higher mortality (1.6 m^2 of basal area lost). Treatment did not affect height growth in either species. Interestingly, burning and the interaction between burning and thinning did not significantly affect stem growth.

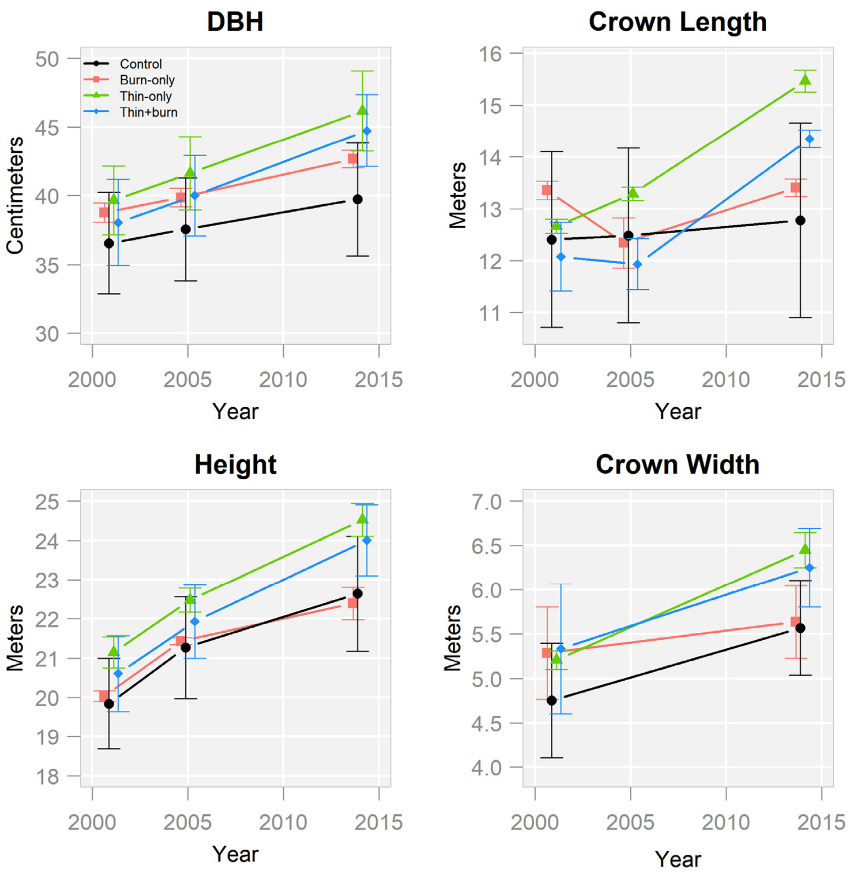


Figure 2. Stem and crown dimensions by treatment and year for ponderosa pine greater than 25 cm dbh.

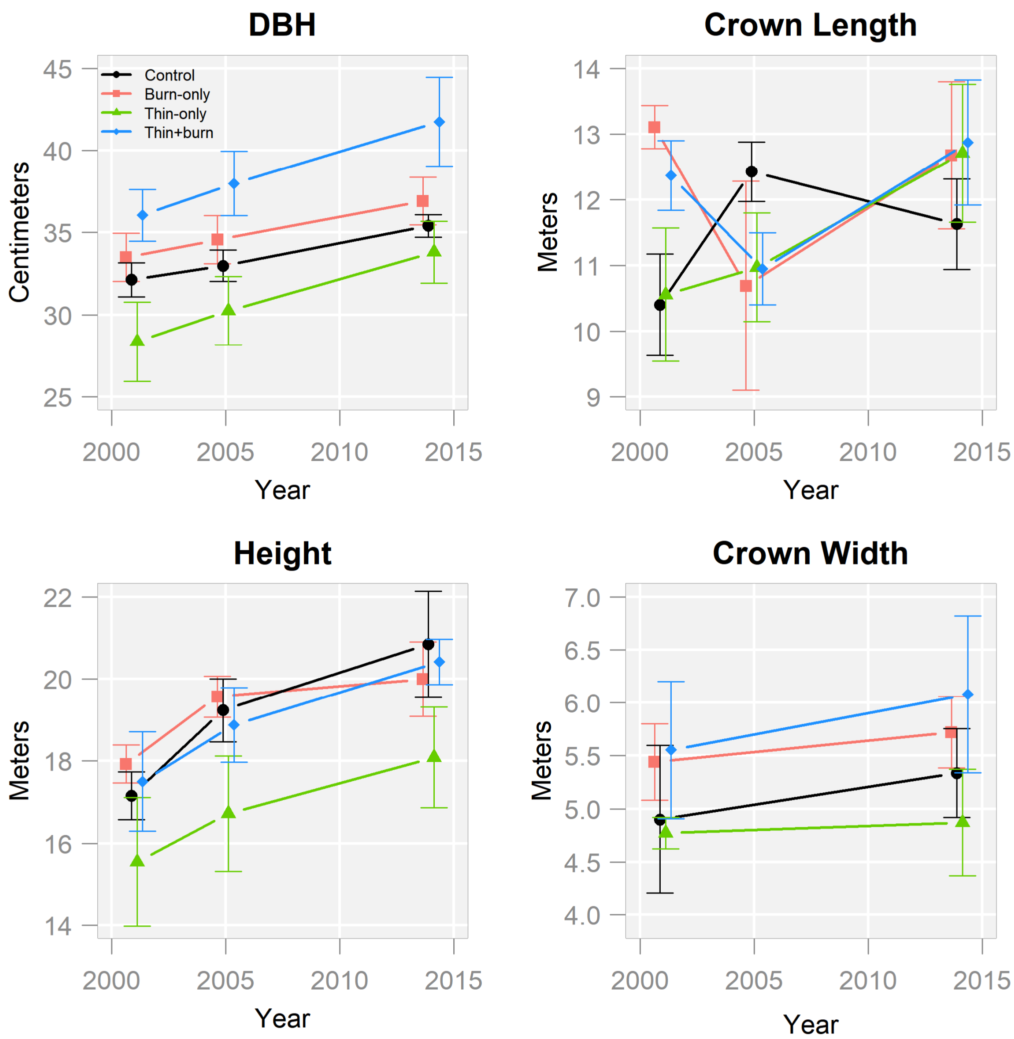


Figure 3. Stem and crown dimensions by treatment and year for Douglas-fir greater than 25 cm dbh.

Table 4. Linear mixed-effects model coefficients for individual tree (DBH > 25 cm) periodic annualized growth responses (i.e., change in DBH, height, crown length, and crown width). The "(Intercept)" coefficient refers to the Control treatment. Note that the "Thinned" factor refers to Thin-only and Thin + Burn treatment units, while the "Burned" factor refers to Burn-only and Thin + Burn treatment units.

		Annual Stem Change Responses				**Annual Crown Change Responses**			
		DBH		**Height**		**Length**		**Width**	
Species	**Coefficient**	**Estimate**	***p* Value**	**Estimate**	***p* Value**	**Estimate**	***p* Value**	**Estimate**	***p* Value**
Pinus ponderosa	(Intercept)	0.243	<0.001	0.274	<0.001	0.207	0.002	0.062	0.026
	Outbreak severity	0.001	0.907	0.009	0.176	0.002	0.816	0.009	0.059
	Initial size	−0.001	0.771	−0.001	0.042	−0.003	0.003	−0.002	0.048
	Thinned	0.253	0.002	0.060	0.208	0.161	0.009	0.054	0.064
	Burned	0.031	0.56	−0.042	0.359	−0.046	0.319	−0.014	0.568
	Thinned×Burned	−0.032	0.651	0.036	0.551	−0.011	0.839	−0.01	0.772
	Marginal R^2	0.39		0.18		0.31		0.15	
	Conditional R^2	0.63		0.53		0.47		0.30	
Pseudotsuga menziesii	(Intercept)	0.181	<0.001	0.513	<0.001	0.255	0.007	0.059	0.254
	Outbreak severity	0.009	0.006	0.004	0.339	−0.024	0.195	−0.014	0.126
	Initial size	0.007	0.001	−0.005	<0.001	−0.004	0.046	−0.002	0.386
	Thinned	0.199	0.005	−0.102	0.316	0.097	0.077	0.019	0.634
	Burned	0.024	0.415	−0.079	0.317	−0.032	0.520	0.022	0.546
	Thinned×Burned	−0.047	0.393	0.159	0.264	−0.080	0.254	−0.022	0.693
	Marginal R^2	0.44		0.26		0.29		0.08	
	Conditional R^2	0.60		0.61		0.35		0.36	

Ponderosa pine and Douglas-fir crowns responded differently to treatments (Figures 2 and 3; Table 4). Although R^2 values for ponderosa pine were low, thinning had a positive effect on crown length and width relative to the unthinned treatment; crown length also depended on initial size while crown width depended on initial size and beetle severity. Thinning caused the trees with shortest crowns (6.6 m) to increase 81% more than trees in unthinned treatments, while the trees with longest crowns (20.4 m) decreased, but the decrease was 72% lower in thinned than unthinned treatments (i.e., thinning minimizes crown length reduction). When compared to the tree height model, coefficients show that crown length growth was 100% of tree height growth for small trees and 86% for large trees in thinned treatments, but for unthinned treatments crown length growth was only 63% of tree height growth for small trees and −40% for large trees. Likewise, thinning increased crown width growth by 111% in the trees with narrowest crowns (2.3 m); the widest crowns (12.6 m) still grew at least 3 cm $year^{-1}$ in thinned treatments, while trees in unthinned treatments reduced in width. The effect of thinning on crown width was moderated by beetle severity, as thinning caused the median tree (5.0 m) to grow 187% more than unthinned treatments where beetles did not kill trees, but only 50% more than unthinned treatments where beetle severity was greatest (0.82 m^2 basal area lost). Burning and the interaction of burning and thinning, however, did not have a significant effect on ponderosa pine growth. Our models show marginal evidence that thinning increased Douglas-fir crown length growth compared to unthinned treatments, but this response varied with initial tree size (49% increases for small crown lengths (6.3 m) and 297% for large lengths (16.5 m)). However, thinning and burning did not affect Douglas-fir crown width.

4. Discussion

4.1. Restoration and Disturbance Resistance

Bark thickness and resistance to cambial kill is dependent on both species and tree diameter [17,49]. Fuel reduction and restoration treatments are specifically designed to retain individual trees that have improved resistance (i.e., thick bark) to fire. For instance, Ryan and Reinhardt [49] found that the probability of fire-caused mortality in Douglas-fir with 1-cm-thick bark was 0.39 if 10% of crown volume was scorched by fire, and 0.98 if 30% was scorched; tree survivorship increased by 40% and 260%, respectively, for a tree with 3-cm-thick bark. Both our ponderosa pine and Douglas-fir bark thickness models corroborate that bark thickness increases with initial tree size. However, after controlling for differences in initial tree size, we found no additional effect of thinning or burning on bark thickness. This disturbance resistance model analysis masks that tree size increased more rapidly in thinning-based treatments, as identified in our tree growth models. Our study supports that thinning improves tree growth and that larger trees are associated with thicker bark (Figure 4). Thicker bark confers improved resistance to surface fire because it insulates stem cambium [50]; therefore, this study indirectly indicates that thinning-based fuel reduction treatment improves surface fire resistance. Land management agencies frequently look for metrics by which to monitor and evaluate tree and stand resistance to future fire. High average tree bark thickness is one metric that managers can use that is not only meaningful, but attainable with thinning-based fuel treatments via their positive effects on diameter distributions and tree growth.

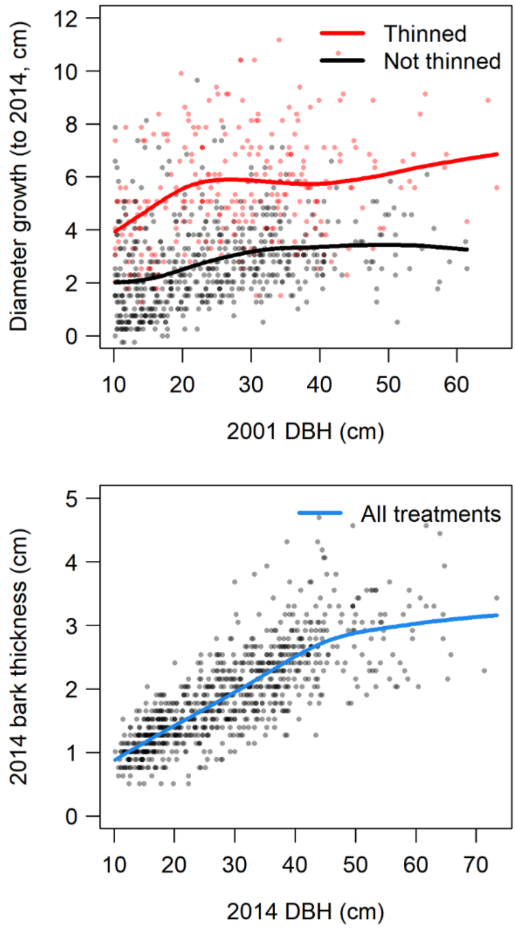
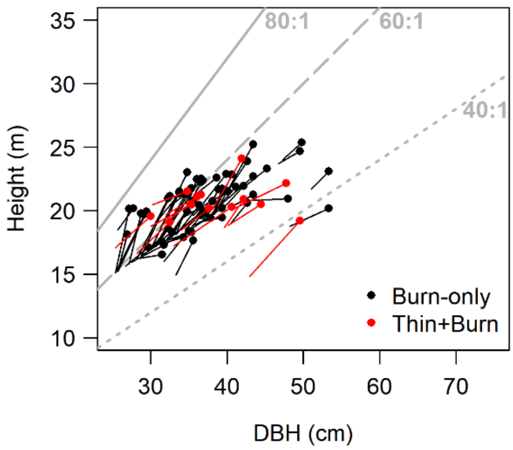


Figure 4. Ponderosa pine periodic dbh growth from 2001 to 2014 by thinning treatment (top panel) and bark thickness by dbh in 2014. Points represent repeat tree measurements, and smooth splines illustrate relationship with tree size.

Previous research has identified a height-to-diameter ratio threshold of approximately 80:1, above which individual tree wind and snow damage is most common [18,19]. Additionally, tree diameter itself is a powerful predictor of resistance to breakage, with resistance proportional to the cube of dbh [51]. Our models showed that the study's trees have low susceptibility to breakage from wind and snow, regardless of treatment (ratio less than 80; Figure 5), but that thinning further increased resistance to breakage in Douglas-fir. This was due to a non-significant decrease in tree height growth that, when paired with diameter growth, caused the height-to-diameter ratio to be marginally influenced by thinning. In other words, tree resistance to breakage was increased by thinning because thinning more positively impacted dbh than height growth. Diameter growth is often more influenced by stand density manipulations than height growth, except in very crowded or stagnated stands [52,53]. In a coastal Douglas-fir Levels of Growing Stock study in Washington, for example, Marshall and Curtis [54] found that 35-year diameter growth in thinned stands was 21% to 90% greater than controls, whereas height growth was only 4% to 10% greater than untreated controls. Similar to our observations, where thinning is done in stands not already susceptible to windthrow and snow breakage, height-to-diameter ratios should remain lower than in untreated counterpart stands and have direct ramifications for tree resistance to breakage [19].



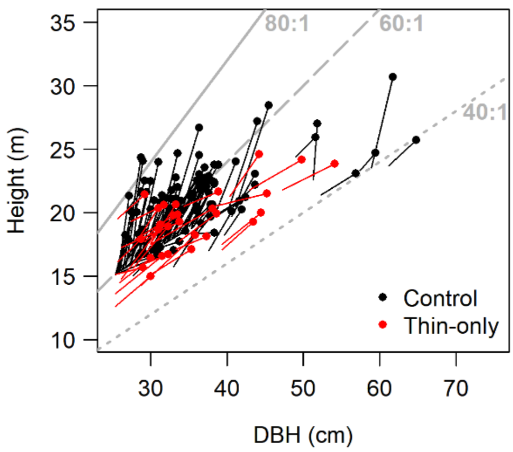


Figure 5. Douglas-fir periodic change in height and diameter relative to height-to-diameter ratio thresholds of 80:1, 60:1, and 40:1. Tree growth is represented from 2001 (segment terminus with no end cap) to 2014 (terminus with circle end cap). To better visualize the significant thinning effect, the top panel shows treatments that used prescribed fire, and the bottom panel shows treatments without prescribed fire.

Fuel reduction and restoration studies do not typically report tree growth efficiency as a treatment response. Although growth efficiency is not a direct resistance metric, Waring [4] identified that it is a "sensitive indicator to environmental stresses" and that increased growth efficiency is associated with decreased tree stress and increased resistance to disease and insect attack. Our models corroborate that thinning, even as a restoration treatment, results in greater growth efficiency in ponderosa pine ([40,55]; but results vary by index in [56]). Furthermore, only 5% of trees in thinned treatments (versus 38% in unthinned treatments) had growth efficiency less than 100 g m^{-2} yr^{-1}, which Larsson et al. [40] identified as a threshold for successful mountain pine beetle attack. We might have expected that trees released to wide spacing become inefficient because of the lack of competitive pressure, as reported by a nearby Douglas-fir study [57]. However, thinning seems to have improved ponderosa pine growth efficiency because it is a shade-intolerant species that thrives in full sun, which the thinning treatments provide by overstory removal. Furthermore, in water-limited ponderosa pine systems, thinning treatments permit trees to invest more in secondary growth, carbon storage, or defensive resins because there is less belowground competition for water [56,58,59].

4.2. Implications of Post-Treatment Growth

Crowns are fundamentally important tree attributes. The tree crown is the photosynthetic machinery that assimilates carbon for cellular respiration, growth, storage, and extractives.

Larger crowns have a greater capacity to produce more photosynthate and meet tree demands. Furthermore, crown dimensions are excellent predictors of tree growth potential (e.g., [60,61]), and they can be more easily measured than tree leaf area. Since thinning-based fuel reduction increases tree carbohydrate source, it subsequently prepares trees for more rapid growth and helps realize potential ecologic or economic gains.

The primary motivation for these treatments was to reduce crown fire potential. Prescribed fire can accomplish this by scorching and killing lower branches, increasing crown base height. Yet, perhaps because burn prescription was conservative and we only considered trees larger than 25 cm dbh, we found no significant effect of fire on crown length. Rather, our models show that thinning-based fuel reduction increased crown length development, especially by arresting crown recession of the smaller overstory trees (crown length growth for a small tree in thinned treatment is equivalent to tree height growth). This has long been known with respect to commercial thinning (e.g., [62,63]), but is rarely discussed in the fuel management literature (but see [64]). Although crown growth should improve overall tree growth, arrested crown recession can be detrimental to tree and stand fire hazard if the gap between crown and surface fuel strata is reduced as ladder and surface fuels aggrade. In fact, crown length reduction ("lifting canopy base height") is one tenet of fuel treatments [1]. This is because low-hanging foliage is more likely to ignite from surface fires and nearby fuel ladders, and because fuller crowns (and higher bulk densities) provide more fuel for crown-to-crown fire transfer. An important consideration is that the gap between surface and overstory fuel strata may be short-lived due to combined slowed recession from above, as this study demonstrates in the thinned treatments, and growth from the understory below. Although trees in both the thin-only and the thin + burn treatments had slowed crown recession, the gap between overstory crown bases (i.e., canopy base height) and understory fuels was more than twice as large in thin + burn because prescribed fire killed understory shrubs, advanced regeneration, and lifted crown base heights [21,48].

Additional crown growth is an ecological advantage of thinning-based treatments. Individual trees with wide crowns and persistent crown bases develop large diameter branches to support the added structure. Large diameter branches are key foundational features that support lichen community development by increasing substrate area and duration for colonization [65]. A healthy lichen community is particularly valuable for managers seeking to improve floristic diversity, arthropod habitat, or herbivore fodder. Deep crowns with large branches also provide better roosting habitats for wildlife such as the turkey, northern goshawk, northern flying squirrel, and fisher [66,67]. Additionally, large branches are ecologically important because they eventually add to a suite of forest floor processes once the branches are shed [68]. These branches become coarse woody debris that persist exponentially longer than fine branch material, providing heterogeneous structure for plant and invertebrate detritivores that drive nutrient cycling [69]. Also, large crowns with high leaf area are associated with increased cone production and frequency [70,71]. One study in California found that full-crowned dominant ponderosa pines produced 99% of total stand cone crop [72]. The ecological benefit of large and frequent cone crops extends beyond more reliable tree regeneration: cone and seed production has a profound impact on food availability for seed consumers such as small rodents and birds, which has cascading effects on ecosystem energetics. Although these stands have a long way to go to emulate the open-canopied uneven-aged structure of fire-maintained old-growth forests, branch development and cone production should be accelerated by thinning-based fuel treatment and restoration (similar to [73]) in a manner that transitions these stands into a position to provide for the ecological processes and habitat needs for complex structures in older forests.

These treatments were not intended to be isolated entries, but rather the first of a multi-entry, treatment regime management strategy, as advocated by Reinhardt et al. [9]. Treatment regimes are a necessary reality (whether or not they are planned for) in dry, fire-prone forests where wildfire is continually excluded. However, treatment regimes require financial remuneration, which in turn is directly affected by how treatments cause tree dimensions to respond. Typically, thinning improves diameter growth, increases the amount of extractable volume per tree, and concentrates stand volume on fewer, more valuable trees than in the unthinned treatments. But thinning for fuel reduction is often severe. As our study suggests, severe thinning improves diameter growth, but increases crown length and width development, extends lower limb retention, and will increase knot presence and size in boards [74,75]. Thus, although thinning-based fuel reduction and restoration treatments increase the extractable product per tree, the quality of extracted timber could potentially detract from final value.

It is interesting to note that starting size did not significantly influence pine dbh or crown width growth. This may mean that the treatment had such a strong effect on this population that the average tree in any given size class grew the maximum average physical limit ("free growth"). That these trees are free to grow is supported by traditional understanding of density-dependent competition measures as interpreted by density management thresholds. Long and Shaw [39] identify a free-to-grow developmental period when Stand Density Index (SDI) is less than 25% of a species' maximum, which stands in thinned treatments remained below in this study (cf 15% of relative density in [76]). Particularly where treatments create a homogeneous structure, planning fuel reduction and restoration treatments can be improved by considering growing stock levels and stand development stages using density management diagrams with known growth-response thresholds.

4.3. Burning versus Thinning

Our models illustrate that thinning-based restoration and fuel reduction (the combined thin-only and thin + burn treatments versus the combined control and burn-only) have the broadest impacts on individual overstory trees, and more so for ponderosa pine than Douglas-fir. Trees in thinned stands have very different morphological characteristics and growth patterns than those in the unthinned treatments. On the other hand, burning-based fuel reduction treatments had comparatively little impact on mid-term tree morphology and growth responses (the combined burn-only and thin + burn treatments versus the combined control and thin-only). We also found no significant effect of treatment interaction; i.e., the thin + burn treatment had no statistically significant effect beyond thinning alone. We believe the lack of burning effect is primarily due to treatment severity and resultant competitive conditions. The prescribed burns in the FFS study had little impact on mature (dbh > 10 cm) stem density (Table 1; [35,77]) and only resulted in minimal perceptible change to residual overstory trees. Although burning improves nutrient availability [78,79], water limitation or competition may be inhibiting full utilization of higher nutrient loads. Low-severity burns are actually common when reintroducing fire (as in [77,80]) for fear of widespread overstory mortality or runaway crown fire that threatens nearby natural resources, structures, or lives. This study provides evidence that single-entry low-severity burning is largely ineffective at changing individual overstory tree growth trends and easy-to-measure tree attributes that confer resistance. Moderate-severity prescribed burns or repeated application of low-severity burning is likely necessary if landowners want to see significant physical change in overstory tree characteristics.

It should be noted that a number of studies have shown that thinning alone insufficiently reduces crown fire potential, though reduction of crown fire potential is the primary objective of fuel reduction treatments (e.g., [24,77,81,82]). This is because thinning alone does not treat dead surface fuels and can even increase loading, may not treat mid-story ladder fuels, does not increase crown base heights as well as burning, and increases in-stand wind speeds, depending on burn prescription. Furthermore, although a one-time low-severity fire may not impact the overstory tree characteristics examined in this study, it may confer increased resistance to disturbances through alternative, chemical pathways (e.g., [25]). We do not negate these findings, but seek to inform multiple-resource managers of the temporal effects of treatments on individual tree growth and attributes.

5. Conclusions

Combined restoration and fuel reduction treatments are common across the western United States because of limited management budgets. Despite being principally engineered to improve stand-level resistance to future surface fire and avoidance of crown fire, the treated areas are almost always multiple-use forests that have a variety of objectives. It is important to consider how these treatments influence objectives other than crown fire hazard reduction. Large trees, in particular, are important structural components to many management objectives. Treatment influence on large trees will subsequently impact stand development and ecology, wildlife use, and potential for economic returns.

Tree attributes that confer resistance varied by restoration treatment, and were influenced only by thinning. Thinning indirectly improved bark thickness via increased dbh growth, which improves tree resistance to surface fire. There was some evidence that thinning-based restoration improved stem resistance to snow and wind breakage in Douglas-fir. Thinning also increased ponderosa pine growth efficiency, which should help trees resist biotic disturbance agents. These results highlight that restorative fuel reduction can have a positive impact on metrics that confer tree resistance to at least three types of disturbances, indicating greater potential for long-term persistence and success in a suite of management goals.

Underlying those resistance metrics are key morphological responses to treatment. We found that tree morphology varied by restoration type. Specifically, thinning-based fuel reduction caused tree stems to grow broader (not taller), and caused ponderosa pine crowns to increase in size altogether. Burning, however, had no effect on measured tree growth. These results do not validate the effectiveness of restoration treatments to reduce crown fire hazard, but they do show the dominant effect of severe thinning-based treatments on growth. Growing differences in morphology have practical impacts on fuel, economic, or ecological objectives that may guide managers' choice in restorative fuel treatment type. Furthermore, these trends may cause unexpected results as we scale up from the tree to consider stand-level growth metrics.

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References

1. Agee, J.K.; Skinner, C.N. Basic principles of forest fuel reduction treatments. *For. Ecol. Manag.* **2005**, *211*, 83–96. [CrossRef]
2. Kolb, T.E.; Agee, J.K.; Fulé, P.Z.; McDowell, N.G.; Pearson, K.; Sala, A.; Waring, R.H. Perpetuating old ponderosa pine. *For. Ecol. Manag.* **2007**, *249*, 141–157. [CrossRef]
3. Sala, A.; Woodruff, D.R.; Meinzer, F.C. Carbon dynamics in trees: Feast or famine? *Tree Physiol.* **2012**, *32*, 764–775. [CrossRef] [PubMed]
4. Waring, R.H. Estimating forest growth and efficiency in relation to canopy leaf area. *Adv. Ecol. Res.* **1983**, *13*, 327–354. [CrossRef]
5. Lutz, J.A.; Larson, A.J.; Swanson, M.E.; Freund, J.A. Ecological importance of large-diameter trees in a temperate mixed-conifer forest. *PLoS ONE* **2012**, *7*. [CrossRef]
6. Scott, V.E. Characteristics of ponderosa pine snags used by cavity-nesting birds in Arizona. *J. For.* **1978**, *76*, 26–27.
7. Meyer, M.D.; Kelt, D.A.; North, M.P. Nest trees of Northern Flying Squirrels in the Sierra Nevada. *J. Mammal.* **2005**, *86*, 275–280. [CrossRef]
8. Scott, J.H. *Fuel Reduction in Residual and Scenic Forests: A Comparison of Three Treatments in a Western Montana Ponderosa Pine Stand*; Research Paper RMRS-RP-5; USDA Forest Service, Rocky Mountain Research Station: Ogden, UT, USA, 1998; 42p.

9. Reinhardt, E.D.; Keane, R.E.; Calkin, D.E.; Cohen, J.D. Objectives and considerations for wildland fuel treatment in forested ecosystems of the interior western United States. *For. Ecol. Manag.* **2008**, *256*, 1997–2006. [CrossRef]
10. Veblen, T. Disturbance patterns in southern Rocky Mountain forests. In *Forest Fragmentation in the Southern Rocky Mountains*; Knight, R., Smith, F., Buskirk, S., Romme, W., Baker, W., Eds.; Colorado State University: Boulder, CO, USA, 2000; pp. 31–54.
11. Bigler, C.; Kulakowski, D.; Veblen, T.T. Multiple disturbance interactions and drought influence fire severity in rocky mountain subalpine forests. *Ecology* **2005**, *86*, 3018–3029. [CrossRef]
12. Covington, W.W.; Moore, M.M. Postsettlement changes in natural fire regimes and forest structure. *J. Sustain. For.* **1994**, *2*, 153–181. [CrossRef]
13. Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* **2006**, *313*, 940–943. [CrossRef]
14. Miller, J.D.; Safford, H.D.; Crimmins, M.; Thode, A.E. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* **2009**, *12*, 16–32. [CrossRef]
15. Miller, J.D.; Skinner, C.N.; Safford, H.D.; Knapp, E.E.; Ramirez, C.M. Trends and causes of severity, size, and number of fires in northwestern California, USA. *Ecol. Appl.* **2012**, *22*, 184–203. [CrossRef] [PubMed]
16. Martin, R.E. Thermal properties of bark. *For. Prod. J.* **1963**, *13*, 419–426.
17. Jones, J.L.; Webb, B.W.; Butler, B.W.; Dickinson, M.B.; Jimenez, D.; Reardon, J.; Bova, A.S. Prediction and measurement of thermally induced cambial tissue necrosis in tree stems. *Int. J. Wildl. Fire* **2006**, *15*, 3–17. [CrossRef]
18. Cremer, K.W.; Borough, C.J.; McKinnell, F.H.; Carter, P.R. Effects of stocking and thinning on wind damage in plantations. *New Zeal. J. For. Sci.* **1982**, *12*, 244–268.
19. Wonn, H.T.; O'Hara, K.L. Height: Diameter ratios and stability relationships for four northern Rocky Mountain tree species. *West. J. Appl. For.* **2001**, *16*, 87–94. [CrossRef]
20. Waring, R.H.; Thies, W.G.; Muscato, D. Stem growth per unit of leaf area: A measure of tree vigor. *For. Sci.* **1980**, *26*, 112–117.
21. Crotteau, J.S.; Keyes, C.R.; Hood, S.M.; Larson, A.J. Vegetation dynamics following compound disturbance in a dry pine forest: Fuel treatment then bark beetle outbreak. *Ecol. Appl.* **2020**, *30*, 1–19. [CrossRef]
22. Harrod, R.J.; Povak, N.A.; Peterson, D.W. Comparing the effectiveness of thinning and prescribed fire for modifying structure in dry coniferous forests. In *Proceedings of the The fire Environment—Innovations, Management, and Policy, Destin, FL, USA, 26–30 March 2007*; Proceedings RMRS-P-46CD; Butler, B.W., Cook, W., Eds.; USDA Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2007; pp. 329–346.
23. Youngblood, A. Thinning and burning in dry coniferous forests of the western united states: Effectiveness in altering diameter distributions. *For. Sci.* **2010**, *56*, 46–59.
24. Fiedler, C.E.; Metlen, K.L.; Dodson, E.K. Restoration treatment effects on stand structure, tree growth, and fire hazard in a ponderosa pine/Douglas-fir forest in Montana. *For. Sci.* **2010**, *56*, 18–31.
25. Hood, S.M.; Baker, S.; Sala, A. Fortifying the forest: Thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. *Ecol. Appl.* **2016**, *26*, 1984–2000. [CrossRef] [PubMed]
26. Van Wagner, C.E. Conditions for the start and spread of crown fire. *Can. J. For. Res.* **1977**, *7*, 23–34. [CrossRef]
27. Waring, R.H.; Running, S.W. *Forest Ecosystems: Analysis at Multiple Scales*, 3rd ed.; Elsevier Inc.: Burlington, MA, USA, 2007.
28. Affleck, D.; Keyes, C.; Goodburn, J. Conifer crown fuel modeling: Current limits and potential for improvement. *West. J. Appl. For.* **2012**, *27*, 165–169. [CrossRef]
29. Pfister, R.D.; Kovalchik, B.L.; Arno, S.F.; Presby, R.C. *Forest Habitat Types of Montana*; General Technical Report INT-GTR-34; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1977; 174p.
30. Nimlos, T.J. *Soils of Lubrecht Experimental Forest*; Montana Forest and Conservation Experiment Station, Miscellaneous Publication No. 44: Missoula, MT, USA, 1986; 36p.
31. PRISM Climate Group, Oregon State University. Available online: http://prism.oregonstate.edu (accessed on 4 February 2004).

32. Grissino-Mayer, H.D.; Gentry, C.M.; Croy, S.Q.; Hiatt, J.; Osborne, B.; Stan, A.; DeWeese Wight, G. *Fire History of Western Montana Forested Landscapes via Tree-Ting Analyses*; Indiana State University, Department of Geography, Geology, and Anthropology, Professional Paper Series 23: Terre Haute, IN, USA, 2006; pp. 47–56.
33. McIver, J.D.; Weatherspoon, C.P. On conducting a multisite, multidisciplinary forestry research project: Lessons from the national Fire and Fire Surrogate study. *For. Sci.* **2010**, *56*, 4–17.
34. McIver, J.; Erickson, K.; Youngblood, A. *Principal Short-Term Findings of the National Fire and Fire Surrogate Study*; General Technical Report PNW-GTR-860; PNW-GTR-860; USDA Forest Service Pacific Northwest Research Station: Portland, OR, USA, 2012; 210p.
35. Metlen, K.L.; Fiedler, C.E. Restoration treatment effects on the understory of ponderosa pine/Douglas-fir forests in western Montana, USA. *For. Ecol. Manag.* **2006**, *222*, 355–369. [CrossRef]
36. Shmida, A. Whittaker's plant diversity sampling method. *Isr. J. Bot.* **1984**, *33*, 41–46.
37. USDA Forest Service, Forest Inventory and Analysis National Program, FIA National Core Field Guide, Volume I: Field Data Collection Procedures for Phase 2 Plots 2020; Version 9.0. Available online: https://www.fia.fs.fed.us/library/field-guides-methods-proc/ (accessed on 20 May 2020).
38. Reineke, L.H. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* **1933**, *46*, 627–638.
39. Long, J.N.; Shaw, J.D. A density management diagram for even-aged ponderosa pine stands. *West. J. Appl. For.* **2005**, *20*, 205–215. [CrossRef]
40. Larsson, S.; Oren, R.; Waring, R.H.; Barrett, J.W. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *For. Sci.* **1983**, *29*, 395–402.
41. Mitchell, R.G.; Waring, R.H.; Pitman, G.B. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *For. Sci.* **1983**, *29*, 204–211. [CrossRef]
42. Faurot, J.L. *Estimating Merchantable Volume and Stem Residue in Four Timber Species: Ponderosa Pine, Lodgepole Pine, Western Larch, Douglas-Fir*; Research Paper INT-196; USDA Forest Service Intermountain Research Station: Ogden, UT, USA, 1977; 55p.
43. Sala, A.; Carey, E.V.; Callaway, R.M. Dwarf mistletoe affects whole-tree water relations of Douglas fir and western larch primarily through changes in leaf to sapwood ratios. *Oecologia* **2001**, *126*, 42–52. [CrossRef] [PubMed]
44. McLeod, S.D.; Running, S.W. Comparing site quality indices and productivity in ponderosa pine stands of western Montana. *Can. J. For. Res.* **1988**, *18*, 346–352. [CrossRef]
45. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Vienna, Austria. 2018. Available online: https://www.R-project.org (accessed on 31 December 2018).
46. Pinheiro, J.; Bates, D.; DebRoy, S.; R Core Team. *Nlme: Linear and Nonlinear Mixed Effects Models*, R package version 3.1-128; 2016. Available online: https://CRAN.R-project.org/package=nlme (accessed on 31 December 2016).
47. Nakagawa, S.; Schielzeth, H. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **2013**, *4*, 133–142. [CrossRef]
48. Crotteau, J.S.; Keyes, C.R.; Hood, S.M.; Affleck, D.L.R.; Sala, A. Fuel dynamics after a bark beetle outbreak impacts experimental fuel treatments. *Fire Ecol.* **2018**, *14*, 13. [CrossRef]
49. Ryan, K.C.; Reinhardt, E.D. Predicting postfire mortality of seven western conifers. *Can. J. For. Res.* **1988**, *18*, 1291–1297. [CrossRef]
50. Pausas, J.G. Bark thickness and fire regime. *Funct. Ecol.* **2015**, *29*, 315–327. [CrossRef]
51. Peltola, H.M. Mechanical stability of trees under static loads. *Am. J. Bot.* **2006**, *93*, 1501–1511. [CrossRef] [PubMed]
52. Langsæter, A. Om tynning i enaldret gran-og furuskog. *Meddelelser fra Det Nor. Skogforsøksves.* **1941**, *8*, 131–216.
53. Oliver, C.D.; Larson, B.C. *Forest Stand Dynamics*; John Wiley & Sons, Inc.: New York, NY, USA, 1996.
54. Marshall, D.D.; Curtis, R.O. *Levels-of-Growing-Stock Cooperative Study in Douglas-Fir: Report No. 15-Hoskins: 1963–1998*; Research Paper PNW-RP-537; USDA Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 2002; 80p.
55. Fajardo, A.; Graham, J.M.; Goodburn, J.M.; Fiedler, C.E. Ten-year responses of ponderosa pine growth, vigor, and recruitment to restoration treatments in the Bitterroot Mountains, Montana, USA. *For. Ecol. Manag.* **2007**, *243*, 50–60. [CrossRef]

56. McDowell, N.G.; Adams, H.D.; Bailey, J.D.; Kolb, T.E. The role of stand density on growth efficiency, leaf area index, and resin flow in southwestern ponderosa pine forests. *Can. J. For. Res.* **2007**, *37*, 343–355. [CrossRef]
57. O'Hara, K.L. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. *Can. J. For. Res.* **1988**, *18*, 859–866. [CrossRef]
58. Breda, N.; Granier, A.; Aussenac, G. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiol.* **1995**, *15*, 295–306. [CrossRef] [PubMed]
59. Kolb, T.E.; Holmberg, K.M.; Wagner, M.R.; Stone, J.E. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. *Tree Physiol.* **1998**, *18*, 375–381. [CrossRef] [PubMed]
60. Dunning, D. Relation of crown size and character to rate of growth and response to cutting in western yellow pine. *J. For.* **1922**, *20*, 379–389.
61. Keen, F.P. Ponderosa pine tree classes redefined. *J. For.* **1943**, *41*, 249–253.
62. Kramer, H. Crown development in conifer stands in Scotland as influenced by initial spacing and subsequent thinning treatment. *Forestry* **1966**, *39*, 40–58. [CrossRef]
63. Siemon, G.R.; Wood, G.B.; Forrest, W.G. Effects of thinning on crown structure in radiata pine. *New Zeal. J. For. Sci.* **1976**, *6*, 57–66.
64. Jain, T.B.; Battaglia, M.A.; Han, H.-S.; Graham, R.T.; Keyes, C.R.; Fried, J.S.; Sandquist, J.E. *A Comprehensive Guide to Fuel Management Practices for Dry Mixed Conifer Forests in the Northwestern United States*; General Technical Report RMRS-GTR-292; USDA Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2012; 331p.
65. Esseen, P.A.; Renhorn, K.E.; Pettersson, R.B. Epiphytic lichen biomass in managed and old-growth boreal forests: Effect of branch quality. *Ecol. Appl.* **1996**, *6*, 228–238. [CrossRef]
66. Boeker, E.L.; Scott, V.E. Roost Tree Characteristics for Merriam's Turkey. *J. Wildl. Manag.* **1969**, *33*, 121–124. [CrossRef]
67. Hagar, J.C. *Key Elements of Stand Structure for Wildlife in Production Forests West of the Cascade Mountains*; General Technical Report PNW-GTR-695; Harrington, T.B., Nicholas, G.E., Eds.; USDA Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 2007; pp. 35–48.
68. Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; Sollins, P.; Gregory, S.V.; Lattin, J.D.; Anderson, N.H.; Cline, S.P.; Aumen, N.G.; Sedell, J.R.; et al. Ecology of Coarse Woody Debris in Temperate Ecosystems. In *Advances in Ecological Research*; MacFadyen, A., Ford, E.D., Eds.; Elsevier Ltd.: Amsterdam, The Netherlands, 1986; Volume 34, pp. 133–302. ISBN 0120139340.
69. Franklin, J.F.; Spies, T.A.; Van Pelt, R.; Carey, A.B.; Thornburgh, D.A.; Berg, D.R.; Lindenmayer, D.B.; Harmon, M.E.; Keeton, W.S.; Shaw, D.C.; et al. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag.* **2002**, *155*, 399–423. [CrossRef]
70. Greene, D.F.; Johnson, E.A. Estimating the Mean Annual Seed Production of Trees. *Ecology* **1994**, *75*, 642–647. [CrossRef]
71. Krannitz, P.G.; Duralia, T.E. Cone and seed production in Pinus ponderosa: A review. *West. North Am. Nat.* **2004**, *64*, 208–218.
72. Fowells, H.A.; Schubert, G.H. *Seed Crops of Forest Trees in the Pine Region of California*; US Department of Agriculture, Technical Bulletin No. 1150: Washington, DC, USA, 1956.
73. Keyes, C.R. Thinning promotes the restoration of branch structure in second-growth redwoods at Redwood National Park. *Ecol. Restor.* **2011**, *29*, 325–327. [CrossRef]
74. Nyland, R.D. *Silviculture: Concepts and Applications*, 3rd ed.; Waveland Press: Long Grove, IL, USA, 2016.
75. Maguire, D.; Kershaw, J.; Hann, D. Predicting the effects of silvicultural regime on branch size and crown wood core in Douglas-Fir. *For. Sci.* **1991**, *37*, 1409–1428.
76. Drew, T.J.; Flewelling, J.W. Stand density management: An alternative approach and its application to Douglas-fir plantations. *For. Sci.* **1979**, *25*, 518–532.
77. Schwilk, D.W.; Keeley, J.E.; Knapp, E.E.; McIver, J.D.; Bailey, J.D.; Fettig, C.J.; Fiedler, C.E.; Harrod, R.J.; Moghaddas, J.J.; Outcalt, K.W.; et al. The national Fire and Fire Surrogate study: Effects of fuel reduction methods on forest vegetation structure and fuels. *Ecol. Appl.* **2009**, *19*, 285–304. [CrossRef]
78. Gundale, M.J.; Metlen, K.L.; Fiedler, C.E.; DeLuca, T.H. Nitrogen spatial heterogeneity influences diversity following restoration in a ponderosa pine forest, Montana. *Ecol. Appl.* **2006**, *16*, 479–489. [CrossRef]

79. Ganzlin, P.W.; Gundale, M.J.; Becknell, R.E.; Cleveland, C.C. Forest restoration treatments have subtle long-term effects on soil C and N cycling in mixed conifer forests. *Ecol. Appl.* **2016**, *26*, 1503–1516. [CrossRef]
80. Skinner, C.N. 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, OR, USA, 18–21 October 2004*; Ritchie, M.W., Maguire, D.A., Youngblood, A., Eds.; USDA Forest Service, Pacific Southwest Forest and Range Experiment Station: Albany, CA, USA, 2005; pp. 245–257.
81. Stephens, S.L.; Moghaddas, J.J. Silvicultural and reserve impacts on potential fire behavior and forest conservation: Twenty-five years of experience from Sierra Nevada mixed conifer forests. *Biol. Conserv.* **2005**, *125*, 369–379. [CrossRef]
82. Stephens, S.L.; Moghaddas, J.J.; Edminster, C.B.; Fiedler, C.E.; Haase, S.M.; Harrington, M.G.; Keeley, J.E.; Knapp, E.E.; McIver, J.D.; Metlen, K.L.; et al. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. *Ecol. Appl.* **2009**, *19*, 305–320. [CrossRef] [PubMed]