

Article

Tree Mortality following Thinning and Prescribed Burning in Central Oregon, U.S.

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Abstract: We examined causes and levels of tree mortality one year after thinning and prescribed burning was completed in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests at Pringle Falls Experimental Forest, Oregon, U.S. Four blocks of five experimental units ($N = 20$) were established. One of each of five treatments was assigned to each experimental unit in each block. Treatments included thinning from below to the upper management zone (UMZ) for the dominant plant association based on stand density index values for ponderosa pine followed by mastication and prescribed burning: (1) 50% UMZ (low density stand), (2) 75% UMZ (medium density stand), (3) 75% UMZ Gap, which involved a regeneration cut, (4) 100% UMZ (high density stand), and (5) an untreated control (high density stand). Experimental units were thinned in 2011 (block 4), 2012 (block 2), and 2013 (blocks 1 and 3); masticated within one year; and prescribed burned two years after thinning (2013–2015). A total of 395,053 trees was inventoried, of which 1.1% (4436) died. Significantly higher levels of tree mortality occurred on 100 UMZ (3.1%) than the untreated control (0.05%). Mortality was attributed to prescribed fire (2706), several species of bark beetles (Coleoptera: Curculionidae) (1592), unknown factors (136), windfall (1 tree), and western gall rust (1 tree). Among bark beetles, tree mortality was attributed to western pine beetle (*Dendroctonus brevicomis* LeConte) (881 trees), pine engraver (*Ips pini* (Say)) (385 trees), fir engraver (*Scolytus ventralis* LeConte) (304 trees), mountain pine beetle (*D. ponderosae* Hopkins) (20 trees), *Ips emarginatus* (LeConte) (1 tree), and *Pityogenes* spp. (1 tree).

Keywords: *Dendroctonus brevicomis*; *Ips pini*; prescribed fire; restoration; *Scolytus ventralis*



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1. Introduction

In a recent review, Achim et al. [1] argue that the science of silviculture must adapt to the reality that many forest ecosystems have been altered significantly by human interventions and climate change. As such, they question the utility of older studies to inform contemporary forest management, and highlight the need for innovative studies at appropriate scales where a range of silvicultural treatments are tested [1]. Many low to mid-elevation (e.g., <2500 m) forests in the Pacific Northwest, U.S. are fire-adapted as wildfire is an integral and predictable part of their ecological functioning [2]. Compared to their historical counterparts, many of these forests have increased tree densities, heavy accumulations of surface fuels, dense forest canopies, increased fuel continuities, and are dominated by more shade-tolerant and fire-intolerant tree species [3]. Wildfire suppression and exclusion, domestic livestock grazing, and selective cutting of large-diameter, fire-tolerant tree species, such as ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), have contributed to the development of these conditions. These changes complicate management of these forests and increase the probability of high-severity wildfire. At the same time, climate change is increasing the number of large wildfires, the length of the wildfire season, and the cumulative area burned in the western U.S. [4], with concomitant increases

in fire suppression costs and risks to homes and other infrastructure [5]. In response, management actions have focused on reducing fire-sensitive vegetation; diversifying tree age-class structure; and reducing surface, ladder, and canopy fuels [6].

A combination of mechanical thinning and prescribed burning has been effective for managing fuels in western forests. For example, the effectiveness of mechanical thinning followed by prescribed burning for reducing the incidence of passive crown fire is well supported by modeling of predicted fire behaviors (e.g., [7,8]), and by empirical research (e.g., [9]). Furthermore, results from the National Fire and Fire Surrogate Study, the largest study of its kind, indicate that the incidence of active crown fire is best reduced by following mechanical fuel treatments (thinning) with prescribed burning [10]. Similarly, Crotteau et al. [11] concluded that thinning and prescribed burning provide the longest lasting benefit for reducing fuels and fire hazards. As a result, thinning and prescribed burning have been widely promoted in the western U.S. to reduce the intensity and severity of future wildfires in forests that were once dominated by short-interval, low- to moderate-intensity fire regimes.

Bark beetles (Coleoptera: Curculionidae) are important disturbance agents in conifer forests [12] and while trees of all species, ages, and sizes may be colonized and killed by bark beetles each species exhibits unique host preferences, life history traits, and impacts. Some bark beetles cause extensive tree mortality as demonstrated by western pine beetle (*Dendroctonus brevicornis* LeConte) in ponderosa pine forests [13], while others cause only limited amounts of tree mortality that often goes unnoticed. When populations are low, bark beetles create small gaps in the forest canopy by killing trees stressed by age or other factors. During outbreaks, large numbers of trees may be killed over extensive areas impacting many ecosystem goods and services [14]. While thinning and prescribed burning are effective for reducing fuels and fire hazards, these treatments may also affect bark beetles as they influence the health and vigor of residual trees, the size, distribution, and abundance of bark beetle hosts, and the physical environment within forests. For example, post-treatment reductions in tree density may alter microclimates, affecting beetle fecundity and fitness as well as the phenology and voltinism of bark beetles and their predators, parasites and competitors. Reductions in tree density can also disrupt pheromone plumes used for recruiting bark beetles to a host tree [15]. Volatiles released by host and nonhost trees during and after thinning and prescribed burning may influence the behavior of bark beetles [16]. For example, Fettig et al. [17] showed that chipping sub- and unmerchantable ponderosa pines and depositing the chips back into treated stands increased the risk of infestation by several species of bark beetles in the southwestern U.S. The effect was due to host volatiles emanating from the chips, which increased bark beetle attraction to treated areas.

During the last two decades, numerous research efforts have examined the effects of thinning and prescribed burning on levels of tree mortality attributed to bark beetles in the western U.S., which varies depending on the tree species, tree size, tree phenology, degree of fire-caused injuries, initial and postfire levels of tree vigor, the postfire environment, and the scale, severity, and composition of bark beetle populations [18]. An important concern has been that bark beetles may colonize and kill fire-injured trees that otherwise would have survived [19], with most studies demonstrating the majority of delayed mortality attributed to bark beetles occurs the first few years following prescribed fire [18]. The objectives of our study were to determine causes and levels of tree mortality one year after thinning and prescribed burning was completed (prescribed burning occurred 2 years after thinning) in ponderosa pine forests at Pringle Falls Experimental Forest, Oregon, U.S. We hypothesized that higher levels of tree mortality attributed to bark beetles would occur following prescribed burns in treatments that retained higher levels of stand density. Our efforts are part of the “Forest Dynamics After Thinning and Fuel Reduction in Dry Forests” study managed by the Pacific Northwest Research Station, USDA Forest Service and provide important baseline information for others (e.g., silviculturists) working on this study.

2. Materials and Methods

2.1. Study Site

This study was conducted on the Lookout Mountain Unit of Pringle Falls Experimental Forest on the Deschutes National Forest (43°42' N, 121°37' W), which lies on an ancient shield volcano. Prior to our study, this forest had undergone little major disturbance since ~1845 when a stand-replacement wildfire occurred. Stands of ponderosa pine occur at lower elevations (up to ~1600 m), and of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Douglas ex D. Don) Lindley), white fir (*Abies concolor* (Gord. and Glend.) Hildebr.), sugar pine (*Pinus lambertiana* Dougl.), western white pine (*Pinus monticola* Dougl. ex D. Don), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) at higher elevations. Four blocks with similar plant associations were delineated for purposes of this study. Five experimental units (originally ranging from ~24 to 155 ha) were established in each block but later adjusted to account for detection of northern spotted owls (*Strix occidentalis caurina* (Merriam)) [20,21]. This also resulted in loss of one experimental unit in block 1 (75 UMZ Gap, below). The northern spotted owl is listed under the U.S. Endangered Species Act as a threatened species in Washington, Oregon, and California, U.S.

2.2. Treatments

One of each of five treatments was assigned to each experimental unit in each block. Treatments included:

- (1) Fifty (50) UMZ (low density stand): Thinned from below to 50% of the upper management zone (UMZ) for the dominant plant association based on stand density index (SDI) values for ponderosa pine. Stand density was reduced by removing trees from the subdominant crown classes to improve residual tree growth and tree vigor. Thinning was followed by mastication and prescribed burning;
- (2) Seventy-five (75) UMZ (medium density stand): Thinned from below to 75% of the UMZ followed by mastication and prescribed burning;
- (3) Seventy-five (75) UMZ Gap: A regeneration cut applied to 75% of the UMZ followed by mastication and prescribed burning. Small gaps in the canopy (~0.1 ha) were created by augmenting existing gaps or creating new gaps;
- (4) One hundred (100) UMZ (high density stand): Thinned from below to 100% of the UMZ followed by mastication and prescribed burning;
- (5) Untreated control (high density stand): No manipulation.

Thinning was conducted in 2011 (block 4, 9.5 million bf (~22,400 m³)), 2012 (block 2, 12.8 million bf (~30,200 m³)), and 2013 (blocks 1 and 3, 13 million bf (~30,700 m³) and 15 million bf (~35,400 m³), respectively). Leave trees were selected (marked) based on fire tolerance and historical tree species compositions. Lodgepole pine (*Pinus contorta* Dougl.), grand fir, white fir, and small-diameter ponderosa pine were preferentially harvested [21]. Mastication was used to reduce ladder fuels (primarily small conifers, shrubs, and slash) within a year of thinning and before prescribed burning. Slash <22.9 cm in diameter on the large end and >0.9 m long was removed, mulched, chopped, lopped, or piled. Slash >22.9 cm on the small end was left in place unless it was within 3 m of a designated leave tree. Prescribed burning required individual burn plans to be developed for each experimental unit to account for differences in fuel accumulations and other factors. Burns were applied in 2013 (block 4), 2014 (block 2), and 2015 (blocks 1 and 3) and included backing and strip head fires applied in spring (April–June, to reduce fire intensity) except for in experimental unit 12. A portion of experimental unit 12 (~50%) had heavy ground and surface fuels [21] and was burned during fall to allow time for these fuels to cure. Burns were applied to achieve 50–100% reduction of 1- and 10-h surface fuels, 25–100% reduction of shrubs, and <50% crown scorch. We refer the reader to [20,21] for more information concerning treatments and their effects on forest structure and composition. Sherman and Anderson [21] provide detailed maps of the study area.

2.3. Data Collection

A 100% cruise (census) was conducted on each experimental unit in late summer and fall in 2014 (block 4), 2015 (block 2), and 2016 (blocks 1 and 3) to locate recently killed trees based on crown fade. All recently killed trees ≥ 10.2 cm dbh (diameter at 1.37 m in height) were tallied, geo-referenced, and the species, dbh, burn severity ranking (below), and cause of death were recorded. Samples of bark ~ 625 cm² were removed from these trees with a hatchet at ~ 2 m in height on at least two aspects to determine if any bark beetle galleries were present. The shape of galleries is used to distinguish bark beetle species [12]. In some cases, deceased bark beetles were found beneath the bark and used to validate identifications based on galleries. Bark removal also served as a means of marking trees that were tallied during our evaluations.

We attributed tree mortality to mountain pine beetle (*Dendroctonus ponderosae* Hopkins), western pine beetle, and fir engraver (*Scolytus ventralis* LeConte) when evidence of colonization was found despite evidence of other bark beetle species in the same tree. Mortality was only attributed to pine engraver (*Ips pini* (Say)) if evidence of colonization was found and evidence of colonization by mountain pine beetle and western pine beetle was absent. Mortality was only attributed to bark beetles when burn severity rankings on individual trees were ≤ 3 (i.e., prescribed fire did not directly kill the tree based on external measures of fire severity) [22,23]. Mortality was attributed to prescribed burns when evidence of bark beetles or other contributing factors was absent and the lower bole had evidence of substantial charring on all sides [22,23]. While red turpentine beetle (*Dendroctonus valens* LeConte) attacks are usually not considered a significant threat to tree health [24], we recorded the number of red turpentine beetle attacks (pitch tubes) on each dead tree. On occasion, other bark beetle genera (e.g., *Hylastes*) were found colonizing trees, but were not considered important tree-killing species [12] and were ignored. Mortality of trees for which no causal agent(s) could be identified was recorded as unknown.

2.4. Analyses

Proportions of trees killed were analyzed using generalized linear mixed effects models with a beta-binomial distribution and a logit link to handle overdispersion and discrete tree counts with a binomial outcome [25,26]. Fit was assessed with residual plots and model selections were informed by AIC values [27]. Treatment and dbh class (10.2–20.3, 20.4–30.5, 30.6–40.6, 40.7–50.8, and >50.8 cm) were fixed effects and block was a random effect. We analyzed several combinations of mortality (i.e., all causes, prescribed fire, bark beetles and individual bark beetle species) and tree groupings (all trees and specific bark beetle hosts). When applicable, differences in mean proportions were analyzed using a post hoc, least square means test with the Tukey's HSD correction. Relationships between quadratic mean diameter (QMD, cm), trees/ha, basal area (m²/ha), and stand density index (SDI), and levels of tree mortality were analyzed using Spearman's Rank correlation test, a non-parametric measure of rank correlation. Analyses were conducted using glmmTMB, DHARMA, emmeans, and stats packages with R Statistical Software (version 3.4.4) via RStudio (version 1.2.1335) [28].

3. Results and Discussion

3.1. Overall Tree Mortality

A total of 395,053 trees was inventoried across all experimental units, including ponderosa pine (300,417), grand fir (53,663), lodgepole pine (35,661), western white pine (3403), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (834), western hemlock (585), Douglas fir (354), sugar pine (84), and white fir (52). Of these, 1.1% (4436) died. Tree mortality was attributed to prescribed fire (2706), several species of bark beetles (1592), unknown factors (136), windfall (1 tree) and western gall rust caused by the fungus *Peridermium harknessii* J. P. Moore (1 tree). Tree size (dbh) had no effect on levels of tree mortality ($p = 0.13$); however, a positive correlation was found between QMD and the percentage of trees killed ($\rho = 0.493$; $n = 19$, $p = 0.03$). Higher levels of tree mortality

occurred on 100 UMZ than the untreated control ($\chi^2 = 13.9$, $df = 4$, $p = 0.008$). No other significant differences were observed (Figure 1). No significant correlations were found between measures of stand density (trees/ha, basal area, and SDI) and the percentage of trees killed ($p > 0.30$, all cases). Only 1.1% of overall tree mortality (48 trees) occurred in the untreated control; however, with time this percentage should increase as higher levels of tree mortality are likely to manifest compared to other treatments due to the high stand densities that remain in the untreated control [21].

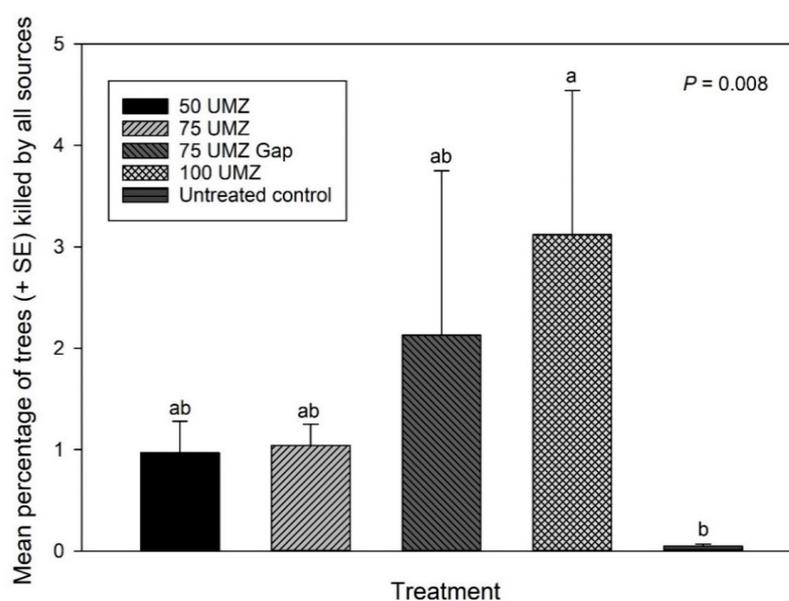


Figure 1. Mean percentage (+SE) of trees killed by all causes following thinning and prescribed burning at Pringle Falls Experimental Forest, Oregon. Means (+SE) followed by the same letter are not significantly different ($p > 0.05$).

3.2. Prescribed Fire-Caused Tree Mortality

Following prescribed fire, tree mortality may be immediate due to heating and consumption of living tissues or it may be delayed [29,30]. The largest source of tree mortality (2706 trees) in our study was prescribed fire. Tree size had no effect on levels of tree mortality attributed to prescribed fire ($p = 0.22$), which is surprising given larger trees tend to be more fire resistant [6]. Higher levels of tree mortality were attributed to prescribed fire on 100 UMZ than 75 UMZ ($\chi^2 = 13.6$, $df = 3$, $p = 0.004$). No other significant differences were observed (Figure 2). No correlations were found between measures of stand density, and the percentage of trees killed by prescribed fire ($p > 0.33$, all cases).

3.3. Bark Beetle-Caused Tree Mortality

Several species of bark beetles were found colonizing and killing trees (1592 trees), including western pine beetle (881 trees), pine engraver (385 trees), and fir engraver (304 trees) which caused enough mortality (>150 trees) to warrant statistical analyses. Mortality was also attributed to mountain pine beetle (20 trees), *Ips emarginatus* (LeConte) (1 tree), and *Pityogenes* spp. (1 tree). All of these species are native to Oregon. Levels of bark beetle-caused tree mortality were low (0.4%, 1592 trees). Tree size (dbh) had a significant effect on tree mortality ($\chi^2 = 11.3$, $df = 4$, $p = 0.02$), with higher levels observed in dbh class 3 than dbh class 1 (1.2 ± 0.4 and $0.3 \pm 0.1\%$, respectively; mean \pm SE). No other significant differences were observed among dbh classes. A significant positive correlation was found between QMD and the percentage of trees killed by bark beetles ($\rho = 0.65$, $n = 19$, $p = 0.002$). Lower levels of bark beetle-caused tree mortality were observed in the untreated control than any other treatment ($\chi^2 = 38.1$, $df = 4$, $p < 0.001$). No other significant differences were observed (Figure 3).

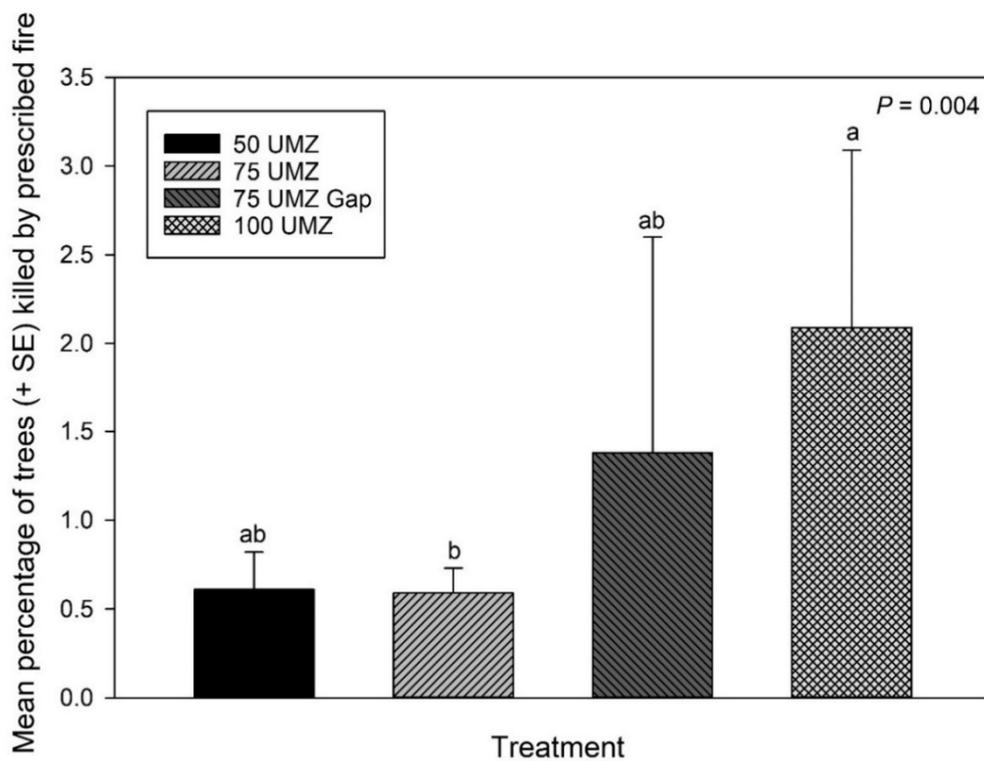


Figure 2. Mean percentage (+SE) of trees killed by prescribed fire following thinning and prescribed burning at Pringle Falls Experimental Forest, Oregon. Means (+SE) followed by the same letter are not significantly different ($p > 0.05$).

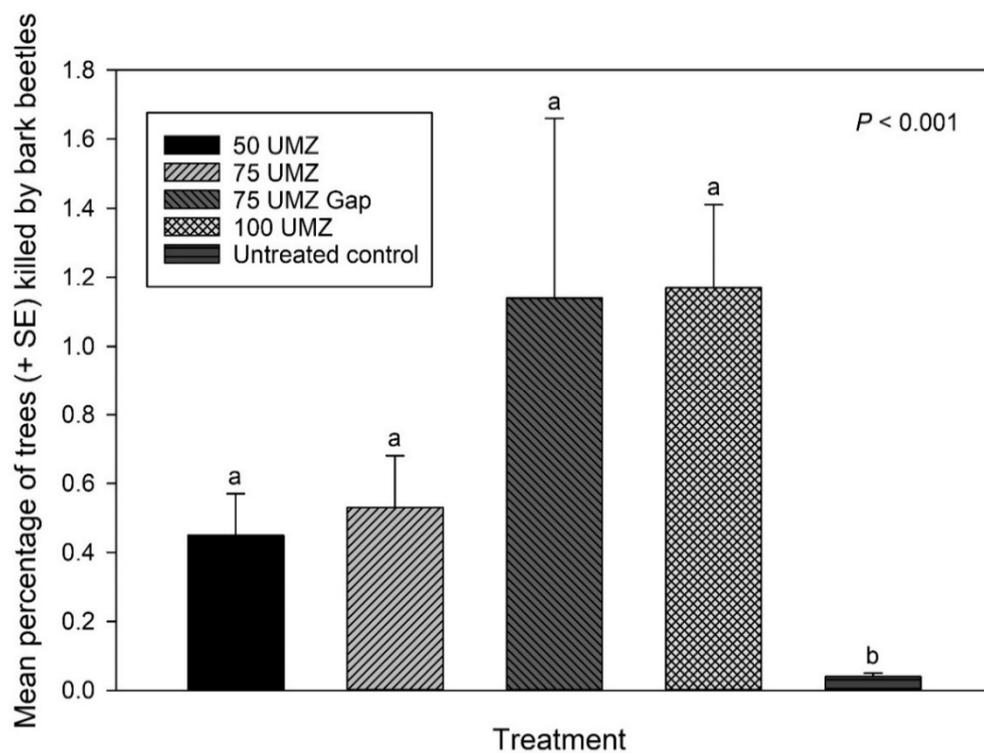


Figure 3. Mean percentage (+SE) of trees killed by bark beetles (all bark beetle species) following thinning and prescribed burning at Pringle Falls Experimental Forest, Oregon. Means (+SE) followed by the same letter are not significantly different ($p > 0.05$).

Fettig and McKelvey [31] reported that 5.6% of trees were killed by bark beetles during a 10-year period following thinning and prescribed burning at Blacks Mountain Experimental Forest, California. In their study, mortality was concentrated on burned-split plots and within the two smallest-diameter classes (19–29.2 and 29.3–39.3 cm dbh). Mortality was highest during the second sample period (3–5 years after prescribed burns) [31]. Westlind and Kerns [32] studied the effects of fuel reduction treatments near Burns, Oregon. Each stand contained an unburned control and four season-by-burn interval treatments. Overall tree mortality was low, only surpassing 2 trees/ha during regional outbreaks of pine butterfly (*Neophasia menapia* C. and R. Felder) and western pine beetle. In a recent review of related research, Fettig et al. [18] concluded that concerns of large increases in bark beetle-caused tree mortality following prescribed burns have been unfounded in most studies. Furthermore, they suggested that one might view the associated increases in bark beetle-caused tree mortality as short-term losses suffered for long-term gains, which agrees with Westlind and Kerns [32]. Of note, Hood et al. [33] demonstrated that low-severity fire increases ponderosa pine defenses against bark beetle attacks by inducing resin duct production, and that resin duct production declines when fire ceases.

3.4. Western Pine Beetle

Western pine beetle causes significant mortality of ponderosa pine throughout much of the western U.S. The only other primary host is Coulter pine (*P. coulteri* D. Don), a species indigenous to the Transverse and Peninsular Ranges of Southern California [34]. Among bark beetles, western pine beetle killed the most trees in our study, but levels were low (Figure 4). Tree size had a significant effect on tree mortality ($\chi^2 = 18.9$, $df = 4$, $p < 0.001$), with higher levels observed in dbh classes 2–5 (range = 0.32–0.89% in class 2 and 3, respectively) than dbh class 1 ($0.07 \pm 0.03\%$). No other significant differences were observed among dbh classes. A positive correlation was found between QMD and the percentage of ponderosa pines killed by western pine beetle ($\rho = 0.463$; $n = 19$, $p = 0.047$). These results are consistent with the beetle's preference for colonizing large-diameter ponderosa pines [34]. In a study conducted on the Tahoe National Forest, California higher levels of tree mortality (all sources) were observed following spring and fall burns compared to the untreated control; however, no significant difference was observed between burn treatments [35]. Most of the large tree (>50.7 cm dbh) mortality occurred following spring burns and was attributed to western pine beetle and mountain pine beetle [35].

Lower levels of tree mortality were attributed to western pine beetle in the untreated control than any other treatment ($\chi^2 = 31.9$, $df = 4$, $p < 0.001$) (Figure 4). We found no correlation between measures of stand density and the percentage of ponderosa pines killed by western pine beetle ($p > 0.18$, all causes). Western pine beetle caused significant tree mortality following prescribed burns in an old-growth ponderosa pine forest in nearby Crater Lake National Park, Oregon [36], with most of the large tree mortality occurring the year following burns [37]. Similarly, both Davis et al. [19] and Westlind and Kelsey [38] noted that most western pine beetle attacks associated with burning occur shortly after fire.

3.5. Pine Engraver

Pine engraver generally colonizes slash, saplings, and weakened pines. Infestations are often short-lived but may increase in scale and duration when host material is plentiful. Among bark beetles, pine engraver killed the second most trees in our study. Tree size had a significant effect on tree mortality ($\chi^2 = 26.6$, $df = 4$, $p < 0.001$), with higher levels observed in dbh classes 1 and 2 (0.28 ± 0.07 and $0.24 \pm 0.09\%$, respectively) than in dbh classes 4 and 5 (0.05 ± 0.03 and $0.01 \pm 0.01\%$, respectively). These results are consistent with the beetle's preference for colonizing small-diameter pines [39]. Lower tree mortality was observed in the untreated control than any other treatment ($\chi^2 = 36.9$, $df = 4$, $p < 0.001$), and higher levels were observed in 100 UMZ than 75 UMZ (Figure 5). We found significant negative correlations between trees/ha ($\rho = -0.567$, $n = 19$, $p = 0.01$), basal area ($\rho = -0.64$, $n = 19$, $p = 0.003$), and SDI ($\rho = -0.617$, $n = 19$, $p = 0.005$), and the

percentage of pines killed by pine engraver. Fettig and McKelvey [31] reported that few trees were killed by engraver beetles following thinning and prescribed burning at Blacks Mountain Experimental Forest (0.3%), and that activity was limited to the first sample period (1–2 years following prescribed burns).

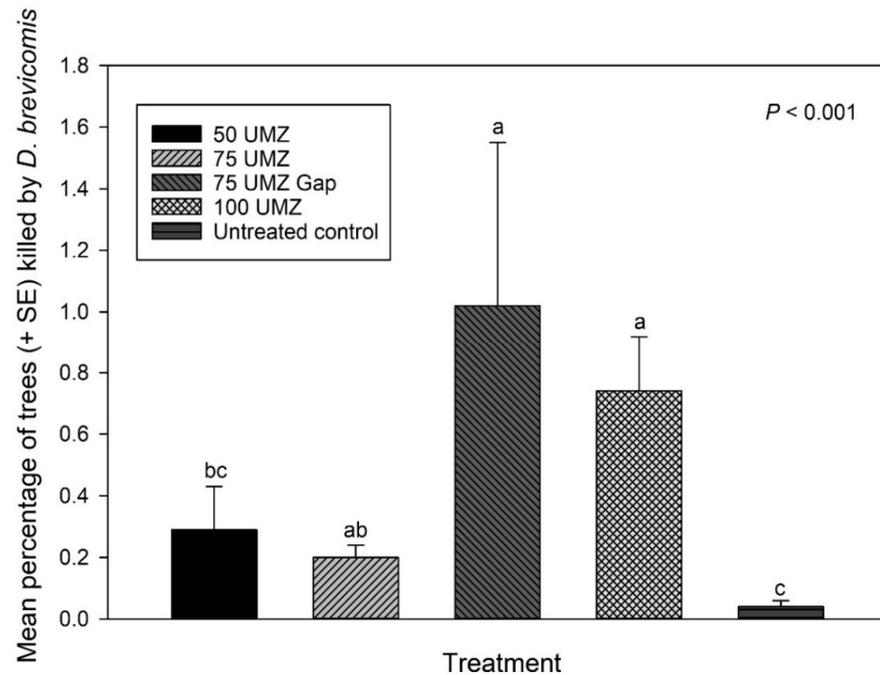


Figure 4. Mean percentage (+SE) of ponderosa pine (*Pinus ponderosa*) killed by western pine beetle (*Dendroctonus brevicornis*) following thinning and prescribed burning at Pringle Falls Experimental Forest, Oregon. Means (+SE) followed by the same letter are not significantly different ($p > 0.05$).

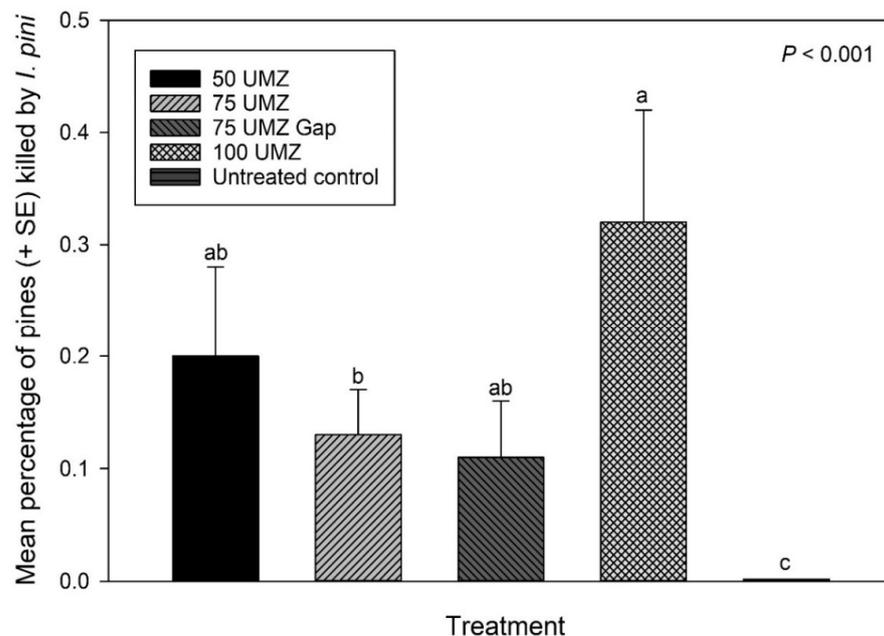


Figure 5. Mean percentage of pines (including ponderosa pine (*Pinus ponderosa*), lodgepole pines (*P. contorta*) and western white pines (*P. monticola*)) killed by pine engraver (*Ips pini*) following thinning and prescribed burning at Pringle Falls Experimental Forest, Oregon. Means (+SE) followed by the same letter are not significantly different ($p > 0.05$).

3.6. Fir Engraver

Fir engraver colonizes several species of fir, but outbreaks are typically associated with trees stressed by drought, defoliation, root pathogens, and other factors [40]. Large numbers of firs may be killed by fir engraver following prescribed burns, particularly in the smaller-diameter classes [41]. Among bark beetles, fir engraver killed the third most trees in our study. Mortality ranged from $0.3 \pm 0.2\%$ in the untreated control to $2.3 \pm 0.6\%$ in 100 UMZ. Our efforts to analyze fir mortality failed, likely as a result of too few trees killed by fir engraver spread across the experimental units and/or blocks, despite efforts to correct for zeros with a zero-inflated term. Significant positive correlations were found between basal area ($\rho = 0.471$, $n = 19$, $p = 0.04$) and SDI ($\rho = 0.482$, $n = 19$, $p = 0.04$), and the percentage of firs killed by fir engraver. Filip et al. [42] examined causes of tree mortality following mixed-severity wildfire in Oregon and reported ~20% of firs were killed by fir engraver two years after the fire.

3.7. Red Turpentine Beetle

Red turpentine beetle attacks are usually confined to the base of weakened or dead and dying pines. In our study, 60% of dead trees (2682 of 4436 trees) were attacked by red turpentine beetle, of which only nine occurred in the untreated control. While we did not attribute tree mortality to red turpentine beetle, six ponderosa pines had ≥ 200 attacks (maximum = 230), and 155 ponderosa pines and one western white pine had ≥ 100 attacks. All occurred on experimental units that were thinned and burned. Similarly, at Blacks Mountain Experimental Forest most trees (96%) with high levels of red turpentine beetle attacks occurred on burned split plots [22]. Westlind and Kelsey [38] examined 7343 ponderosa pines following prescribed burns and wildfires in Oregon and Washington. They reported that most red turpentine beetle attacks occurred the first year following fire.

3.8. Stand Density

As discussed above, we found no correlations, significant negative correlations, and significant positive correlations between measures of stand density and the percentage of trees killed by western pine beetle, pine engraver, and fir engraver, respectively. Fettig et al. [43] reviewed tree and stand factors associated with bark beetle infestations in the western U.S. In short, they described the benefits of thinning in reducing stand susceptibility to bark beetles as manifested through reductions in stand density that affect microclimate, inter-tree spacing and tree vigor. Microclimate affects beetle survival, fitness and fecundity, among other factors, but notably reductions in tree density often result in increased wind speeds and turbulences within stands that disrupt pheromone plumes [15]. This reduces tree colonization rates as large numbers (hundreds to thousands) of beetles are required to mass attack a host tree and overwhelm its defenses, which for most tree-killing species is facilitated by aggregation pheromones. Killing groups of trees is fundamental to growth of bark beetle infestations (e.g., [44]), and as inter-tree spacing increases the probability of successful host colonization decreases. However, in ponderosa pine the importance of increases in tree vigor following thinning have been most heavily emphasized [45]. Notably, our results reflect the short-term (3 years after thinning and 1 year after prescribed burning) effects of thinning and prescribed burning on stand susceptibility to bark beetles (e.g., primarily due to release of attractive tree volatiles during and after treatments, increased stress due to fire-related injuries and changes in microclimate); and not the effects of changes in stand structure and composition (e.g., due to increases in tree vigor associated with increased growing space), which take longer to fully manifest [43].

4. Conclusions

In this study, most tree mortality was attributed to prescribed fire (61%). Fuel reduction goals were met [21] and initial concerns regarding high levels of bark beetle-caused tree mortality following spring burns (as reported in some studies, e.g., [46]) were unfounded. This is encouraging as the need to increase the pace and scale of thinning and prescribed

burning is paramount in many forests in the western U.S. [47]. To address this, managers increasingly rely on conducting burns whenever suitable conditions exist, such as during spring when atmospheric conditions and fuel moistures tend to be favorable even though historically most wildfires occurred in late summer and early fall. Further evaluations of these treatments are necessary to facilitate a better understanding of the effects of thinning and prescribed burning on resistance and resilience to bark beetles and other disturbances at Pringle Falls Experimental Forest. Given climate change, this is of utmost importance [1,48].

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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