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Long-term sensitivity of ponderosa pine axial resin ducts to harvesting and prescribed burning

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ABSTRACT

Forest restoration treatments primarily aimed at reducing fuel load and preventing high-severity wildfires can also influence resilience to other disturbances. Many pine forests in temperate regions are subject to tree-killing bark beetle outbreaks (e.g., *Dendroctonus*, *Ips*), whose frequency and intensity are expected to increase with future climatic changes. Restoration treatments have the potential to increase resistance to bark beetle attacks, yet the underlying mechanisms of this response are still unclear. While the effect of forest restoration treatments on tree growth has been studied, less is known about their impact on resin-based defenses. We measured axial resin ducts in the earlywood and latewood of ponderosa pines (*Pinus ponderosa*) in western Montana, USA, 20 years before and after the implementation of restoration treatments, with the aim to elucidate changes in the yearly and interannual investment in resin duct defenses following treatments and their sensitivity to climate. Two experiments were established in 1992: a moderate thinning and a retention shelterwood, with 35 % and 57 % basal area reduction, respectively. Each experiment comprised four treatments with three replicates per treatment: cutting only, cutting followed by prescribed burning in either spring or fall or under wet or dry duff moisture conditions, and an untreated control. Cutting treatments stimulated a long-term, sustained increase in resin duct production, more pronounced in the earlywood, which we attribute to a higher availability of resources due to reduced tree density. Prescribed burning following cutting induced a short-term increase in resin ducts, likely aiding in the compartmentalization of fire-killed cambium and enhancing the resistance of fire-injured trees to bark beetle attack. However, the fire-induced spike in duct production was not related to the degree of crown scorch. Treatments had little effect on climate-defense relationships, as ducts remained positively correlated to winter precipitation and, though less significantly, negatively correlated to spring maximum temperature. Our findings show that by reducing stand density, forest restoration treatments induce the synthesis of resin ducts, which are key in mitigating vulnerability of ponderosa pine to mountain pine beetle (*D. ponderosae*) attacks, thus promoting forest resilience to multiple disturbances.

1. Introduction

Forest management treatments, such as cutting and prescribed burning, are often used to increase timber production, reduce fuels and fire hazard, or restore vegetation and fuel structure associated with historical fire regimes. Yet, their benefits are manifold and often extend beyond their initial objectives. By modifying forest structure and enhancing tree vigor, these treatments are key in shaping how trees respond to various disturbances including pest outbreaks, droughts, and wildfires (Sohn et al., 2016; Vilà-Vilardell et al., 2024). Bark beetle

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outbreaks (Coleoptera: Curculionidae, Scolytinae) are the predominant biotic disturbance in conifer forests worldwide and their occurrence is often associated with drought (Gaylord et al., 2013). As drought and bark beetle outbreaks become increasingly prevalent with climate change (Seidl et al., 2017), understanding how tree defense investment, forest structure, and climate are intertwined is essential.

Pine species (*Pinus* spp.) have a network of constitutive and induced resin ducts or canals which remain functional for several years after synthesis. As sites of resin synthesis, storage, and delivery, resin ducts provide conifers a lasting defense mechanism (Hudgins and Franceschi, 2004). Because resin ducts are produced from the vascular cambium as wood develops, they are embedded in the secondary xylem and serve as a retrospective record of the interannual variation of tree defenses, allowing the study of the effect of environmental factors on tree defense investment over time (Vázquez-González et al., 2020b). Resin ducts are produced both in the earlywood and latewood, and their relative proportion is under strong genetic control (Vázquez-González et al., 2020a). Duct density is typically greater in the latewood (Saracino et al., 2017), which is formed later in the growing season when competition for resources with other tree functions is presumably lowest (Herms and Mattson, 1992). Consistently, Rigling et al. (2003) showed that management treatments that ameliorate resource availability stimulate the synthesis of resin ducts in the earlywood. More research is needed to understand the different responses of earlywood and latewood ducts to external stimuli.

While a number of studies have shown the efficacy of resin ducts in providing tree resistance to bark beetle-related mortality (e.g., Ferrenberg et al. 2023, Hood et al. 2015, Kane and Kolb 2010, Sangüesa-Barreda et al. 2015, and Valor et al. 2021), relatively few have focused on how forest treatments and forest structure influence the production of resin ducts and several uncertainties remain. First, reported effects of prescribed burning on the production of resin ducts in pines are inconclusive, with some studies reporting a short-term spike when prescribed burning was implemented in combination with thinning (Bernal et al., 2023) or tapping (Rodríguez-García et al., 2018), while others have found no significant effect of prescribed burning alone or combined with thinning (Hood et al., 2016) or even a reduction in resin duct size following smoldering fire (Slack et al., 2016). Secondly, reported effects of thinning treatments followed by prescribed burning are also mixed: while Hood et al. (2016) found that thinning, rather than prescribed burning, promoted the production of new resin ducts, Bernal et al. (2023) found that thinning increased resin duct defenses particularly when followed by prescribed burning. These mixed results could reflect the diverse effects of different cutting intensities, burning seasons, or burning under different moisture conditions on resin duct investment, a topic that remains unexplored.

Understanding the sensitivity of resin ducts to forest management treatments helps to elucidate the underlying mechanism that triggers the synthesis of resin-based defenses and thus, the resistance to beetle-related mortality. For example, a greater investment in resin ducts after prescribed burning would be related to the role of low-intensity fire in stimulating resin-based defenses (Hood et al., 2015), while a greater investment after thinning would be associated with the greater availability of resources due to reduced tree density and competition (Hood et al., 2016). Moreover, the season of burning can affect tree resin defenses (Cannac et al., 2009), either because of the different phenological status of the tree at the time of burning (Valor et al., 2017) or as a result of the fire intensity and crown scorch derived (Wallin et al., 2003).

Climate is an important driver of physiological processes like tree growth and investment in resin defenses (Rigling et al., 2003). Climate influence on resin duct defenses is particularly intricate in water-limited environments, where soil-water availability for physiological processes depends not only on precipitation and temperature patterns (Saracino et al., 2017) but also on forest structure and tree vigor (Tepley et al., 2020). In the context of climate change, disentangling the influence of both forest structure and climate on tree resin defenses is essential for anticipating and predicting future responses.

Here, we use tree ring chronologies to examine the sensitivity of resin duct defenses in ponderosa pine to forest restoration treatments and climate in western Montana, USA. Treatments included two independent cutting experiments with and without subsequent prescribed burning (cut-burn and cut-only, respectively), implemented either in spring or fall or under wet or dry duff moisture conditions. Specifically, we study the interannual (whole tree rings) and intra-annual (earlywood vs. latewood) variation in resin duct production along a 40-year period, covering 20 years before and after the treatments. We seek to answer:

(1) How do the different treatments affect the inter- and intra-annual production of resin duct defenses? We expect to see (H1.1) higher resin duct defenses in treatments relative to control and (H1.2) a relatively higher increase in earlywood than in latewood ducts;
(2) Are resin duct defenses sensitive to prescribed burning? (H2.1) We expect a more pronounced response in cut-burn treatments than in cut-only treatments. Further, if the fire effect is mediated via heating stress and fire-caused injury, (H2.2) we expect a greater response in trees with intermediate crown scorch compared to low or no crown scorch;
(3) Do treatments influence the sensitivity of resin ducts to climate? (H3) We expect that treatments will reduce sensitivity of tree resin duct defenses to climate by reducing tree competition that lessens drought stress.

2. Methods

2.1. Study site and treatments

The study took place in the Lick Creek Demonstration-Research Forest, located in the Bitterroot National Forest in southwestern Montana, USA (46º5’N, 114º15’W). The site is a south-facing slope dominated by ponderosa pine (*Pinus ponderosa* var. *ponderosa* Dougl. ex Laws.) with scattered Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and its elevation ranges from 1300 to 1500 m.a.s.l. Mean maximum and minimum temperatures are 13.1 ºC and −2.7 ºC, respectively, and mean annual precipitation is 380 mm (period 1958–2017). Ponderosa pine is a widely distributed species in western North America, ranging from southwestern Canada to northern Mexico, and the primary bark beetles that affect it are western pine beetle (*Dendroctonus brevicomis* LeConte) and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Smith and Arno, 1999). These native beetles are commonly associated with virulent blue-stain fungi, a group of unrelated genera of ascomycetes, that play an important role in killing the tree (Franceschi et al., 2005).

The area was first harvested in 1906 and part of it was additionally cut in 1955, 1967, and 1979 (Smith and Arno, 1999). In spring 1992, forest restoration treatments were implemented with the goals of reducing fire hazard and susceptibility to insects and diseases and improving timber production and wildlife habitat. Towards that end, efforts were directed at reducing stand density and fuels, increasing dominance of ponderosa pine, and retaining the largest, most vigorous trees. The treatments consisted of two independent cutting experiments: moderate intensity thinning from below, which promotes tree growth, and retention shelterwood, which promotes tree growth and pine regeneration. The moderate thinning, hereafter referred to as the thinning experiment, reduced basal area by 35 % and tree density by 42 %, while the retention shelterwood, hereafter referred to as the shelterwood experiment, reduced basal area by 57 % and density by 64 % (Table 1). Part of the thinning experiment had been last harvested in 1979 (Smith and Arno, 1999). Both experiments were divided into 12 management units of 1–2 ha, allowing the following four treatments to be replicated three times within each experiment: a cut-only treatment, two cutting followed by prescribed burning treatments (cut-burn: spring vs. fall burn in the thinning experiment and burning under moist vs. dry

Table 1
Mean (SE) of stand and tree characteristics before (Pre), right after (Post-1), and 13 years after treatments (Post-13). Measurements are for all live trees > 15.24 cm dbh.

		Thinning				Shelterwood			
		Control	Cut-only	Spring-burn	Fall-burn	Control	Cut-only	Wet-burn	Dry-burn
Stand density (trees ha^{-1})	Pre		332 (17)	310 (16)	358 (20)		405 (30)	375 (25)	358 (24)
	Post−1	352 (22)	178 (9)	200 (10)	200 (9)	328 (23)	141 (11)	120 (9)	148 (11)
	Post−13	364 (22)	188 (9)	200 (13)	216 (11)	314 (23)	138 (11)	119 (10)	130 (10)
Stand basal area (m^2 ha^{-1})	Pre		20.6 (0.7)	18.8 (0.9)	22.4 (1.3)		28.1 (1.4)	25.2 (1.1)	25.0 (1.7)
	Post−1	23.6 (1.1)	13.0 (0.6)	13.0 (0.6)	14.2 (0.6)	25.6 (1.4)	11.9 (0.6)	10.1 (0.5)	11.7 (0.6)
	Post−13	29.9 (1.3)	17.4 (0.5)	16.8 (0.7)	18.8 (0.8)	28.5 (1.5)	15.0 (0.7)	12.5 (0.8)	13.3 (0.6)
DBH (cm)	Pre		27.1 (0.3)	26.8 (0.3)	27.2 (0.3)		28.4 (0.4)	27.7 (0.4)	28.4 (0.4)
	Post−1	28.2 (0.3)	29.3 (0.4)	27.8 (0.3)	28.9 (0.3)	30.1 (0.4)	29.5 (0.5)	29.3 (0.5)	29.9 (0.4)
	Post−13	31.0 (0.4)	33.7 (0.5)	31.4 (0.5)	32.1 (0.5)	32.3 (0.5)	35.4 (0.8)	34.4 (0.8)	34.4 (0.7)
Height (m)	Pre		16.3 (0.2)	16.1 (0.2)	16.1 (0.1)		20.3 (0.2)	18.9 (0.2)	18.0 (0.2)
	Post−1	16.2 (0.1)	16.0 (0.1)	15.6 (0.1)	16.0 (0.1)	20.4 (0.2)	21.1 (0.2)	19.7 (0.2)	18.8 (0.2)
	Post−13	18.8 (0.1)	18.7 (0.2)	17.5 (0.2)	18.0 (0.2)	23.2 (0.2)	23.9 (0.4)	21.8 (0.3)	20.8 (0.3)

duff in the shelterwood experiment), and an untreated control. Within each of the 12 units, 12 circular plots of 0.04 ha (radius 11.35 m) were established on a systematic grid to measure stand characteristics and assess tree responses.

The treated units were randomly assigned, while the untreated units were placed according to logistical needs for the prescribed burns. In the thinning experiment, prescribed burning was implemented in fall 1993 (fall-burn, 20 % duff moisture content) and spring 1994 (spring-burn, 30 % duff moisture content). In the shelterwood experiment, units were all burned in spring 1993, either under wet conditions (wet-burn, 50 % duff moisture content) or under dry conditions (dry-burn, 16 % duff moisture content) (Fig. 1). Although both cutting experiments are density reduction treatments, they differ in environmental site conditions (the thinning treatment was on the upper slope and the shelterwood on the lower slope) and in their primary objective (promotion of tree growth vs. regeneration); thus, they are considered independent in this study and have been analyzed separately. Similarly, burning treatments were implemented under different conditions in each experiment (spring vs. fall, wet vs. dry) and have also been considered separately. Further details on harvesting prescriptions and burning conditions are given in Smith and Arno (1999).

A number of studies have reported treatment responses at Lick Creek including studies on initial (Ayers et al., 1999; Smith and Arno, 1999) and long-term carbon responses (Clyatt et al., 2017), soil nitrogen

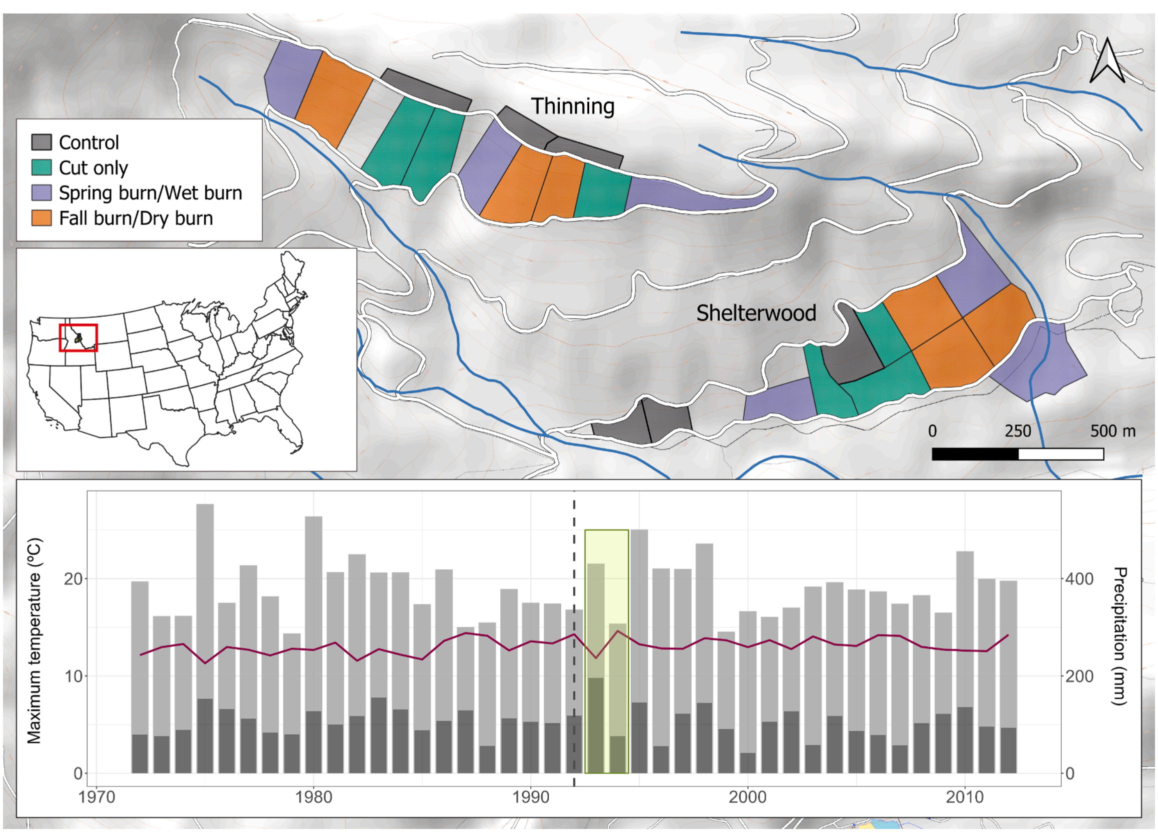

Fig. 1. Location of the treatment units in the Lick Creek Demonstration-Research Forest in southwestern Montana, USA. The lower inset displays total annual precipitation in light grey overlaid by the total precipitation during the growing season (June through August) in dark grey, and mean annual maximum temperature from 1972 to 2012 (purple line). Vertical dashed line denotes year of cutting treatments (1992). The light-green rectangle highlights the 2 years after cutting treatments, when prescribed burns were implemented.

dynamics (DeLuca and Zouhar, 2000), tree physiology (Sala et al., 2005), cone production (Peters and Sala, 2008), forest structural and fuel load responses (Hood et al., 2020a), understory vegetation (Jang et al., 2021) and tree growth, physiological activity, and mortality (Tepley et al., 2020).

2.2. Data collection

All trees larger than 15.24 cm in diameter at breast height (dbh) inside the 12 circular plots were measured in 1991 (pre-cutting) and in 1993, 2005, and 2015 (post-cutting) to estimate stand basal area and tree density. After the prescribed burning treatments, percent crown scorch was visually assessed. In 2016, 8 of the 12 circular plots per unit were randomly selected for collecting increment cores for dendrochronological analyses. Two ponderosa pine trees from each of the 8 randomly selected plots were chosen for coring: the closest large (> 25.4 cm dbh) and small (15.2 – 25.4 cm dbh) tree to the plot center, resulting in 16 trees per unit, 48 per treatment within each experiment, and 192 trees per experiment. Two increment cores were collected from each tree on opposite sides perpendicular to the slope at a mean height of 51 cm with an increment borer of 5.15 mm diameter. Basal area increment (BAI) was calculated based on the cross-dated tree-ring width and the distance to the pith. See Tepley et al. (2020), for a detailed description of cross-dating methods and growth characterization. Climatic variables were retrieved at 4-km resolution from the TerraClimate database (Abatzoglou et al., 2018), and included monthly maximum temperature, precipitation, and the Palmer Drought Severity Index (PDSI).

2.3. Axial resin ducts

We quantified resin duct metrics on one of the two cored trees per plot, and one of the two increment cores collected from that tree, as a compromise between measurement effort and obtaining a sample size large enough to identify common patterns in resin duct defenses, resulting in 8 cores per unit, 24 per treatment within each experiment, and 96 cores per experiment. To quantify resin ducts, cores were sanded using a belt sander with a progression of 120- to 400-grit, then progressively hand-polished with 40- to 9-micron polishing paper, and finally scanned at 1200 dpi. Resin ducts in the earlywood and the latewood were measured in ImageJ (version 1.8.0_112, National Institutes of Health, Bethesda, MD, USA) using the ellipse tool and adding calendar years to the measurements. We measured resin ducts formed between 1972 and 2012, to analyze a 20-year time interval before and after the treatments (1992 was designated as the treatment year since the harvests took place at that time, though the prescribed burns were conducted in 1993 and 1994). We estimated the annual earlywood, latewood, and whole ring investment in resin ducts by calculating absolute and relative to ring area metrics: duct size, duct production, and total duct area as absolute (unstandardized) metrics, and duct density and relative duct area as relative (standardized) metrics following Hood et al. (2020b). Ring area, needed to calculate the standardized resin duct metrics, was calculated as ring width x tree core diameter (5.15 mm). The latest version of the R script used to assign calendar years to ducts in both the earlywood and latewood can be found at https://github.com/jeffkane/resinduct/ (Vilà-Vilardell et al., 2024).

2.4. Data analysis

To study the impact of cutting and prescribed burning on resin ducts, we compared the response over the 20-year intervals before and after treatments. Specifically, we evaluated the changes in duct size, duct production, total duct area, duct density, and relative duct area in response to the treatments. We chose a 20-year interval as a measure of the long-term response to management treatments.

We modelled the effect of treatments on the 20-year mean resin duct values per core of earlywood, latewood, and whole-ring resin ducts using generalized linear mixed-effects models (GLMMs). We fit separate models for both the thinning and shelterwood experiments for all duct metrics, using treatment *type* (categorical with four levels) and its interaction with treatment *period* (categorical with two levels: pre and post) as fixed factors and *tree* as random intercept, to account for repeated measures of the same tree.

We also explored the effects of crown scorch and stand structure on whole-ring resin ducts as proxies of prescribed burning and cutting impacts, respectively. Because measures of crown scorch and stand structure were taken only in specific years, we used relative duct measurements to smooth out the extremes of individual trees in those years. Relative duct measurements were calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Crown scorch was modelled using only burned units. To model the crown scorch effect on resin ducts, we fitted models using percent *crown scorch* (continuous standardized) and *year* (categorical with two levels: Post-1 and Post-2; see below) as fixed factors and treatment *type* nested in *experiment* (thinning and shelterwood) as random intercept. As year, we used the two years following treatments (Post-1 and Post-2: 1993 and 1994, or 1994 and 1995, depending on the treatment completion date). To model the stand structure effect we fit GLMMs on the mean duct metrics per plot using *stand basal area* of the plot (continuous standardized), *tree density* of the plot (continuous standardized), and *year* (categorical with three levels: Pre, Post-1, and Post-13; see below) as fixed factors and treatment *unit* nested in treatment *type* and *experiment* (thinning and shelterwood) as random intercept, to account for dependency among observations of the same treatment unit. As year of the stand structure models, we used a before-treatment year (Pre: 1991) and two after-treatment years (Post-1: 1993 or 1994, depending on the treatment completion date; and Post-13: 2005). These two after-treatment years were the years when plots were resampled. Control plots were not sampled until 1993, but since we assume minimal changes in forest structure over two years, we used data of 1993 structure as the before-treatment structure. Model selection led to models without *tree density* as a covariate.

Depending on the distribution of the data, we fit Gamma, zero-inflated Gamma, or Conway-Maxwell Poisson (COM-Poisson) GLMMs with a log link function, or Gaussian GLMMs with an identity link function. We used the COM-Poisson distribution to account for underdispersed data. We used Akaike's Information Criteria (AIC) to select the best models, and when AIC < 2 we kept the most parsimonious model. Pairwise differences among treatment units were tested using least-square means, adjusting the significance level ($\alpha = 0.05$) with a Holm correction factor to account for multiple comparisons and reduce the risk of type I errors. The differences between resin duct measurements before and after treatments separately for both earlywood and latewood were also assessed using pairwise comparisons with a Holm correction factor. Model assumptions were verified ensuring the absence of residual patterns by plotting residuals versus fitted values and each covariate (Zuur and Ieno, 2016). All analyses were done using R v.4.3.1 (R Core Team, 2023), including *lme4* v.1.1–34 (Bates et al., 2015), *glmmTMB* v.1.1.7 (Brooks et al., 2017), *DHARMa* v.0.4.6 (Hartig, 2022), and *emmeans* v.1.8.8 packages (Lenth, 2023).

Finally, we explored the sensitivity of resin duct defenses to climate before and after treatments. Climate-defense relationships were assessed by treatment unit, treatment period (pre and post), and cutting experiment separately ($n = 20$) with Pearson's correlation analyses between resin duct measurements and monthly maximum temperature and precipitation, using *treeclim* R package v.2.0.6.0 (Zang and Biondi, 2015). Correlation analyses were conducted separately for earlywood, latewood, and whole ring measurements from September of the previous year to August of the current year. Confidence intervals were bootstrapped to test for significant correlations ($\alpha = 0.05$). Because correlations consisted of a 20-year interval, we relied upon the principle of uniformity, assuming that the statistical relationship between resin duct measurements and the climate variable is stable over time. This principle has been discussed in dendrochronology for many years, particularly in climate reconstruction studies (Peltier and Ogle, 2020; Wilmking et al., 2020), yet the time interval in our analysis is relatively short compared to these studies. In the following sections, the term "treatment year" refers to the year of the harvests (1992) unless explicitly clarified, even though the prescribed burns were conducted over 1993 and 1994. Because duct size and total duct area are correlated with resin flow in ponderosa pine (Hood and Sala, 2015), and the focus of this study is consequences of forest management on resin ducts as a proxy for defense, for simplicity, we chose to focus primarily on these metrics in the results section. Results of the other metrics are reported in Appendix A, B, and C.

3. Results

3.1. Resin ducts responses to cutting and prescribed burning

After treatments, there was an increase in duct production and duct area that lasted throughout the 20-year period analyzed (Fig. 2). During this period, both metrics were 2-fold higher in the treated units compared with the control ($p < 0.05$; Fig. 4, Fig. A.1). In the thinning experiment, ducts of treated trees were on average 27 % larger than ducts of control trees, while in the shelterwood experiment, only ducts in the cut-only and wet-burn units were larger, by 17 % ($p < 0.01$; Fig. 4). All unstandardized metrics (i.e., size, total area, and production) tended to decline over time in the control units of both experiments (Fig. 2). Duct density and relative duct area in the treated units of the shelterwood experiment exhibited a spike following treatments (Fig. 3), particularly in the earlywood (EW) in the dry-burn units, but also in the wet-burn ones (Fig. B.4, Fig. B.5). Thereafter, they gradually decreased, reaching similar levels to those of the control trees four years after the cutting treatments. A similar, but smaller peak in duct density and relative duct area was observed in the fall-burn units of the thinning experiment (Fig. 3). The variance explained by fixed factors alone (R^2m) was relatively low, ranging from 3 % to 22 % (Fig. 4, Fig. A.1, Table D.1 to D.10), indicating that treatments and period contributed moderately to the interannual variation in resin ducts, and that a greater proportion was explained by variation within the tree itself (R^2c, ranging from 37 % to 87 %).

3.2. Differences between earlywood and latewood duct responses

Treatments had a comparatively smaller effect on latewood (LW) resin ducts compared to EW ducts in the shelterwood experiment for all metrics but size (Fig. 5, Fig. A.2). Control units had smaller ducts that occupied a smaller portion of the EW and LW after treatments in both experiments. Average EW and LW duct size was larger in the cut-only and in the spring-burn or wet-burn units after treatments ($p < 0.05$; Fig. 5). Average total duct area did not change after treatments in the thinning experiment, but it increased in the EW of all treated units ($p < 0.05$) and in the LW of the cut-only units ($p < 0.001$) of the shelterwood experiment (Fig. 5).

3.3. Resin duct sensitivity to crown scorch and stand structure

Crown scorch had little impact on resin duct responses, explaining less than 9 % of the total variance in relative duct size and total area (Fig. 6a, Table D.11).

Stand basal area was negatively related to duct size before and 13 years after treatments (Post-13). Immediately after treatments (Post-1), duct size did not change with basal area. Post-1 ducts were larger than both the pre-treatment and the Post-13 ducts, especially in the units where stand basal area was high ($p < 0.01$; Fig. 6b). Total duct area was

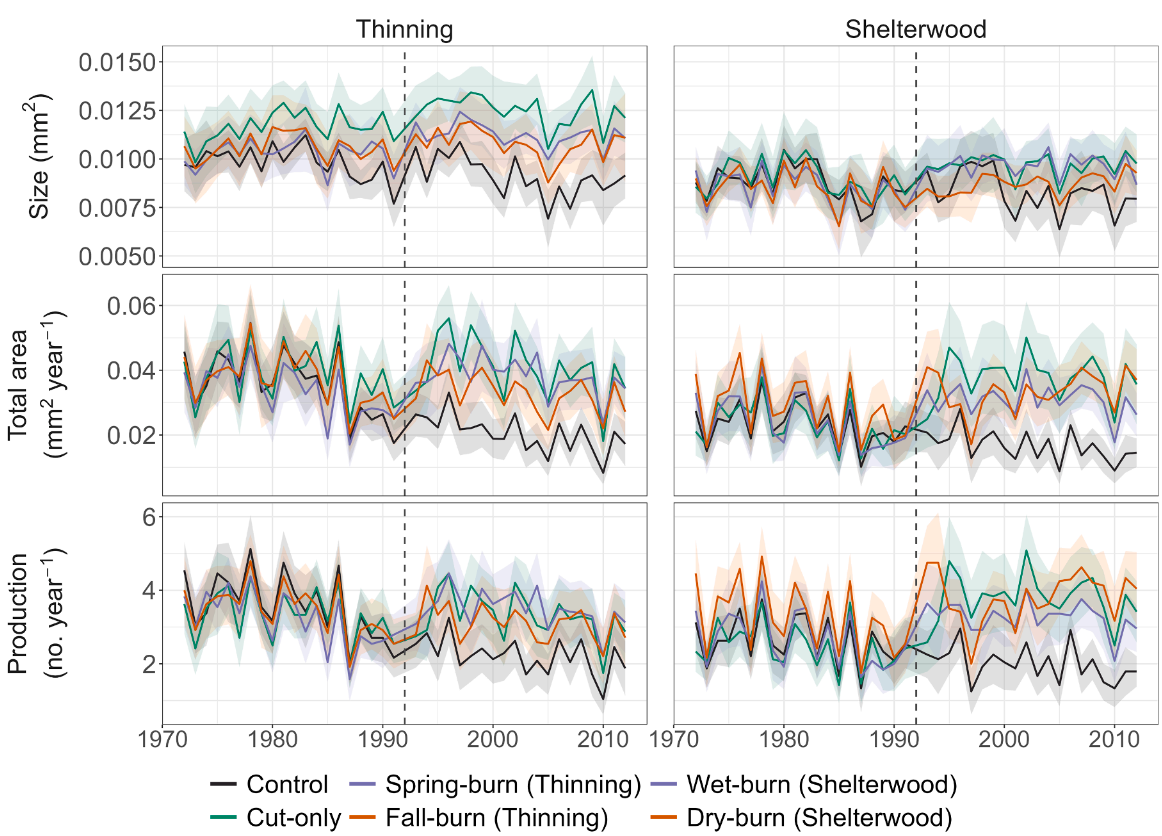

Fig. 2. Mean annual variation of duct size, total duct area, and duct production in the whole ring by experiment. Shaded areas represent the 95 % confidence interval. N = 192 trees were analyzed across the period 1972–2012. The vertical dashed line denotes year of cutting treatments (1992).

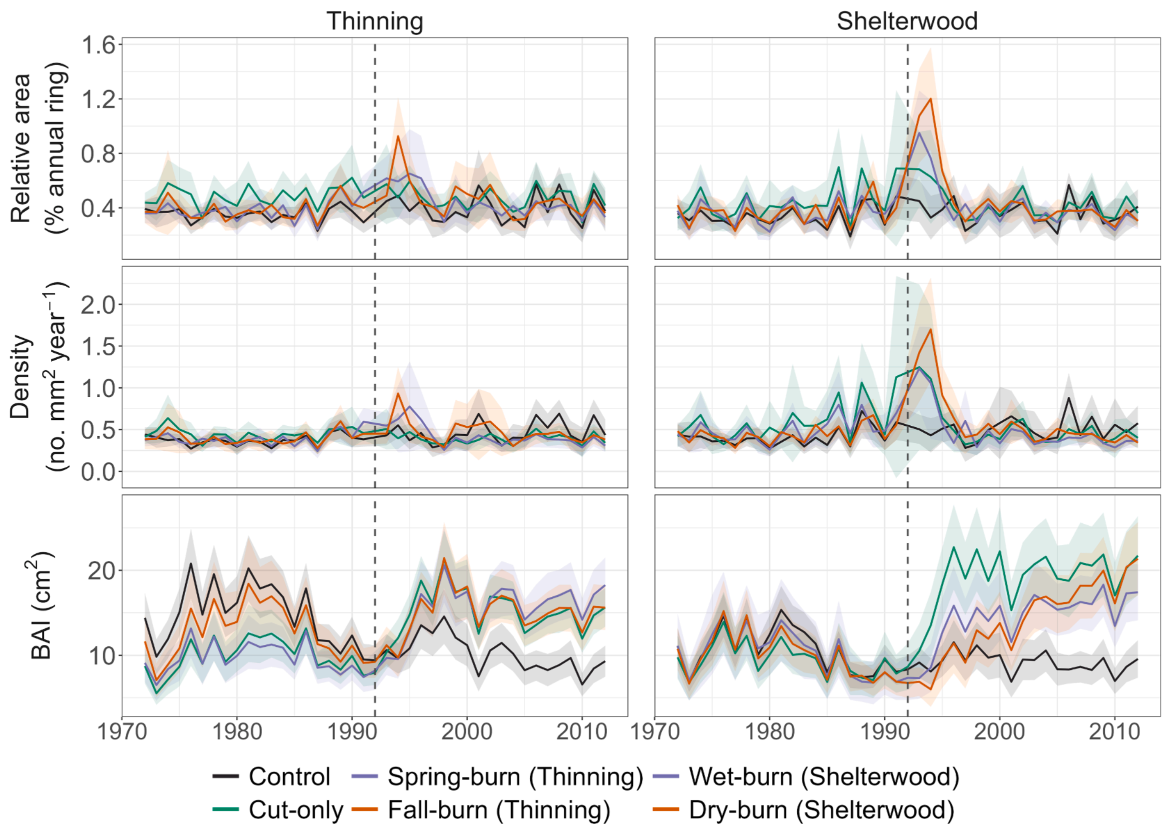

Fig. 3. Mean annual variation of relative duct area, duct density, and basal area increment (BAI) in the whole ring by experiment. Shaded areas represent the 95 % confidence interval. N = 192 trees were analyzed across the period 1972–2012. Vertical dashed line denotes year of cutting treatments (1992).

not related to stand basal area before treatments; however, their relationship became increasingly negative over time. Thirteen years after treatments (Post-13), greater duct area was observed in units with lower stand basal area ($p < 0.01$, significant Post-13 x stand basal area interaction; Fig. 6b). However, the variance in resin ducts explained by stand basal area is relatively small ($R^2c < 0.19$) (Table D.12).

3.4. Relationships between climate and defenses

The correlation between duct defenses and climate did not show any trend linked to treatment type (Fig. 7). Winter precipitation was positively correlated with duct size and total duct area before and after treatments in treated and control units of both experiments; yet the correlation with total duct area was weaker in virtually all units during the post-treatment period. Similarly, but in the opposite direction, mid-spring to mid-summer maximum temperature was more strongly negatively correlated with duct defenses before than after treatments in treated and control units of both experiments. Additionally, July precipitation and maximum temperature were positively and negatively correlated with duct size, respectively, mostly at the latewood (LW) ducts and weaker after treatments, particularly in the treated units of the shelterwood experiment (Fig. C.1). Similarly, the positive and negative correlation of April precipitation and maximum temperature with total duct area before treatments, respectively, became weaker after treatments (Fig. 7).

4. Discussion

Forest restoration treatments aimed at shifting structure and composition towards historical levels and increasing resistance to high-severity wildfires, may also have the additional benefit of boosting tree resistance to bark beetles. Our findings show that cutting and burning treatments increased resin duct defenses and that this response lasted for at least 20 years (H1.1 accepted; Fig. 2). Thus, they provide insight into the mechanism driving the increased resistance to the mountain pine beetle outbreak that impacted the Lick Crick area from 2011 to 2014 (Martin, 2024), where tree mortality in treated units was less than half that in control units (Tepley et al., 2020). The greatest increase in resin duct defenses was observed in the earlywood of the shelterwood experiment (H1.2 accepted; Fig. 5). Cut-burn and cut-only treatments induced a similar increase in resin duct defenses in the long run (H2.1 rejected; Fig. 4). Yet, the addition of prescribed burning led to a short-term increase in resin duct defenses compared with cut-only and control treatments, particularly in the shelterwood experiment (Fig. 3). However, this increase in the burned units was not associated to the degree of tree crown scorch (H2.2 rejected, Fig. 6a).

4.1. Stand density reduction stimulates resin duct investment

Trees in the shelterwood experiment (57 % basal area reduction) experienced the greatest increase in resin duct area (Fig. 2) along with the greatest growth release (Fig. 3). In the thinning experiment (35 % basal area reduction), treatments stabilized duct area, in contrast to the decrease observed in the untreated control units. Greater resin duct defenses in treated units relative to control persisted for at least 20 years following treatments in both experiments, in agreement with our hypothesis (H1.1; Fig. 4). Yet, contrary to our hypothesis H2.1, no differences in resin duct investment between cut-only and cut-burn units were observed. This result aligns with those reported by Tepley et al. (2020) and Sala et al. (2005) at the same study site in Lick Creek, who found that the physiological differences among treatments were small relative to the physiological differences between treatments and control.

The increase in resin duct investment following cutting with or without subsequent prescribed burning may be attributed to the

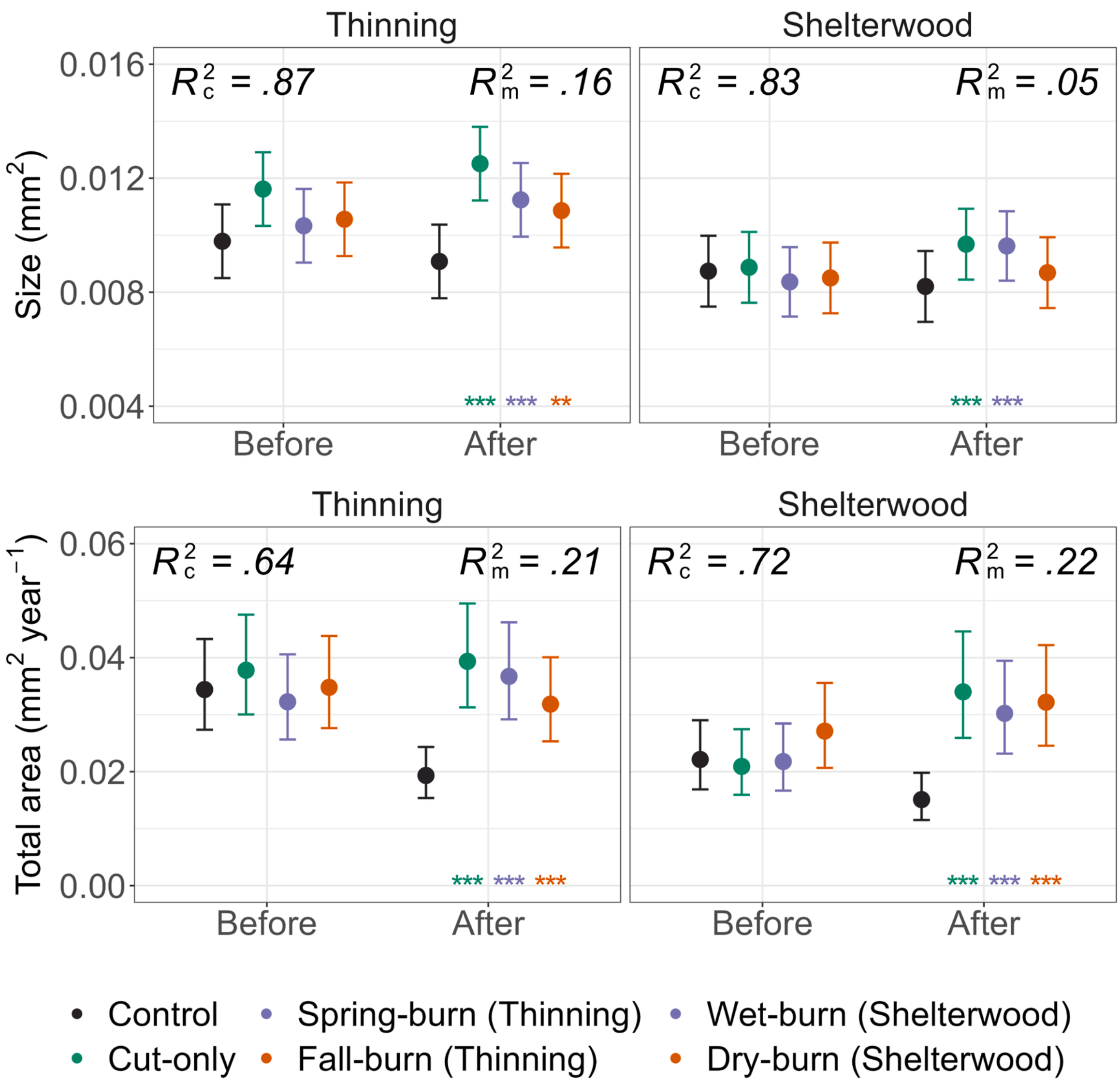

Fig. 4. Estimated marginal means and confidence intervals (95 %) of the mixed-effects models for duct size and total duct area in the whole ring using the mean value of a 20-year interval before and after treatments. Marginal (R^2m) and conditional (R^2c) variance of the models and significance (*p<0.05; **p<0.01; ***p<0.001) of the estimated marginal means relative to control units (α < 0.05).

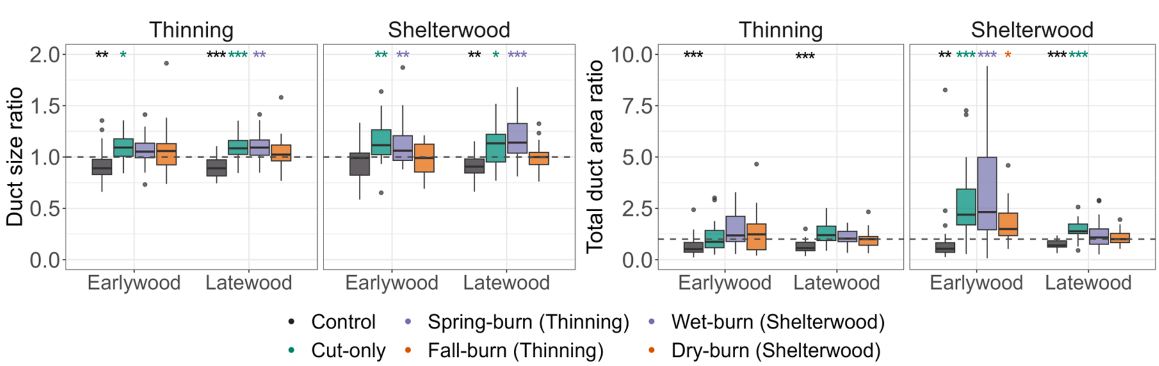

Fig. 5. Mean departure from average duct size and total duct area in earlywood and latewood, calculated for each tree as the ratio between the 20-year core average after treatments and the 20-year core average before. Significance (*p<0.05; **p<0.01; ***p<0.001) of the estimated marginal means relative to pre-treatments (α < 0.05). The horizontal dashed line denotes no departure from pre-treatments 20-year core average, above denotes increase, and below, decrease.

favorable conditions created by the reduction in stand density and tree competition (Bernal et al., 2023; Hood et al., 2016). The greater availability of resources for trees likely resulted in increased photosynthetic rate and stomatal conductance (Sala et al., 2005) and consequently, in more carbon to invest in both growth (Tepley et al., 2020) and defenses (Hood et al., 2016) in the long term. The increase in resin ducts was

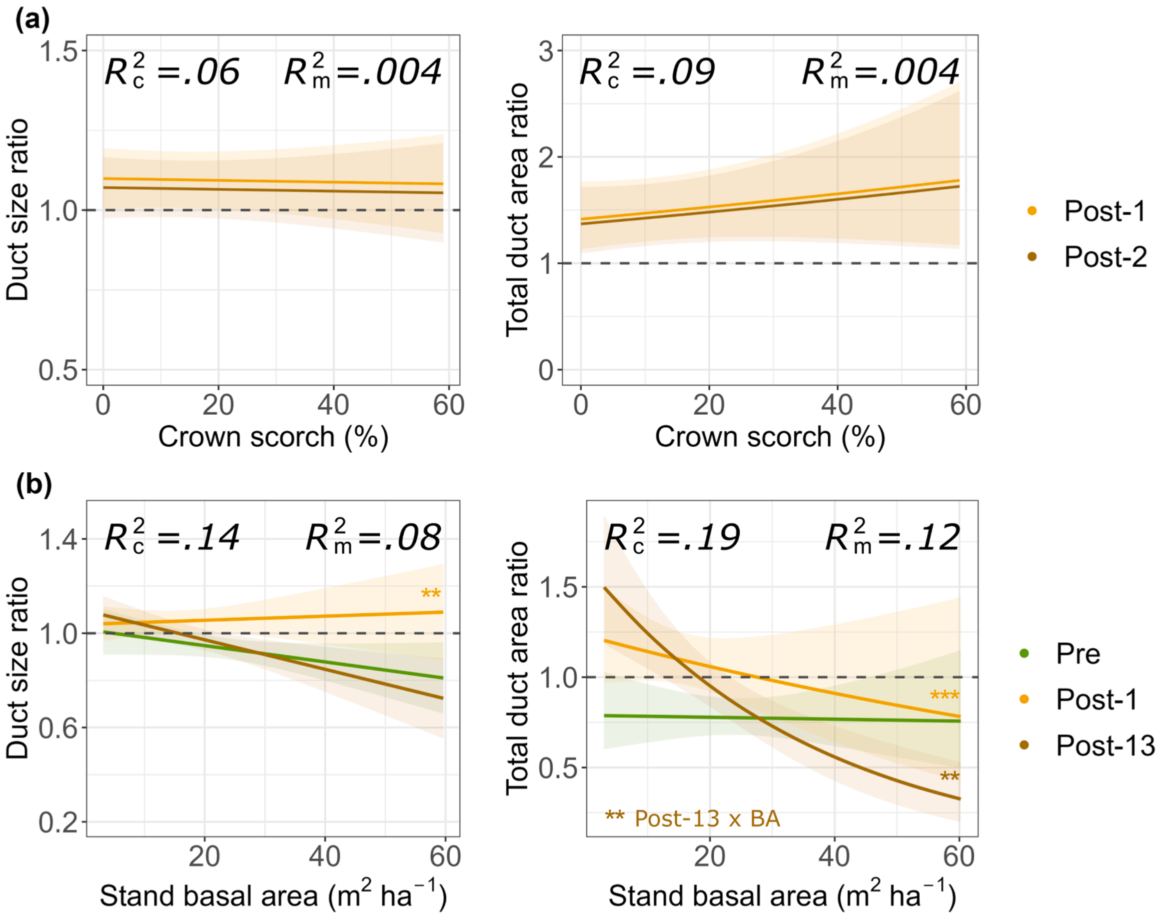

Fig. 6. Mixed-effects models of whole ring relative duct metrics as a function of (a) crown scorch and (b) stand basal area. Relative duct metrics were calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Crown scorch models were fit using only the burned units for the two years following prescribed burning (Post-1 and Post-2). Stand basal area models were fit in all units before (Pre), right after (Post-1), and 13 years after treatments (Post-13). Shaded areas represent the 95 % confidence interval. Marginal (R^2m) and conditional (R^2c) variance of the models and significance (*p<0.05; **p<0.01; ***p<0.001) of the estimated marginal means comparing resin ducts following treatments to pre-treatments are shown (α < 0.05). Horizontal dashed line denotes no departure from pre-treatments 20-year core average, above denotes increase and below, decrease.

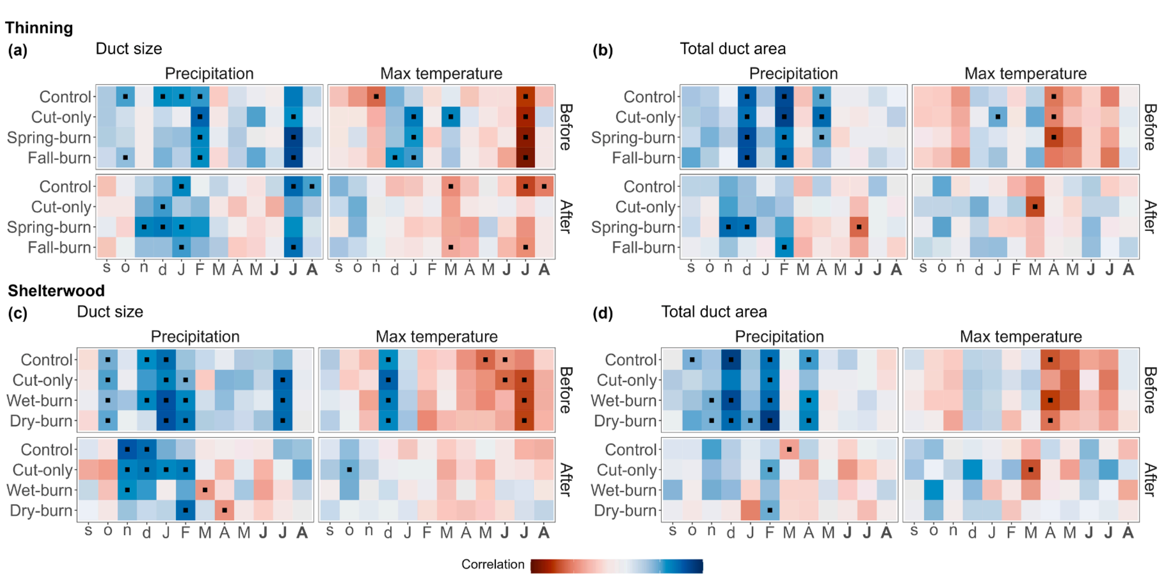

Fig. 7. Pearson correlation coefficients between monthly precipitation and maximum temperature and duct size (a, c) or total duct area (b, d) in the whole ring, 20 years before and after treatments for the thinning (a, b) and the shelterwood (c, d) experiments. Tiles marked with a dot denote significant correlation (α < 0.05) using regular bootstrapping. Months in lowercase letters correspond to previous year and capital letters to current year (September previous year to August current year); months in bold denote the growing season.

probably also influenced by the fact that both cutting experiments retained the most vigorous trees. However, resin ducts often show contrasting responses in different studies, including a decline in trees growing under favorable conditions (Vázquez-González et al., 2020a) and a slightly positive correlation between tree competition (i.e., unfavorable conditions) and resin duct area (Slack et al., 2017), suggesting variability in response to site productivity and resource availability in the different studies.

We found a positive response of duct size to treatments, yet in different directions depending on the cutting experiment: ducts became larger in treated units of the thinning experiment, did not change in treated units of the shelterwood, and became smaller in control units of both experiments (Fig. 2). Smaller ducts in control units may be associated with the long-term, cumulative effect of high competition (Slack et al., 2017). Duct size and duct area are correlated to resin flow (Hood and Sala, 2015), and resin flow is related to the chances of surviving a bark beetle attack (Perrakis et al., 2011). Therefore, changes in duct size and total area after treatments likely explain the observed low mortality rates in the treatments of both experiments relative to the controls during the 2011–2014 mountain pine beetle outbreak, as reported in Tepley et al. (2020) and consistent with Hood et al. (2016), who reported higher total duct area and lower mountain pine beetle-caused mortality in thinned treatments.

4.2. *Earlywood resin ducts are more sensitive to treatments than latewood ducts*

Our findings illustrate the greater sensitivity of earlywood (EW) ducts to treatments, particularly in the shelterwood experiment (Fig. 5, Fig. A.2), in agreement with our hypothesis (H1.2). These changes may be relevant for increased resistance to bark beetles, as timing of EW xylem production in late-spring through mid-summer (Ziaco et al., 2018) coincide with the timing of western pine beetle (Gaylord et al., 2006) and mountain pine beetle flight (Jackson et al., 2008). However, despite remaining active for years (Hudgins and Franceschi, 2004), it is unknown if recently formed ducts contribute more to resin flow than older ducts or whether there are functional differences between EW and LW ducts. Hood and Sala (2015) found positive, but slightly weaker correlations between resin flow and 10-year average duct size and total duct area than between resin flow and 5-year averages, suggesting a decline in resin flow with resin duct age.

Although before treatments most of the resin ducts were synthesized in the latewood (LW), treatments led to a shift in the relative proportion between EW and LW ducts, with the exception of duct size, which was the only metric that changed proportionally in both EW and LW following treatments. Prior to treatments, higher density of resin ducts in LW can be explained by the harsher environmental conditions and limited availability of resources experienced by plants during LW formation. According to the growth-differentiation balance hypothesis (GDBH), when resources are limited, growth is more constrained than photosynthesis, leading to a larger relative allocation of carbon to defenses than when resources are abundant (Herms and Mattson, 1992). For example, factors such as high vapor pressure deficit and low soil moisture later in the growing season induce water stress and promote differentiation processes, leading to a greater relative investment in defenses in LW (Saracino et al., 2017). While we did not explicitly test the GDBH, our results support its predictions, with higher investments in growth and ducts in the EW and increased ducts in the LW in the density reduction treatments. After treatments, higher relative proportion of resin ducts in the EW of the shelterwood experiment may be attributed to an increase in resource availability as suggested by Rigling et al. (2003), who found greater proportion of ducts in the EW of irrigated trees. Our findings are consistent with Tepley et al. (2020) results based on carbon isotope discrimination, who observed that treatments enhanced carbon assimilation in ponderosa pine early in the growing season when water is available, but also allowed continued assimilation late in the growing season under more severe water stress. Higher photosynthesis early in the growing season may allow both growth and resin duct production.

4.3. *Burning after cutting induces a short-term increase in resin duct investment*

Although stand density reduction had a greater effect in resin defenses in the long term, prescribed burning stimulated a sharp, but short-term increase in resin ducts. Burning after cutting triggered a short-term increase in earlywood (EW) resin duct density and relative duct area in both experiments, but especially in the shelterwood (Fig. 3, Fig. B.4, Fig. B.5), where the increase of resin ducts stimulated by the fire preceded the growth release caused by cutting. The increase in resin duct production began immediately after treatments, while the increase in growth rate (i.e., BAI) began two years after and reached its peak at year three or four. An immediate response of resin ducts and delayed response in the growth of ponderosa pine after cutting and burning treatments was also reported by Hood et al. (2016).

Low-intensity fire stimulates resin flow (Cannac et al., 2009; Knebel and Wentworth, 2007; Lombardero and Ayres, 2011) and the effect can last for up to 4 years (Perrakis et al., 2011). The increase in resin flow occurs within days to weeks, likely via upregulation of resin synthesis in existing ducts, and it persists as new resin ducts are formed and become functional (Hood et al., 2015). However, an increase in the number of ducts after fire does not always translate into higher resin flow (Rodríguez-García et al., 2018), and more research is needed to understand the fire intensity required to elicit resin flow responses. Increases in resin production in pines after low-intensity fire likely aids in compartmentalization of fire-killed cambium (Verrall, 1938; Wallin et al., 2004) and in resisting post-fire bark beetle attacks (Hood et al., 2015; Valor et al., 2021), both of which increase tree survival.

While prescribed fire stimulated resin duct synthesis in the short term, crown scorch explained only a limited amount of the variation in resin ducts (Fig. 6a), contrary to our hypothesis (H2.2). Our results agree with Sparks et al. (2017), who found no clear correlation between fire intensity and resin duct responses following prescribed burning, with fires of a wide range of intensities increasing duct production, total duct area, and duct size. Resin flow is inversely related to crown scorch after fire (Lombardero and Ayres, 2011), particularly in cases of severe scorch (75 %) (Wallin et al., 2003) due to a reduction in the photosynthetic capacity of the tree (Valor et al., 2018). In our study area, most trees exhibited $<$ 25 % crown scorch, with almost all falling below 50 %. Low-intensity fire mostly affects the lower-crown foliage, and these levels of lower foliage loss are likely insufficient to significantly affect the photosynthetic rate (Gomez-Gallego et al., 2020) and, consequently, the synthesis of resin defenses. Additionally, ponderosa pine buds can survive if the temperature that reaches the surrounding needles is enough to scorch but not to consume the foliage (Fowler et al., 2010), in which case, the buds flush new needles that contribute to post-fire recovery (Reed and Hood, 2024). The narrow range of observed crown scorch in our study limits our ability to test its effects on resin duct responses and additional research is needed.

The spike in resin duct synthesis was especially evident in the EW of trees in the shelterwood experiment (Fig. B.4, Fig. B.5), particularly within the dry-burn units, which burned under the driest moisture conditions. Prescribed burning in the shelterwood experiment was applied in spring of 1993 (before the second growing season following the cutting treatments), while in the thinning experiment it was applied in fall of 1993 and spring of 1994 (before the third growing season following the cutting treatments). The difference in response to prescribed burning between the two experiments could be partly explained by the substantially different weather patterns during the years following the cutting treatments: 1993 was a notably wet year, particularly during the growing season (PDSI = 3.0), with below-average maximum temperature (Fig. 1). In 1994, the situation was quite the opposite, as it was a dry year with warm, dry conditions during the growing season (PDSI = −4.9), and the maximum temperature was higher than the average, causing high evaporative demand and stress for the trees. In brief, the growing season following prescribed burning in the shelterwood was an unusually wet season, while in the thinning experiment it was an unusually dry season.

Besides differences in weather conditions, prescribed burning in the thinning experiment was conducted in fall of 1993 and spring of 1994, meaning that the trees had two full growing seasons to respond to the thinning before showing additional responses to the burning treatments. The earlier growth response to reduced competition could have masked the spike in duct density and relative area stimulated by the burning treatments. We observed a delay in tree growth during the two years after the treatments that could be explained because trees first invest in increasing leaf area index with new foliage and buds (i.e., larger crown) and in new roots. A larger crown allows for an increase in the photosynthetic capacity and carbon assimilation that can eventually be allocated to growth (Waring and Pitman, 1985). Yet, immediately after cutting treatments, trees may already benefit from increased resource availability. The unusually wet year that followed cutting might have allowed trees to not only invest in new foliage but also in defenses. Additionally, a short-term increase in soil nitrogen content immediately following prescribed burning treatments (DeLuca and Zouhar, 2000) could increase photosynthetic rates and thus, resin duct production (Mason et al., 2019). Considering that resin ducts remain functional for several years after their synthesis (Hudgins and Franceschi, 2004), the current investment in anatomical defenses is expected to provide defenses in the future. However, for how long and whether older resin ducts can produce the same volume of resin as the new ducts remains uncertain.

Dry-burn and fall-burn units, the units that burned under drier conditions, in the shelterwood and the thinning experiment, respectively, were the ones with the greatest spike in resin ducts. This could indicate a stronger stress response under higher fire intensity, which would be consistent with the increase in resin ducts observed after wildfire but not necessarily after prescribed burning (Hood et al., 2015, 2016). However, the fact that burning treatments were not implemented under consistent conditions (spring vs. fall and moist vs. dry) limits our ability to draw conclusions.

4.4. *Treatments have a minor impact on climate-defense relationships*

Treatments did not influence the sensitivity of resin ducts to climate (Fig. 7), contrary to our third hypothesis (H3). Resin duct investment seemed to be less sensitive to climate after treatments, yet there was a different range of weather conditions over the 20-year intervals before and after treatments, characterized by a decline in annual precipitation and a rise in temperature, and a 20-year window may be too short to quantify statistically significant changes in the response to climate. Winter precipitation was positively correlated to duct defenses. These findings align with those reported for longleaf pine (*Pinus palustris*) (Slack et al., 2016) but differ from those reported for whitebark pine (*Pinus albicaulis*) (Kichas et al., 2020) or Bosnian pine (*Pinus leucodermis*) (Saracino et al., 2017), which might be explained by the different environments in which these pines grow: ponderosa and longleaf pine in moisture-limited environments, while whitebark and Bosnian pine in energy-limited environments near the treeline where precipitation is abundant. In moisture-limited environments, trees use water originating from winter precipitation even in the peak of summer (Martin et al., 2018). The generally positive correlation between winter precipitation and duct defenses in all units before and after treatments may be partially explained by the also positive correlation between winter precipitation and latewood (LW) growth found by Tepley et al. (2020), as more LW growth leads to a generally greater investment in duct defenses.

The reduced sensitivity following treatments observed in both treated and untreated trees indicates that changes in climate-defense relationships cannot be attributed to the treatments but to weather pattern changes. Trends towards less snowfall and earlier beginning of the growing season have been documented in western United States (Knowles et al., 2006; Stewart et al., 2005). Indeed, we observed that the negative correlation between spring maximum temperature and duct area moved from April, before treatments, to March, after treatments (Fig. 7), which we attributed to the increasing trend in March maximum temperature over the 40-year period analyzed, leading to an earlier snowmelt. We found slightly different responses to climate between EW and LW duct investment (Fig. C.1 to C.5), which could be explained because they are produced asynchronously, and sensitivity of resin duct production to weather conditions may change.

5. Conclusions

Our findings highlight the additional benefits of forest restoration treatments primarily aimed at mitigating high-severity fire in also boosting resistance to bark beetle outbreaks. Previous research showed that cutting with or without subsequent prescribed burning stimulates resistance to drought and reduces tree mortality during a mountain pine beetle outbreak (Tepley et al., 2020). Here, we further established that these restoration treatments increase resistance to bark beetles by inducing the production of resin ducts, providing a mechanism for the observed reductions in beetle-caused mortality during the 2011–2014 mountain pine beetle outbreak. Our results showed that density reduction treatments stimulated a long-term, sustained increase in resin duct production, thereby providing long-term benefits for mitigating future outbreaks (Hood et al., 2016). Additionally, when cutting was followed by prescribed burning it triggered a short-term increase in resin ducts. This spike was especially evident in the lower residual basal area shelterwood treatment, where prescribed burning was implemented right before a particularly wet growing season. Given that these ducts remain functional for several years, the investment likely bolsters the resistance of fire-injured trees to bark beetle pressure, which often temporarily increases after low and mixed-severity fires (Davis et al., 2012; Powell et al., 2012). Overall, our findings confirm that trees are better prepared to resist bark beetle attacks after density reduction treatments when trees experience faster growth rates. Moreover, the short-term positive effect of prescribed burning should be taken into consideration when planning management actions, as prescribed burning is usually repeated at regular intervals to ensure that its primary objective, fire hazard reduction, is maintained. Future climatic changes will likely increase the frequency and intensity of coupled disturbances such as drought episodes and pest outbreaks, and forest treatments that reduce tree density are key in promoting tree adaptation to the anticipated harsher conditions.

CRediT authorship contribution statement

Sharon M. Hood: Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization. **Pere Casals:** Writing – review & editing. **Anna Sala:** Writing – review & editing. **Alan J. Tepley:** Writing – review & editing, Resources. **Lena Vilà-Vilardell:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared the link to my code at the Attach Files step Code from: Long-term sensitivity of ponderosa pine axial resin ducts to harvesting and prescribed burning (Original data) (Figshare)

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122301.

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