

Contents lists available at ScienceDirect

Forest Ecology and Management



journal homepage: www.elsevier.com/locate/foreco

Repeated fall prescribed fire in previously thinned *Pinus ponderosa* increases growth and resistance to other disturbances

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Douglas J. Westlind^{*}, Becky K. Kerns

USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331, USA

ARTICLE INFO

Black stain root disease

Keywords:

Dendroctonus

Leptographium

Pine butterfly

Ponderosa pine

Neophasia

ABSTRACT

In western North America beginning in the late 19th century, fire suppression and other factors resulted in dense ponderosa pine (Pinus ponderosa) forests that are now prone to high severity wildfire, insect attack, and root diseases. Thinning and prescribed fire are commonly used to remove small trees, fire-intolerant tree species, and shrubs, and to reduce surface and aerial fuels. These treatments can be effective at lowering future fire severity, but prescribed burns must be periodically repeated to maintain favorable conditions and are feasible only outside the historical summer wildfire season. This study examines tree growth and mortality associated with spring and fall burning repeated at five (5 yr) and fifteen-year (15 yr) intervals in six previously thinned ponderosa pine stands in the southern Blue Mountain Ecoregion near Burns, Oregon, USA. Each stand consisted of an unburned control, and four season-by-burn interval treatments: spring 5 yr, spring 15 yr, fall 5 yr, and fall 15 yr. Burning was initiated in fall 1997 and spring 1998. Pine height and diameter growth was evaluated in 2013, 15 years following initial treatment. Mortality was assessed annually from 2002 to 2017, when these stands experienced severe defoliation from pine butterfly (PB, Neophasia menapia), followed by a moderate outbreak of western pine beetle (WPB, Dendroctonus brevicomis), allowing us to examine resistance to these disturbances. Pine in the 5 yr fall treatments added more diameter than spring 15 yr and marginally more than spring 5 yr, while fall 15 yr added marginally more diameter than spring 15 yr. In addition, the fall 5 yr treatments had lower mortality associated with prescribed fire, PB, WPB, Ips spp., red turpentine beetle (RTB, D. valens), and mountain pine beetle (MPB, D. ponderosae), but the effect was not always significant. Annosus root disease (ARD, caused by Heterobasidion irregulare) and black stain root disease (BSRD, caused by Leptographium wagneri var. ponderosum) appear to be unaffected by burning. However, BSRD occurrence dramatically declined in all treatments, probably a result of thinning prior to study initiation. Results from this study demonstrate that repeated fall burning, especially at 5-year intervals, improves ponderosa pine diameter growth and may provide resistance to future biotic and abiotic disturbances while spring burning, regardless of frequency, does not.

1. Introduction

Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests of the western US were historically adapted to fire (Weaver, 1943; Agee, 1993). Both wildfires and fires intentionally ignited by Native Americans were frequent and generally of low severity (Agee, 1993; Covington and Moore, 1994; Boyd, 1999; Heyerdahl et al., 2001; Hessburg and Agee, 2003; Fule et al., 2009). Frequent fires reduced the occurrence of small pines, fire-intolerant conifers (e.g., Abies), seedlings, and shrubs, resulting in a mixed-age mosaic of large widely scattered trees and tree clusters, and grassy openings with scattered shrubs and few seedlings (Hessburg et al., 2000; Collins et al., 2015). High-severity fires were rare

in most ponderosa pine forests because surface fuel was generally light and widely scattered, and tree canopies were high and open with few ladder fuels (Keane et al., 2002). However, beginning in the late 19th century, fire suppression, livestock grazing, and selective logging interrupted the disturbance role of fire, allowing younger pines and fireintolerant species to survive, while litter, duff, and woody fuels accumulated, fueling high-severity wildfire (Agee, 1993; Covington and Moore, 1994; Belsky and Blumenthal, 1997; Hessburg et al., 2005; Marlon et al., 2012; Dennison et al., 2014). Anthropogenic climate change is also contributing to increasing frequency of large wildfires and cumulative area burned (Littell et al., 2009; Dennison et al., 2014), largely through reduced fuel moisture (Peterson and Marcinkowski,

* Corresponding author. *E-mail addresses:* doug.westlind@usda.gov (D.J. Westlind), becky.kerns@usda.gov (B.K. Kerns).

https://doi.org/10.1016/j.foreco.2020.118645

Received 8 April 2020; Received in revised form 11 June 2020; Accepted 19 September 2020 Available online 10 October 2020 0378-1127/Published by Elsevier B.V. 2014; Abatzoglou and Williams, 2016). In addition, forest densification and increasing drought can expand the occurrence of other disturbances such as disease and insect attack (Castello et al., 1995; Covington et al., 1997; Fettig et al., 2007, 2019).

In an effort to mitigate these unsustainable conditions, forest managers are applying thinning treatments, where fire-intolerant tree species and smaller pines are removed, followed by prescribed burning to reduce fuel (Agee and Skinner, 2005). These treatments can increase forest resilience to wildfire (Pollet and Omi, 2002; Fulé et al., 2012; Stephens et al., 2012; McIver et al., 2013). But prescribed burning must be periodically repeated to keep tree seedlings and fine fuel at low levels necessary to maintain this resiliency (Battaglia et al., 2008; Reinhardt et al., 2008; Westlind and Kerns, 2017).

The complex and often competing effects of thinning and prescribed fire treatments on future forest health is a major area of concern. Reductions in stand density through thinning can increase available water (McDowell et al., 2003; Skov et al., 2004) positively affecting tree growth (Cochran and Barrett, 1993; Busse et al., 2009; Zhang et al., 2013; Tappeiner et al., 2015; Vernon et al., 2018) and drought resistance (Sohn et al., 2016; Bradford and Bell, 2017; Vernon et al., 2018), as well as reduce tree mortality attributed to insects (Fettig et al., 2007; Zhang et al., 2013). But mechanical thinning can release monoterpene attractants leading to increases in bark beetle attack (Fettig et al., 2006), and damage to the residual trees may also lead to increases in root pathogens (Ferrell, 1996). The impact of prescribed fire on growth of remaining trees is highly variable with some studies indicating increases (Hatten et al., 2012; McCaskill, 2019), decreases (Landsberg et al., 1984; Landsberg, 1992; Busse et al., 2000), or no change (Sala et al., 2005). Results depend upon the severity (Landsberg et al., 1984), season (Hatten et al., 2012; Thies et al., 2013), and interval of burning (Peterson et al., 1994). Additionally, the impact of fire on tree growth may take several years to become apparent (Thies et al., 2013). Prescribed fire may also cause undesirable mortality to highly valued large trees (Kolb et al., 2007; Hood, 2010) and lead to increases in tree mortality attributed to bark beetles (Schwilk et al., 2006; Maloney et al., 2008; Fettig et al., 2010a; Davis et al., 2012). Many of these effects change over time, adding further complexity when evaluating thinning and burning treatments. Fire-related tree mortality rates generally drop to those of unburned stands within a few years (Thies et al., 2005), and increases in bark beetle attack associated with fire are usually shortlived (Davis et al., 2012; Westlind and Kelsey, 2019).

In western US forests, most prescribed burns are conducted in the spring and late fall because personnel are available and weather conditions are favorable for maintaining control, but how burn season and repeat interval interact with other stress agents and affect future stand health is not well known. Spring burning coincides with peak annual activity periods for many bark beetle species, and this timing may contribute to increased tree mortality from the beetles or the pathogens they vector. But fall burns are typically higher in severity (Ryan and Reinhardt, 1988; Thies et al., 2005; Fettig et al., 2010b), due to lower fuel moisture following the typically dry summer season (Estes et al., 2012). Higher fall fire severity also increases the likelihood of bark beetle attack (Negrón et al., 2016; Westlind and Kelsey, 2019) that may offset the effect of burning during periods of high beetle activity in spring (Ganz et al., 2002; Schwilk et al., 2006). The interval between prescribed burns can impact growth (Peterson et al., 1994), as short intervals may not allow trees to fully recover and longer intervals allow more fuel to accumulate leading to higher burn severity.

In response to concerns of Malheur National Forest personnel in the southern Blue Mountain Ecoregion of Oregon, regarding perceived increases in spread of black stain root disease (BSRD, caused by *Leptographium wageneri* (W.B. Kendr.) M.J. Wingf.) following spring burns, a study was initiated in 1997 to investigate the impacts of prescribed burning on BSRD (Thies et al., 2005). During the course of this study beginning in 2010, the area experienced widespread defoliation from a pine butterfly (PB, *Neophasia menapia* C. & R. Felder) outbreak, lasting

three years, peaking in 2011 at over 100,000 ha (Flowers et al., 2011, 2012, 2013), and resulting in mean defoliation of 67% by 2012 (DeMarco, 2014). The PB outbreak was followed by a widespread eruption of western pine beetle (WPB, *Dendroctonus brevicomis* LeConte) from 2015 to 2017 (Buhl et al., 2016, 2017, 2018). These conditions created a unique opportunity to investigate the impacts of prescribed burning on these and other mortality agents of ponderosa pine.

The fungus *L. wageneri* causing BSRD, colonizes water conducting tissues in host roots and lower stem, restricting water movement. Three fungal variants have been identified, each with specific host preferences: *L. wageneri* var. *ponderosum* infects ponderosa pine and Jeffrey pine (*P. jeffreyi* Grev. & Balf.), *L. wageneri* var. *pseudotsugae* infects Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and *L. wageneri* var. *wageneri* infects pinyon pine (*P. edulis* Engelm.) (Hessburg et al., 1995). Virulence of the disease appears to vary with host species and tree size. Healthy ponderosa pine may be able to survive by outgrowing infections (Owen et al., 2005), whereas, in Douglas fir, infections are typically fatal, with young fir usually succumbing within a year or two, while older firs may take 6 to 8 years to die (Hessburg et al., 1995). The disease can spread by root and lower bole feeding bark beetles and root weevils, and once established on a site, by root to root contact.

Pine butterfly outbreaks are relatively rare events generally lasting from two to six years, but defoliation can be severe and cover large geographic areas. The worst documented outbreak occurred on the Yakima Indian Reservation from 1893 through 1895 affecting 65,000 ha, and in association with bark beetles, destroying over two million cubic meters of ponderosa pine volume (Hopkins, 1907; Weaver, 1961). What causes endemic PB populations to outbreak is not known, as there are no clear links with any environmental factors (DeMarco, 2014). Outbreaks typically end due to a combination of predators, parasites, and bacterial or viral diseases (Furniss and Carolin, 1977; Scott, 2012). During the summer, PB adults lay eggs on current year needles that hatch the following spring to begin feeding on the mature needles. During an outbreak, larvae can consume all mature needles and all but the base of current year needles (Evenden, 1940; Furniss and Carolin, 1977; Scott, 2012) (Fig. 1). Other mortality events associated with PB outbreaks have been recorded near McCall, Idaho, USA in 1922-23, where 11,000 ha were affected and an estimated 25% of mature pine were killed (Evenden, 1940), and in southern Idaho in 1950-54, where 100,000 ha were affected, but mortality of < 2% was attributed to aerial



Fig. 1. Severe defoliation from pine butterfly (*Neophasia menapia*) of ponderosa pine (*Pinus ponderosa*) in 2012 at the season and interval of burn study in the southern Blue Mountain Ecoregion, Oregon, USA. Most trees ultimately recovered but a portion succumbed to attack by western pine beetle (*Dendroctonus brevicomis*) two to three years following defoliation. Photo credit: Doug Westlind. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pesticide application at the outbreak peak (Cole, 1966). In documented outbreaks a significant portion of pine mortality occurred in subsequent years being attributed to attack by WPB, and mountain pine beetle (MPB, *D. ponderosae* Hopkins), on trees stressed by the prior defoliation (Hopkins, 1907; Evenden, 1940; Furniss and Carolin, 1977).

WPB typically attack ponderosa pine stressed by other agents (Moeck et al., 1981) and are associated with excessive competition and periods of drought (Fettig et al., 2019). Adult WPB have no known primary attraction kairomone, they initiate attack through random landing and sampling of trees until a suitable host is found (Moeck et al., 1981; Raffa et al., 1993). But once attack is initiated, other WPB are drawn to the attacked tree by strong attraction to their pheromones, exo- and *endo*-brevicomin, and frontalin overwhelming tree defenses through high numbers (Bedard et al., 1980).

Increasing the resilience of dry western forests using restoration treatments of thinning and prescribed burning began in response to large and severe wildfires altering the fundamental character of forests (Agee and Skinner, 2005; Fitzgerald, 2005). But climate and disturbance are so closely linked that climate change is fundamentally altering forest disturbance regimes (Seidl et al., 2016). In addition to increasing fire occurrence and size, fire seasons are growing longer due to earlier snowmelt (Westerling et al., 2006), insect reproductive rates are increasing and winter mortality is declining (Creeden et al., 2014), and the increasing occurrence and severity of drought weakens tree defenses to insect attack (Bentz et al., 2010; Fettig et al., 2019). The effects of thinning and prescribed burning restoration treatments on forest resistance to this broader set of disturbances is not well known and better understanding is vital in planning restoration treatments. Our research objective here is to quantify differences between restoration treatments of no-burn (control), and four season-by-burn interval treatments: spring 5 yr, spring 15 yr, fall 5 yr, and fall 15 yr on tree growth, and mortality from prescribed burning, BSRD, insects, and other root diseases in previously thinned ponderosa pine stands in the southern Blue Mountain Ecoregion of Oregon, USA. Our expectations were that; 1) fall and more frequent burning would reduce tree growth due to higher fall fire severity and more frequent disturbance, 2) spring burning would increase mortality from BSRD based on prior observation of forest managers, and 3) spring burning would increase insect mortality, resulting from burning during period of high activity of most bark beetles.

2. Materials and methods

2.1. Study sites and experimental design

2.1.1. Season of burn

In summer 1996, six replicate mixed-age ponderosa pine stands (40 – 56 ha) in the Emigrant Creek Ranger District, of the southern Blue

Table 1

Tree size and stand density estimated means (95% CI below in parentheses) of ponderosa pine (*Pinus ponderosa*) by treatment in 2013, 15 years after initiating the season and interval of burn study in the Blue Mountain Ecoregion, Oregon, USA. Within columns, treatments with the same letter superscript are not different at $\alpha = 0.05$

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Mountain Ecoregion near Burns, OR, USA were selected from a larger set of stands planned to receive burn treatments. Four stands are in the eastern portion of the district near Driveway Springs (43° 48' N, 118° 59' W) designated DW14, DW17, DW26, DW28, and two stands are in the western part of the district near Idlewild campground (43° 48' N, 118° 59' W) designated as Trout Creek and Kidd Flat. The stands were predominately 80 to 100 years old with varying numbers of individuals up to 250 years old developed from native primary forest with a history of selective harvest beginning in the 1920's and natural regeneration following fire suppression beginning in the early 1900's. All stands received a low thinning in 1994 or 1995 to 181 to 252 trees ha $^{\text{-}1}$ with mean dbh from 25.5 to 31.8 cm and basal area of 17.2 to 19.4 m² ha $^{-1}$ (Thies et al., 2005). Each replicate stand was divided into three areas (4.5 - 20.5 ha) and randomly assigned treatments of fall burn, spring burn, and unburned control. Prescribed burns were conducted in October 1997 (fall) and June 1998 (spring). Tree morphology characteristics and burn damage were evaluated in 1998 following all burns using six systematically placed 0.20 ha sampling plots in each treatment (Thies et al., 2005). Results for stand structure, tree mortality attributed to fire, and BSRD incidence were previously reported through 2001, four vears following initial prescribed burns (Thies et al., 2005).

2.1.2. Interval of burn

In 2002, the study was expanded to include intervals of re-entry burns, hereafter referred to as reburns. Each season of burn treatment unit described above was divided roughly in half and randomly assigned a reburn frequency treatment of either five years or 15 years with reburns always the same season as the original treatment, control units were not subdivided. Selection of reburn frequencies was designed to bracket what was known at the time of historical mean fire return intervals for the area (Soeriaatmadja, 1966; Bork, 1984; Heyerdahl et al., 2001). This resulted in each of the six replicate stands (n = 6) having five individual treatments; the unburned control with six 0.20 ha sampling plots, and four burn season-by-frequency treatments of: (1) fall 5 yr, (2) fall 15 yr, (3) spring 5 yr, and (4) spring 15 yr, each with three 0.20 ha sampling plots. The first and second 5 yr reburns were conducted in October 2002 and 2007 (fall) and June 2003 and 2008 (spring). The third 5 yr, and first 15 yr reburns were conducted on two stands in October 2012 and May 2013, but weather conditions delayed burning the remaining four stands until October 2013 and May 2014. For all burns, mean air temperature at the time of burning averaged 6.2 °C higher during spring burns (15.5 to 30.0 °C) than fall burns (10.0 to 20.6 °C), but conditions were similar between the two seasons for relative humidity (12 to 54%), wind speed (0.0 to 11.4 km hr⁻¹), and flame length (0.0 to 1.5 m). Detailed information regarding prescribed burn dates and conditions have been described previously (Westlind and Kerns, 2017, Table 1).

0.03.						
Treatment* (n = 6)	HT ^{**}	DBH	TPH	BA	SDI	QMD
Control	16.2	31.9 ^{ab}	232	22.0 ^a	371 ^a	35.1
	(14.3 to 18.1)	(27.6 to 36.2)	(180 to 284)	(19.3 to 24.7)	(321 to 420)	(31.3 to 39.0)
Fall 5	17.3	33.7 ^{ab}	186	17.3 ^b	297 ^b	36.1
	(15.3 to 19.2)	(29.4 to 38.0)	(133 to 238)	(14.6 to 20.0)	(247 to 346)	(32.3 to 40.0)
Fall 15	17.6	35.6 ^a	167	17.8 ^b	290 ^b	38.0
	(15.7 to 19.6)	(31.4 to 39.9)	(115 to 219)	(15.1 to 20.5)	(240 to 339)	(34.1 to 41.8)
Spring 5	16.4	31.9 ^{ab}	216	20.7 ^{ab}	347 ^{ab}	35.3
	(14.4 to 18.3)	(27.7 to 36.2)	(164 to 268)	(18.0 to 23.5)	(297 to 396)	(31.5 to 39.2)
Spring 15	15.9	30.4 ^b	224	20.4 ^{ab}	334 ^{ab}	34.5
	(14.0 to 17.8)	(26.1 to 34.7)	(172 to 276)	(17.7 to 23.1)	(285 to 384)	(30.6 to 38.3)

* Treatments: Control = unburned, Fall 5 = prescribed burned in fall every 5 years, Fall 15 = prescribed burned in fall every 15 years, Spring 5 = prescribed burned in spring every 5 years, Spring 15 = prescribed burned in spring every 15 years.

^{**} Variables: HT = tree height (m), DBH = diameter breast height (cm), TPH = trees ha⁻¹ (ponderosa pine > 7.5 cm), BA = basal area (m² ha⁻¹), SDI = mixed-age stand density index, QMD = quadratic mean diameter (cm).

2.2. Sampling

In late summer of 2013, height and stem diameter was measured for all trees >7.6 cm dbh on sampling plots using laser hypsometers and diameter tapes, respectively. From 2002 through 2017 tree mortality was monitored annually in the fall and each new dead tree, with no green needles, was assessed for potential non-fire agents contributing to death. Attack by WPB, Ips spp. (species not identified), and MPB were assessed by removing bark to determine their presence from feeding and nuptial gallery patterns as described in Furniss and Carolin (1977). Red turpentine beetle (RTB, D. valens LeConte) attack was identified by the characteristically large pitch tubes typically occurring below breast height on the lower bole and root collar (Owen et al., 2010). Suppression (SP) mortality was recorded in the absence of other mortality agents when a tree was completely overtopped, and prior live crown % was very low. All new dead trees, depending on size, had two or three roots inspected at the root collar to determine presence of Annosus root disease (ARD, caused by Heterobasidion irregulare (Fr.) Bref.) and BSRD. Following the fire treatments in 1998, 2003, 2008 and 2014, trees were assessed for stem charring and crown scorch.

Ponderosa pine growth was evaluated in 2013 on all trees after the spring 2013 reburns, or 15 years after study initiation. Stands rescheduled for burning in fall 2013 and spring 2014 were included, as their reburn delay impact on the previous 15 years of growth was considered negligible. As mentioned previously, mortality from 1998 through 2001 was reported in Thies et al. (2005). Here we report mortality from 2002 through 2017 when 5 yr treatments had received three reburns and the 15 yr treatment had been reburned once.

2.3. Statistical analysis

The division of the burn treatments to study reburn frequency resulted in a randomized block, incomplete split-plot study design replicated in each of the six stands. Season of burn represents the whole plot (control, fall, and spring) and reburn frequency as the split-plot (5 yr or 15 yr). The unburned control treatment is the incomplete split, as these plots were not burned. The 2013 tree height and diameter data were used to calculate trees ha ⁻¹ (TPH), basal area (BA, m² ha⁻¹), quadratic mean diameter (QMD, cm) and stand density index (SDI, no units; Reineke, 1933) modified for mixed-age stands following the summation method described in Shaw (2006). Tree growth for the study period was calculated by subtracting the 1998 height and diameter values from those taken in 2013. From 2002 to 2017, total combined tree mortality was summed by treatment and normalized to a perhectare basis. Each contributing mortality factor including fire, PB, WPB, Ips spp., RTB, MPB, BSRD, ARD, and SP were similarly summed and normalized per hectare but, sums by contributing factors can be higher than total mortality as dead trees may be represented more than once where multiple factors contributed to mortality. Treatment means were then calculated by experimental unit (stand by treatment) for analysis. Stand descriptor means by treatment of tree height, diameter, TPH, BA, QMD, and SDI, were compared using ANOVA, with treatment modeled as a fixed effect and stand as a random effect. Tree growth and mortality analyses used the same design, but after testing all stand structure variables, the study period initial (i.e. 1998 for growth, 2002 for mortality) TPH value was used as a covariate using ANCOVA to control for treatment density differences because it was typically the only significant stand descriptor covariate or was most significant (lowest α). Because of the independent control split-plot design, response to the five treatments (control, fall 5 yr, fall 15 yr, spring 5 yr, and spring 15 yr) was compared using paired contrasts (Aastveit et al., 2009). Assumptions of normality and equal variance of residuals was checked during analysis through use of quantile-quantile and residual versus predicted plots, respectively. No transformation of response variables was necessary. To balance the possibility of type I and II error in such a large field experiment we chose to not correct for multiple comparisons. We considered effects significant based upon $\alpha = 0.05$, and marginally significant when $\alpha > 0.05$ to $\alpha \le 0.10$. All analyses were completed using the Mixed procedure of SAS 9.4 (SAS, 2014).

3. Results

3.1. Stand structure

Stand descriptor means and 95% confidence limits by treatment in 2013 for tree height, diameter, TPH, BA, SDI, and QMD are presented in Table 1. Tree height in fall 15 yr treatments was 1.7 m taller than trees in the spring 15 yr treatments (marginally significant, $t_{15.5} = 1.80$, P = 0.091), with no other height differences. Similarly, diameter of fall 15 yr trees was 5.1 cm greater than the spring 15 yr trees ($t_{15.3} = 2.40$, P = 0.030). There was 65 more TPH in the control treatments than in the fall 15 yr (marginally significant, $t_{14.4} = 1.96$, P = 0.069). BA for control treatments was 4.7 and 4.2 m² ha ⁻¹ greater than the fall 5 yr ($t_{23.9} = 2.53$, P = 0.018) and fall 15 yr ($t_{23.9} = 2.24$, P = 0.034) respectively, with no other BA differences. The control treatments SDI was 74 and 81 units greater than the fall 5 yr ($t_{21.9} = 2.40$, P = 0.025) treatments, respectively, with no other SDI differences. QMD did not differ by treatment (all P > 0.135).

3.2. Growth and mortality

Diameter growth in fall burns was 20 to 27% greater than in spring burns, and 17% above the unburned controls, but differences were only significant between the fall 5 yr and spring 15 yr treatments (P = 0.046), and marginally significant between fall 15 yr and spring 15 yr treatments (P = 0.057), and fall 5 yr and spring 5 yr treatments (P = 0.100) (Fig. 2). Height growth did not differ among treatments (all P > 0.604).

Across all treatments, annual tree mortality from 2002 to 2017 was generally low, < 2 TPH except for a moderate increase during the PB outbreak, and a more severe increase from during the WPB outbreak (Fig. 3). By treatment, overall tree mortality ha ⁻¹ was lowest in the fall and highest in the spring treatments regardless of the burn interval. Total mortality from all causes in the fall 5 yr treatments was 19.3 and 17.2 TPH less than the spring 5 yr (P = 0.043) and spring 15 yr (P = 0.070, marginally significant) treatments respectively, and total mortality in the fall 15 yr was 20.5 and 18.5 TPH less than the spring 5 yr (P



Fig. 2. Diameter growth (cm) of ponderosa pine (*Pinus ponderosa*) from 1998 through 2013 at the season and interval of burn study in the Blue Mountain Ecoregion, Oregon, USA. Bars represent 95% confidence limits. Treatments (n = 6) include an unburned control (Control), and prescribed burns repeated in fall every 5 years (Fall 5 yr), fall every 15 years (Fall 15 yr), spring every 5 years (Spring 5 yr), and spring every 15 years (Spring 15 yr). Treatments with the same letter are not different at $\alpha = 0.05$.



Fig. 4. Overall ponderosa pine (Pinus ponderosa) mortality (trees ha⁻¹) from 2002 through 2017 at the season and interval of burn study in the Blue Mountain Ecoregion, Oregon, USA. Bars represent 95% confidence limits. Treatments (n = 6) include an unburned control (Control), and prescribed burns repeated in fall every 5 years (Fall 5 yr), fall every 15 years (Fall 15 yr), spring every 5 years (Spring 5 yr), and spring every 15 years (Spring 15 yr). Treatments with the same letter are not different at $\alpha = 0.05$.

= 0.040) and spring 15 yr (P = 0.064, marginally significant) treatments respectively (Fig. 4). Direct fire mortality sustained in the reburns was very low, < 4 TPH due to limited fire severity, though slightly higher in the spring units, the differences were not significant (all P > 0.211). Mortality associated with the PB outbreak was also lowest in the fall treatments, but again not statistically different from either the control or both spring burn treatments (all P > 0.163). Mortality associated with WPB in fall 5 vr burn treatments was 9.2 and 9.3 TPH less than the control (P = 0.040) and spring 5 yr (P = 0.036) treatments respectively (Fig. 5). Mortality associated with other stressors trended lower with fall burning but was not always significant (Table 2). Mortality associated with Ips spp. did not differ by treatment (all P > 0.207). RTB associated mortality was 5.9, 5.5, 5.0 and 3.7 TPH less than the spring 15 yr treatment for the fall 5 yr ($t_{15.7} = 3.17$, P = 0.006), control ($t_{16.8} = 2.79$, P = 0.013), fall 15 yr ($t_{15.9} = 2.53$, P = 0.022), and spring 5 yr ($t_{15.7} =$ 1.98, P = 0.065, marginally significant) treatments respectively. Mortality associated with MPB in the control was 1.0 and 1.1 TPH less than the spring 5 yr ($t_{20.0} = 1.79$, P = 0.089) and spring 15 yr ($t_{20.0} = 2.05$, P= 0.054) treatments respectively, but the effect was only marginally significant. Mortality from BSRD and ARD did not differ by treatment (all P > 0.228).

Fig. 3. Annual pine mortality (trees ha⁻¹) across all treatments from 2002 through 2017 showing increased mortality from pine butterfly (PB, Neophasia menapia) and western pine beetle (WPB, Dendroctonus brevicomis) outbreaks at the season and interval of burn study in the Blue Mountain Ecoregion, Oregon, USA. Drip torch figure represents fall and spring burn years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 5. Western pine beetle (WPB, Dendroctonus brevicomis) associated mortality (trees ha⁻¹) of ponderosa pine (*Pinus ponderosa*) from 2002 through 2017 at the season and interval of burn study in the Blue Mountain Ecoregion, Oregon, USA. Bars represent 95% confidence limits. Treatments (n = 6) include an unburned control (Control), and prescribed burns repeated in fall every 5 years (Fall 5 yr), fall every 15 years (Fall 15 yr), spring every 5 years (Spring 5 yr), and spring every 15 years (Spring 15 yr). Treatments with the same letter are not different at $\alpha = 0.05$.

4. Discussion

4.1. Stand structure

2017

In 2013 SDI values ranging from 290 to 371 represent 32% to 41% of the recommended 900 biological maximum for even-age ponderosa pine managed for timber production (DeMars and Barrett, 1987; Oliver, 1995). These values are considered moderate density and below the 50% of maximum considered as the density dependent mortality range. While the fall treatments had lower tree density following the higher severity initial 1997 fall burns (Thies et al., 2005), the range of 167 to 232 TPH for all treatments remains considerably higher than the 35 to 125 TPH reported as historically typical for pre-settlement ponderosa pine stands (Covington et al., 1997; Harrod et al., 1999; Youngblood et al., 2004; Churchill et al., 2017). Further reductions in stand density to levels more historically typical would likely add disturbance resistance to the ecosystem and have elsewhere been shown to increase growth efficiency, water relations, and resin flow for the remaining trees (McDowell et al., 2003; Skov et al., 2005; Zausen et al., 2005) promoting

Table 2

Non-fire stress agents contributing to ponderosa pine (*Pinus ponderosa*) mortality (ha⁻¹) from 2002 to 2017 at the season and interval of burn study in the Blue Mountain Ecoregion, Oregon, USA. Values are estimated treatment means (95% CI below in parentheses). Within columns, treatments with the same letter superscript are not different at $\alpha = 0.05$.

	Insects	Insects			Root diseases	
Treatment* $(n = 6)$	Ips **	RTB	MPB	BSRD	ARD	SP
Control	2.6 (0 to 9.0)	3.8 ^b (0.5 to 7.1)	1.3 ^a (0.5 to 2.1)	1.7 (0 to 3.6)	0.2 (0 to 1.5)	5.3 ^{ab} (0 to 10.8)
Fall 5	0.0 (0 to 5.6)	$3.4^{\rm b}$ (0.3 to 6.5)	0.7^{ab} (0 to 1.4)	1.5 (0 to 3.1)	0.8 (0 to 2.0)	2.2^{ab} (0 to 7.3)
Fall 15	0.0 (0 to 6 0)	$4.3^{\rm b}$ (1.0 to 7.7)	$0.0^{\rm b}$	1.5 (0 to 3.3)	0.9 (0 to 2.3)	0.0^{b} (0 to 5.5)
Spring 5	1.7 (0 to 7.8)	5.6^{ab}	0.3^{ab}	(0.2 to 3.5)	1.0	8.1^{a}
Spring 15	(0 to 10.2)	9.3 ^a (6.1 to 12.5)	$0.2^{\rm b}$ (0 to 1.0)	(0.2 to 3.9) 2.2 (0.5 to 3.9)	1.3 (0 to 2.5)	(1.7 to 12.4)

* Treatments: Control = unburned, Fall 5 = prescribed burned in fall every 5 years, Fall 15 = prescribed burned in fall every 15 years, Spring 5 = prescribed burned in spring every 5 years, Spring 15 = prescribed burned in spring every 15 years.

** Mortality agents: Ips = Ips spp., RTB = red turpentine beetle, MPB = mountain pine beetle, BSRD = black stain root disease, ARD = Annosus root disease, SP = suppression.

additional resistance to bark beetle attack (Fettig and McKelvey, 2010), and drought (Bottero et al., 2017).

4.2. Tree growth

Increases in ponderosa pine radial growth in response to thinning have been well documented relative to decreased competition for resources, including light, nutrients, and water (Covington et al., 1997; Sala et al., 2005; McDowell et al., 2006). The increases in growth for fall 5 yr and fall 15 yr treatments we document are contrary to our expectation that more frequent fall burning would reduce growth due to higher fall fire severity and more frequent stress. While modest the increases in growth with fall burning, if continued over time, could result in substantial treatment diameter differences, and since all treatments here were thinned prior to the initial burns, this increased growth is in addition to the thinning response. Earlier reports from this same study found no diameter growth differences among treatments (Hatten et al., 2012; Thies et al., 2013), but growth responses to burning may take years to develop, because they could be masked by increases resulting from prior thinning, or simply delayed as trees recover from injuries sustained in the burns (Sutherland et al., 1991). At year 10, Thies et al. (2013) found that trees in all treatments were adding radial growth faster after thinning, when compared to the same trees prior to thinning, but without differences for either season or frequency of burn, however trees in fall treatments were adding diameter faster in years five to 10 than in years zero to five post fire. The increase in diameter growth documented here for the fall treatments suggests that trend continued through year 15, resulting in significantly increased diameter growth.

There are several factors that might be related to the growth patterns we observed. Two measurements from other work at these same sites imply improved water availability in the fall burn treatments. First, fall 5 yr treatments consistently had higher summer and fall soil moisture measured at 7.5 cm depth (Hatten et al., 2012), and second, analysis of carbon isotope discrimination from foliage collected in the upper third of dominant tree crowns in 2015 indicated increased stomatal conductance and photosynthetic rate (Hatten, 2020, personal communication). These patterns in water availability may be related to; 1) rapid reduction and maintenance of low litter and duff levels decreases rain interception resulting in faster infiltration to mineral soil and decreased evaporation back to the atmosphere (Hatten et al., 2012), 2) reduced surface root uptake and transpiration before reaching the mineral soil (Smith et al., 2004), and 3) reduced competition from high numbers of pine seedlings and saplings (Westlind and Kerns, 2017) (Fig. 6). In addition to water, other factors potentially contributing to increased fall 5 yr and fall 15 yr growth are increases in available nutrients such as nitrogen and phosphorous following fall burning, and longer calculated growing season due to increased solar heating and better water infiltration to mineral soil, as a result of maintained low litter and duff levels, especially in fall 5 yr treatments, (Hatten et al., 2012).

Lack of a corresponding height growth increase is not surprising, because a height growth response is more complex, and may take longer periods to become evident (Oliver, 1979), and also depends upon tree size, age, and site productivity (Tappeiner et al., 2015).

4.3. Tree mortality

4.3.1. Overall mortality

Overall mortality during the 16 years from 2002 through 2017 was generally low, only surpassing two TPH yr^{-1} during the PB defoliation and six TPH yr^{-1} during the modest WPB outbreak. However, mortality was lowest in the fall treatments regardless of reburn interval, suggesting increased tree vigor and resistance to disturbances with fall reburns, likely due to increased water and nutrient availability and longer growing season as discussed above. While the levels of mortality encountered during this study are relatively modest regardless of



Fig. 6. High number of pine seedlings and saplings developed after thinning in unburned control (left) versus reburn (right) in 2010 at the season and interval of burn study in the Blue Mountain Ecoregion, Oregon, USA. Path in center of photo is the fire line between treatments. Photo credit: Doug Westlind. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

treatment, the percentage reduction is high and if sustained over time could become quite substantial, especially under more frequent and severe disturbances expected with future changing climate. Specific mortality agents of interest encountered in this study are discussed below.

4.3.2. Mortality from fire

Mortality from the initial 1997/98 burns was either immediate, resulting from consumption or lethal heating of crown or bole tissues, or delayed over the first three years, from sublethal damage to the crown, bole and roots reducing their physiological function. Both types of mortality were significantly higher in fall than spring burns. But by year four, all treatments had low mortality rates similar to the unburned controls (Thies et al., 2005). Reburns at 5 yr or 15 yr reported here, were of very low severity with minimal immediate or delayed mortality attributed to fire, and bole or crown scorch beyond that initially observed in 1997/1998 burns was rare regardless of season (spring or fall) or interval (Westlind and Kerns, 2017; Kerns and Day, 2018). Fall reburn timing was restricted to late season periods with lower temperature and higher humidity, plus much of the litter, duff, and fine fuel that drives fire severity was previously consumed during the initial 1997 burns. Spring reburn severity, while still low, was slightly higher due to more litter, duff, and fine fuel remaining following the 1998 spring burns (Westlind and Kerns, 2017), but spring reburn severity remained low due to the higher fuel moisture content (Estes et al., 2012). Consequently, additional thinning by fire to further reduce stand density will require increases in burn severity; however, with fuels already reduced from prior burns, this will likely require a change in burn prescriptions toward warmer and lower humidity periods of late summer, or early fall when natural fires historically occurred.

4.3.3. Mortality from black stain root disease

Contrary to the prior observation of increased mortality from BSRD with spring burning, we found no effect from either burn season or interval. Low BSRD related mortality across all treatments here suggests low virulence in ponderosa pine of this area. After initial burns, Thies et al. (2005) estimated 22% of the trees in these stands were infected with BSRD based on examination of trees killed immediately by fire damage in fall 1997 and spring 1998 burns. However, low BSRD related mortality was recorded in unburned control stands, suggesting BSRD either takes a long time to kill ponderosa pine, or a low percentage of infected trees die. Potential insect vectors of BSRD include RTB and Hylastes macer (LeConte) among others (Goheen and Cobb, 1978; Goheen et al., 1985; Owen et al., 2005), both are attracted to fire damaged pines producing ethanol combined with pine monoterpenes (Kelsey and Joseph, 2003; Kelsey and Westlind, 2017), potentially increasing the spread of BSRD in burned stands. Indeed, by fall 1998, one season after the initial prescribed burns, RTB had attacked 6.2%, 24.3%, and 30.8% of the control, spring and fall treatment trees, respectively (Niwa, 1998, unpublished data). Yet, these differences in beetle attacks did not lead to differences in BSRD mortality, and appears not to have spread this disease, or it would have been recorded in our dead tree assessments for mortality agents. Rather, our results suggest BSRD infection rates in these stands declined markedly from the 22% reported by Thies et al. (2005). Of the trees that died from 2002 to 2017, only 6% had BSRD as a contributing factor, a proportion close to the 8.1% infection level reported in nearby unburned stands where entire root systems of 284 trees were examined (Kelsey et al., 2006). Our estimates were from root collar examination, and are probably lower than actual infection levels, as some roots are likely infected, but not detected. It is possible the high BSRD rate of infected trees reported by Thies et al. (2005) was a short-term response to elevated insect activity generated by the prior thinning activity and logging slash as demonstrated following Douglas fir pre-commercial thinning (Harrington et al., 1983; Hessburg et al., 2001). But in the long-term, thinning has been shown to reduce BSRD mortality in ponderosa pine from both sides of the Sierra Nevada in Northern CA (Otrosina et al., 2007; Woodruff et al., 2019). Mechanisms reducing incidence of BSRD after thinning are most likely; a) improved tree vigor in thinned stands is enough to outgrow the fungus influence, b) wider tree separation disrupts disease spread via root contact between trees, as seen in other root diseases, and c) wider separation may decrease the trees likelihood of being encountered by pathogen vectoring bark beetles (Owen et al., 2005; Woodruff et al., 2019).

4.3.4. Mortality from pine butterfly

The slight uptick in mortality associated with PB reported here was largely confined to less vigorous small trees with a tertiary or suppressed crown position. Though the differences were not significant, mortality associated with PB was lowest in the fall units burned every five years. Lower mortality in the fall 5 yr treatments aligns with our previous report from the same area where we found slightly less defoliation (5%) with fall 5 yr burning (Kerns and Westlind, 2013). Generally, defoliation episodes in conifers don't cause significant mortality themselves until defoliation exceeds 90% but can result in reduced carbon stores affecting tree growth and vigor (Cole, 1966; Schowalter, 2016), but with PB, survival depends upon tree health prior to defoliation (DeMarco, 2014). Improved water and nutrient availability in the fall 5 yr reburn units may have increased tree vigor and carbohydrate storage enough that they better withstand multiple years of defoliation.

4.3.5. Mortality from western pine beetle

The lower WPB mortality we found is also likely tied to increased tree vigor with fall 5 yr burning, as healthy ponderosa pines typically produce enough resin to either eject the attacking beetles or flood the larval gallery limiting larval development (DeMars and Roettgering, 1982). Chemical defense to attack can also be enhanced as trees respond to frequent burning with increases in resin duct development resulting in enhanced resin flow (Perrakis and Agee, 2006; Hood et al., 2015).

The WPB outbreak two years following the PB defoliation is consistent with their preference for attacking ponderosa pine stressed by other agents (Moeck et al., 1981), and the timing is similar to the earlier PB outbreak near McCall, Idaho, where defoliation peaked in 1922 and substantial WPB mortality was noted from 1924 to 1927 (Evenden, 1940). High numbers of trees stressed by multiple years of PB defoliation allow WPB populations to increase, peaking a few years after the defoliation event. Then, as surviving trees recover and become less suitable hosts, WPB populations return to endemic levels as seen here and following previous PB outbreaks.

The lack of increased WPB attack associated with the reburns is not surprising. Heat scorch of the tree bole is the primary factor contributing to post fire attack by WPB (Westlind and Kelsey, 2019) and was not present due to very low reburn severity.

5. Conclusions

Following thinning and prescribed fire as fuel reduction treatments, pine stand densities remained higher than historically typical, regardless of season or reburn interval. However, we have some evidence that fall prescribed burning, especially at more frequent intervals (e.g., repeat three times at 5-year intervals in this study), may provide additional forest health benefits. Ponderosa pine stands burned frequently in the fall added diameter faster and had less overall tree mortality, as well as less mortality during an outbreak of western pine beetle than stands burned in spring at the same frequency. Other trends with fall burning indicated increased forest health and resistance to disturbances, such as PB outbreak, and attack by RTB and Ips spp. The increased growth and lower mortality we found, while modest over the course of our study, could become substantial over longer periods. Further reductions in stand density to typical historical levels, through either mechanical thinning, or thinning by higher severity reburning, may provide additional resistance to more frequent disturbances predicted for the future.

CRediT authorship contribution statement

Douglas J. Westlind: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing - original draft, Project administration, Funding acquisition. **Becky K. Kerns:** Conceptualization, Methodology, Writing - review & editing, Project administration, Supervision, Funding acquisition.

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.

Acknowledgements

This study was funded by the Joint Fire Sciences Program, National Fire Plan, Forest Health Protection (USDA Forest Service, Special Technology Development Program) and the Pacific Northwest Research Station (USDA Forest Service). We thank W. G. Thies for initiating the study, the Malheur National Forest and the Emigrant Creek Ranger District for support and providing crews to implement the prescribed fires, Ariel Muldoon for statistical guidance, and Mee-Sook Kim, Tim Harrington, Rick Kelsey, and the anonymous reviewers for helpful comments during manuscript development.

References

- Aastveit, A.H., Almøy, T., Mejza, I., Mejza, S., 2009. Individual control treatment in splitplot experiments. Statistical Papers 50, 697–710.
- Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. 113, 11770–11775.
- Agee, J.K., 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, DC, USA.
- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manag. 211, 83–96.
- Battaglia, M.A., Smith, F.W., Shepperd, W.D., 2008. Can prescribed fire be used to maintain fuel treatment effectiveness over time in Black Hills ponderosa pine forests? For. Ecol. Manag. 256, 2029–2038.
- Bedard, W.D., Wood, D.L., Tilden, P.E., Lindahl, K.Q., Silverstein, R.M., Rodin, J.O., 1980. Field responses of the western pine beetle and one of its predators to host-and beetle-produced compounds. J. Chem. Ecol. 6, 625–641.
- Belsky, A.J., Blumenthal, D.M., 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the Interior West. Conserv. Biol. 315–327.
- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects. Bioscience 60, 602–613.
- Cascades. Oregon State University, USA.
- Bottero, A., D'Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., Asherin, L.A., 2017. Density-dependent vulnerability of forest ecosystems to drought. J. Appl. Ecol. 54, 1605–1614.
- Boyd, R., 1999. Indians, fire and the land. Oregon State University Press Corvallis, p. 54. Bradford, J.B., Bell, D.M., 2017. A window of opportunity for climate-change adaptation:
- easing tree mortality by reducing forest basal area. Front. Ecol. Environ. 15, 11–17. Buhl, C., Kanaskie, A., Navarro, S., Norlander, D., Williams, W., Heath, Z., Schroeter, R., Smith, B., 2017. Forest Health Highlights in Oregon–2016. Oregon Department of
- Forestry, USDA Forest Service, p. 34.
 Buhl, C., Kanaskie, A., Navarro, S., Williams, W., Norlander, D., Nelson, A., Schroeter, R., 2016. Forest Health Highlights In Oregon - 2015. Oregon Department of Forestry, USDA Forest Service. p. 30.
- Buhl, C., Navarro, S., Norlander, D., Williams, W., Heath, Z., Ripley, K., Schroeter, R., Smith, B., 2018. Forest Health Highlights In Oregon–2017. Oregon Department of Forestry, USDA Forest Service, p. 36.Busse, M.D., Cochran, P., Hopkins, W.E., Johnson, W.H., Riegel, G.M., Fiddler, G.O.,
- Busse, M.D., Cochran, P., Hopkins, W.E., Johnson, W.H., Riegel, G.M., Fiddler, G.O., Ratcliff, A.W., Shestak, C.J., 2009. Developing resilient ponderosa pine forests with mechanical thinning and prescribed fire in central Oregon's pumice region. Can. J. For. Res. 39, 1171–1185.
- Busse, M.D., Simon, S.A., Riegel, G.M., 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned Pinus ponderosa forests of central Oregon. For. Sci. 46, 258–268.
- Castello, J.D., Leopold, D.J., Smallidge, P.J., 1995. Pathogens, patterns, and processes in forest ecosystems. Bioscience 45 (1), 16–24.
- Churchill, D.J., Carnwath, G.C., Larson, A.J., Jeronimo, S.A., 2017. Historical forest structure, composition, and spatial pattern in dry conifer forests of the western Blue Mountains, Oregon. Gen. Tech. Rep. PNW-GTR-956. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 93 p. 956.

Cochran, P., Barrett, J.W., 1993. Long-term response of planted ponderosa pine to thinning in Oregon's Blue Mountains. West. J. Appl. For. 8, 126–132.

- Cole, W.E., 1966. Effect of pine butterfly defoliation on ponderosa pine in southern Idaho. US Dept. of Agriculture, Forest Service, Intermountain Forest & Range Experiment Station, Ogden, UT.
- Collins, B.M., Lydersen, J.M., Everett, R.G., Fry, D.L., Stephens, S.L., 2015. Novel characterization of landscape-level variability in historical vegetation structure. Ecol. Appl. 25, 1167–1174.
- Covington, W.W., Fule, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. J. Forest. 95, 23.
- Covington, W.W., Moore, M.M., 1994. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. J. Sustainable For. 2, 153–181.
- Creeden, E.P., Hicke, J.A., Buotte, P.C., 2014. Climate, weather, and recent mountain pine beetle outbreaks in the western United States. For. Ecol. Manag. 312, 239–251.
- Davis, R.S., Hood, S., Bentz, B.J., 2012. Fire-injured ponderosa pine provide a pulsed resource for bark beetles. Can. J. For. Res. 42, 2022–2036.
- DeMarco, A.T., 2014. Pine butterfly (Neophasia menapia) outbreak in the Malheur National Forest, Blue Mountains, Oregon: examining patterns of defoliation. Oregon State University, USA.
- DeMars, C.J., Roettgering, B.H., 1982. Western pine beetle. USDA For. Serv., For. Insect Dis. Leaflet 1. US Department of Agriculture, Forest Service, Washington, D.C.
- DeMars, D.J., Barrett, J.W., 1987. Ponderosa pine managed-yield simulator: PPSIM users guide. Gen. Tech. Rep. PNW-GTR-203. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 36 p 203.
- Dennison, P.E., Brewer, S.C., Arnold, J.D., Moritz, M.A., 2014. Large wildfire trends in the western United States, 1984–2011. Geophys. Res. Lett. 41, 2928–2933.
- Estes, B.L., Knapp, E.E., Skinner, C.N., Uzoh, F.C., 2012. Seasonal variation in surface fuel moisture between unthinned and thinned mixed conifer forest, northern California, USA. Int. J. Wildland Fire 21, 428–435.
- Evenden, J.C., 1940. Effects of defoliation by the pine butterfly upon ponderosa pine. J. Forest. 38, 949–955.
- Ferrell, G.T., 1996. The influence of insect pests and pathogens on Sierra forests. In: Davis, C.A. (Ed.), Sierra Nevada Ecosystem Project: Final Report to Congress. University of California Centers for Water and Wildland Resources, pp. 1177–1192.
- Fettig, C., Borys, R., Dabney, C., 2010a. Effects of fire and fire surrogate treatments on bark beetle-caused tree mortality in the Southern Cascades. California. For. Sci. 56, 60–73.
- Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negrón, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For. Ecol. Manag. 238, 24–53.
- Fettig, C.J., McKelvey, S.R., 2010. Bark beetles responses to stand structure and prescribed fire at Black Mountain Experimental Forest, California, USA: 5-year data. Fire Ecology 6 (2): 26-42 6, 26-42.
- Fettig, C.J., McKelvey, S.R., Cluck, D.R., Smith, S.L., Otrosina, W.J., 2010b. Effects of prescribed fire and season of burn on direct and indirect levels of tree mortality in ponderosa and Jeffrey pine forests in California. USA. For. Ecol. Manag. 260, 207–218.
- Fettig, C.J., McMillin, J.D., Anhold, J.A., Hamud, S.M., Borys, R.R., Dabney, C.P., Seybold, S.J., 2006. The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. For. Ecol. Manag. 230, 55–68.
- Fettig, C.J., Mortenson, L.A., Bulaon, B.M., Foulk, P.B., 2019. Tree mortality following drought in the central and southern Sierra Nevada, California. US. For. Ecol. Manag. 432, 164–178.
- Fitzgerald, S.A., 2005. Fire ecology of ponderosa pine and the rebuilding of fire-resilient ponderosa pine ecoystems.
- Flowers, R., Kanaskie, A., McWilliams, M., Mathiason, R., Schroeter, R., 2011. Forest Health Highlights in Oregon-2010. Oregon Department of Forestry, USDA Forest Service, p. 26.
- Flowers, R., Kanaskie, A., McWilliams, M., Nelson, A., Schroeter, R., 2012. Forest Health Highlights in Oregon- 2011. Oregon Department of Forestry, USDA Forest Service, p. 24.
- Flowers, R., Kanaskie, A., McWilliams, M., Williams, W., Nelson, A., Schroeter, R., 2013. Forest Health Highlights In Oregon–2012. Oregon Department of Forestry, USDA Forest Service, p. 26.
- Fulé, P.Z., Crouse, J.E., Roccaforte, J.P., Kalies, E.L., 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? For. Ecol. Manag. 269, 68–81.
- Fule, P.Z., Korb, J.E., Wu, R., 2009. Changes in forest structure of a mixed conifer forest, southwestern Colorado. USA. For. Ecol. Manag. 258, 1200–1210.
- Furniss, R.L., Carolin, V.M., 1977. Western forest insects. US Department of Agriculture, Forest Service, Washington D.C.
- Ganz, D.J., Dahlsten, D.L., Shea, P.J., 2002. The post-burning response of bark beetles to prescribed burning treatments. In: Omi, P.N., Joyce, L.A. (Eds.), Fire, Fuel Treatments, and Ecological Restoration: Conference Proceedings, April 16–18. USDA, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, p. 29.
- Goheen, D., Cobb, F., Wood, D., Rowney, D., 1985. Visitation frequencies of some insect species on *Ceratocystis wageneri* infected and apparently healthy ponderosa pines. Can. Entomol. 117, 1535–1543.
- Goheen, D.J., Cobb, F., 1978. Occurrence of Verticicladiella wagenerii and its perfect state, Ceratocystis wageneri sp. nov., in insect galleries. Phytopathology 68, 192–1191.

Harrington, T., Reinhart, C., Thornburgh, D., Cobb Jr, F., 1983. Association of black-stain root disease with precommercial thinning of Douglas-fir. For. Sci. 29, 12–14.

Harrod, R.J., McRae, B.H., Hartl, W.E., 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. For. Ecol. Manag. 114,

433–446. Hatten, J., 2020. personal communication. Forest Engineering Resources and

Management Dept. Oregon State University, Corvallis, Oregon.

- Hatten, J., Zabowski, D., Ogden, A., Thies, W., Choi, B., 2012. Role of season and interval of prescribed burning on ponderosa pine growth in relation to soil inorganic N and P and moisture. For. Ecol. Manag. 269, 106–115.
- Hessburg, P., Smith, B., Salter, R., Ottmar, R., Alvarado, E., 2000. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests. USA. For. Ecol. Manag. 136, 53–83.
- Hessburg, P.F., Agee, J.K., 2003. An environmental narrative of inland northwest United States forests, 1800–2000. For. Ecol. Manag. 178, 23–59.

Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. For. Ecol. Manag. 211, 117–139.

Hessburg, P.F., Goheen, D.J., Bega, R.V., 1995. Black stain root disease of conifers, USDA For. Serv., For. Insect Dis. Leaflet 145. US Department of Agriculture, Forest Service.

Hessburg, P.F., Goheen, D.J., Koester, H., 2001. Association of black stain root disease with roads, skid trails, and precommercial thinning in Southwest Oregon. West. J. Appl. For. 16, 127–135.

Heyerdahl, E.K., Brubaker, L.B., Agee, J.K., 2001. Spatial controls of historical fire

regimes: a multiscale example from the interior west, USA. Ecology 82, 660–678. Hood, S., Sala, A., Heyerdahl, E.K., Boutin, M., 2015. Low-severity fire increases tree defense against bark beetle attacks. Ecology 96, 1846–1855.

Hood, S.M., 2010. Mitigating old tree mortality in long-unburned, fire-dependent forests: a synthesis. General Technical Report RMRS-GTR-238. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Hopkins, A.D., 1907. Notable depredations by forest insects. In: Yearbook of Department of Agriculture for 1907. USDA, Washington, DC, pp. 149–164.

Keane, R.E., Ryan, K.C., Veblen, T.T., Allen, C.D., Logan, J.A., Hawkes, B., 2002. The cascading effects of fire exclusion in Rocky Mountain ecosystems. Rocky Mount. Futures Ecolog. Perspective 133–152.

Kelsey, R.G., Joseph, G., 2003. Ethanol in ponderosa pine as an indicator of physiological injury from fire and its relationship to secondary beetles. Can. J. For. Res. 33, 870–884.

Kelsey, R.G., Thies, W.G., Schmitt, C.L., 2006. Using chemical markers to detect root disease in stressed ponderosa pine stands with a low incidence of disease in eastern Oregon. For. Ecol. Manag. 232, 205–215.

Kelsey, R.G., Westlind, D.J., 2017. Ethanol and primary attraction of red turpentine beetle in fire stressed ponderosa pine. For. Ecol. Manag. 396, 44–54.

Kerns, B.K., Day, M.A., 2018. Prescribed fire regimes subtly alter ponderosa pine forest plant community structure. Ecosphere 9, e02529.

Kerns, B.K., Westlind, D.J., 2013. Effect of season and interval of prescribed burn on ponderosa pine butterfly defoliation patterns. Can. J. For. Res. 43, 979–983.

Kolb, T.E., Agee, J.K., Fulé, P.Z., McDowell, N.G., Pearson, K., Sala, A., Waring, R.H., 2007. Perpetuating old ponderosa pine. For. Ecol. Manag. 249, 141–157.

Landsberg, J.D., 1992. Response of ponderosa pine forests in central Oregon to prescribed underburning. In: Forest Science. Oregon State University, Corvallis, OR, p. 307. Ph.D. Thesis.

Landsberg, J.D., Cochran, P., Finck, M., Martin, R., 1984. Foliar nitrogen content and tree growth after prescribed fire in ponderosa pine. Res. Note PNW-RN-412. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 16 p 412.

Littell, J.S., McKenzie, D., Peterson, D.L., Westerling, A.L., 2009. Climate and wildfire area burned in western US ecoprovinces, 1916–2003. Ecol. Appl. 19, 1003–1021.

Maloney, P.E., Smith, T.F., Jensen, C.E., Innes, J., Rizzo, D.M., North, M.P., 2008. Initial tree mortality and insect and pathogen response to fire and thinning restoration treatments in an old-growth mixed-conifer forest of the Sierra Nevada. California. Can. J. For. Res. 38, 3011–3020.

Marlon, J.R., Bartlein, P.J., Gavin, D.G., Long, C.J., Anderson, R.S., Briles, C.E., Brown, K. J., Colombaroli, D., Hallett, D.J., Power, M.J., 2012. Long-term perspective on wildfires in the western USA. Proc. Natl. Acad. Sci. 109, E535–E543.

McCaskill, G., 2019. The Hungry Bob Fire & Fire Surrogate Study: A 20-Year Evaluation of the Treatment Effects. Forests 10, 15.

McDowell, N., Brooks, J.R., Fitzgerald, S.A., Bond, B.J., 2003. Carbon isotope discrimination and growth response of old Pinus ponderosa trees to stand density reductions. Plant Cell Environ. 26, 631–644.

McDowell, N.G., Adams, H.D., Bailey, J.D., Hess, M., Kolb, T.E., 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. Ecol. Appl. 16, 1164–1182.

McIver, J.D., Stephens, S.L., Agee, J.K., Barbour, J., Boerner, R.E., Edminster, C.B., Erickson, K.L., Farris, K.L., Fettig, C.J., Fiedler, C.E., 2013. Ecological effects of alternative fuel-reduction treatments: highlights of the National Fire and Fire Surrogate study (FFS). Int. J. Wildland Fire 22, 63–82.

Moeck, H.A., Wood, D.L., Lindahl Jr, K.Q., 1981. Host selection behavior of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. J. Chem. Ecol. 7, 49–83.

Negrón, J.F., McMillin, J., Sieg, C.H., Fowler, J.F., Allen, K.K., Wadleigh, L.L., Anhold, J. A., Gibson, K.E., 2016. Variables associated with the occurrence of Ips beetles, red turpentine beetle and wood borers in live and dead ponderosa pines with post-fire injury. Agric. For. Entomol. 18 (4), 313–326.

Niwa, C.G., 1998. USDA Forest Service, Pacific Northwest Research Station. Unpublished data, Corvallis, OR (retired).

- Oliver, W.W., 1979. Fifteen-year growth patterns after thinning a ponderosa-Jeffrey pine plantation in northeastern California. Res. Pap. PSW-RP-141. Berkeley, CA: US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 10 p 141.
- Oliver, W.W., 1995. Is self-thinning in ponderosa pine ruled by Dendroctonus bark beetles? US Department of Agriculture, Forest Service GTR-213, Rocky Mountain Research Station.

Otrosina, W., Kliejunas, J., Smith, S., Cluck, D., Sung, S., Cook, C., 2007. Black stain root disease studies on ponderosa pine parameters and disturbance treatments affecting infection and mortality. Acta Silva. Lign. Hung., Spec. Ed. 247–251.

Owen, D.R., Smith, S.L., Seybold, S.J., 2010. Red turpentine beetle. USDA For. Serv., For. Insect Dis. Leaflet 55. USDA Forest Service, Pacific Northwest Region (R6), Portland, OR.

Owen, D.R., Wood, D.L., Parmeter, J.R., 2005. Association between *Dendroctonus valens* and black stain root disease on ponderosa pine in the Sierra Nevada of California. Can. Entomol. 137, 367–375.

Perrakis, D.D.B., Agee, J.K., 2006. Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. Can. J. For. Res. 36, 238–254.

Peterson, D.L., Marcinkowski, K.W., 2014. Recent changes in climate and forest ecosystems. In: Peterson, D.L., Vose, J.M., Patel-Weynand, T. (Eds.), Climate Change and United States Forests, Advances in Global Change Research 57. Springer, New York, NY, pp. 3–11.

Peterson, D.L., Sackett, S.S., Robinson, L.J., Haase, S.M., 1994. The effects of repeated prescribed burning on Pinus ponderosa growth. Int. J. Wildland Fire 4, 239–247.

Pollet, J., Omi, P.N., 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. Int. J. Wildland Fire 11, 1–10.

Raffa, K.F., Phillips, T.W., Salom, S.M., 1993. Strategies and mechanisms of host colonization by bark beetles. In: Schowalter, T.D., Filip, G.M. (Eds.), Beetle-pathogen interactions in conifer forests. Academic Press Inc., San Diego, CA, pp. 103–128.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. f Agri. Res. 46, 627–638.

Reinhardt, E.D., Keane, R.E., Calkin, D.E., Cohen, J.D., 2008. Objectives and considerations for wildland fuel treatment in forested ecosystems of the interior western United States. For. Ecol. Manag. 256, 1997–2006.

Ryan, K.C., Reinhardt, E.D., 1988. Predicting postfire mortality of seven western conifers. Can. J. For. Res. 18, 1291–1297.

Sala, A., Peters, G.D., McIntyre, L.R., Harrington, M.G., 2005. Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season. Tree Physiol. 25, 339–348.

SAS, 2014. Base SAS 9.4 Procedures Guide. SAS Institute Inc., Cary, NC.

Schowalter, T.D., 2016. Insect ecology: an ecosystem approach. Academic Press. Schwilk, D.W., Knapp, E.E., Ferrenberg, S.M., Keeley, J.E., Caprio, A.C., 2006. Tree

mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. For. Ecol. Manag. 232, 36–45.

Scott, D.W., 2012. Pine Butterfly, Forest Insect and Disease Leaflet 66. USDA Forest Service, Pacific Northwest Region (R6), Portland, Oregon.

Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hicke, J.A., 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J. Appl. Ecol. 53, 120–129.

Shaw, J.D., 2006. Reineke's stand density index: where are we and where do we go from here?, in: Proceedings: Society of American Foresters 2005 National Convention; October 19-23, 2005, Fort Worth, Texas, Bethesda, MD: Society of American Foresters:[1]-13.

Skov, K.R., Kolb, T.E., Wallin, K.F., 2004. Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. For. Sci. 50, 81–91.

Skov, K.R., Kolb, T.E., Wallin, K.F., 2005. Difference in radial growth response to restoration thinning and burning treatments between young and old ponderosa pine in Arizona. West. J. Appl. For. 20, 36–43.

Smith, J.E., McKay, D., Niwa, C.G., Thies, W.G., Brenner, G., Spatafora, J.W., 2004. Short-term effects of seasonal prescribed burning on the ectomycorrhizal fungal community and fine root biomass in ponderosa pine stands in the Blue Mountains of Oregon. Can. J. For. Res. 34, 2477–2491.

Soeriaatmadja, R., 1966. Fire history of the ponderosa pine forests of the Warm Springs Indian Reservation. Oregon State University, USA.

Sohn, J.A., Saha, S., Bauhus, J., 2016. Potential of forest thinning to mitigate drought stress: A meta-analysis. For. Ecol. Manag. 380, 261–273.

Stephens, S.L., McIver, J.D., Boerner, R.E., Fettig, C.J., Fontaine, J.B., Hartsough, B.R., Kennedy, P.L., Schwilk, D.W., 2012. The effects of forest fuel-reduction treatments in the United States. Bioscience 62, 549–560.

Sutherland, E.K., Covington, W.W., Andariese, S., 1991. A model of ponderosa pine growth response to prescribed burning. For. Ecol. Manag. 44, 161–173.

Tappeiner, I., John, C., Bailey, J.D., Harrington, T.B., Maguire, D.A., 2015. Silviculture and ecology of western US forests. Oregon State University Press.

Thies, W.G., Westlind, D.J., Loewen, M., 2005. Season of prescribed burn in ponderosa pine forests in eastern Oregon: impact on pine mortality. Int. J. Wildland Fire 14, 223–231.

Thies, W.G., Westlind, D.J., Loewen, M., 2013. Field Note: Impact of Spring or Fall Repeated Prescribed Fire on Growth of Ponderosa Pine in Eastern Oregon. USA. West. J. Appl. For. 28, 128–132.

Vernon, M.J., Sherriff, R.L., van Mantgem, P., Kane, J.M., 2018. Thinning, tree-growth, and resistance to multi-year drought in a mixed-conifer forest of northern California. For. Ecol. Manag. 422, 190–198.

Weaver, H., 1943. Fire as an ecological and silvicultural factor in the ponderosa-pine region of the pacific slope. J. Forest. 41, 7–15.

Weaver, H., 1961. Ecological changes in the ponderosa pine forest of Cedar Valley in southern Washington. Ecology 42, 416–420.

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Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. science 313, 940–943.

- Westlind, D.J., Kelsey, R.G., 2019. Predicting post-fire attack of red turpentine or western pine beetle on ponderosa pine and its impact on mortality probability in Pacific Northwest forests. For. Ecol. Manag. 434, 181–192.
- Westlind, D.J., Kerns, B.K., 2017. Long-term effects of burn season and frequency on ponderosa pine forest fuels and seedlings. Fire Ecology 13, 42–61.
- Woodruff, W., Greenberg, D., Cannon, P., 2019. Results of a thinning study in a black stain (Leptographium wageneri)-infested Jeffrey/ponderosa pine forest in northern California. For Pathol. e12551.
- Youngblood, A., Max, T., Coe, K., 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. For. Ecol. Manag. 199, 191–217.
- Zausen, G., Kolb, T., Bailey, J., Wagner, M., 2005. Long-term impacts of stand management on ponderosa pine physiology and bark beetle abundance in northern Arizona: a replicated landscape study. For. Ecol. Manag. 218, 291–305.
- Zhang, J., Ritchie, M.W., Maguire, D.A., Oliver, W.W., 2013. Thinning ponderosa pine (Pinus ponderosa) stands reduces mortality while maintaining stand productivity. Can. J. For. Res. 43, 311–320.