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Impacts of fire radiative flux on mature *Pinus ponderosa* growth and vulnerability to secondary mortality agents

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Abstract. Recent studies have highlighted the potential of linking fire behaviour to plant ecophysiology as an improved route to characterising severity, but research to date has been limited to laboratory-scale investigations. Fine-scale fire behaviour during prescribed fires has been identified as a strong predictor of post-fire tree recovery and growth, but most studies report these metrics averaged over the entire fire. Previous research has found inconsistent effects of low-intensity fire on mature *Pinus ponderosa* growth. In this study, fire behaviour was quantified at the tree scale and compared with post-fire radial growth and axial resin duct defences. Results show a clear dose–response relationship between peak fire radiative power per unit area (W m^{-2}) and post-fire *Pinus ponderosa* radial growth. Unlike in previous laboratory research on seedlings, there was no dose–response relationship observed between fire radiative energy per unit area (J m^{-2}) and post-fire mature tree growth in the surviving trees. These results may suggest that post-fire impacts on growth of surviving seedlings and mature trees require other modes of heat transfer to impact plant canopies. This study demonstrates that increased resin duct defence is induced regardless of fire intensity, which may decrease *Pinus ponderosa* vulnerability to secondary mortality agents.

Additional keywords: conifers, fire behaviour, fire severity, post-fire impacts.

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Introduction

Low-intensity surface fires have a well-documented role in maintaining healthy ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests (Agee 1998; Heyerdahl *et al.* 2001; Baker 2009). Surface fires can reduce susceptibility to high-intensity, stand-replacing fires by consuming surface fuels, thinning understorey trees and shrubs, and increasing canopy base height of dominant trees (Steele *et al.* 1986; Busse *et al.* 2000; Strom and Fulé 2007). Changes in climate and widespread fire exclusion have led to fuel accumulation and forest structural changes resulting in higher-intensity fires across the western United States (Stephens *et al.* 2009). To counter this trend, management efforts have included low-intensity prescribed fires as a tool to help return these forests to characteristic stand densities and fuel loadings (Agee and Skinner 2005). The resulting range of surface fire intensity (wildfire to prescribed fire) in *Pinus ponderosa* forests is large, and varies considerably depending on the fuel complex structure, ignition pattern, burning conditions, slope and other factors (Alexander and Cruz 2012). High variability in fire intensity, coupled with secondary mortality agents such as bark beetles and disease, have resulted in considerable uncertainties in identifying the causes and magnitudes of tree vulnerability, recovery and mortality post-fire. Although many fire effects models exist, none spatially quantify post-fire ecological and physiological characteristics, limiting our understanding of ecosystem carbon dynamics and our ability to manage landscapes pre- and post-fire (Reinhardt and Dickinson 2010; Smith *et al.* 2016).

The effects of fire on tree growth and physiology are a consequence of the transfer of heat into the roots, bole and crown (Michaletz and Johnson 2007). Heat-induced cell necrosis can reduce growth by damaging apical and lateral meristems and can eventually lead to tree mortality. Many empirical studies have linked visual assessments of crown and bole damage with post-fire tree mortality and recovery (Ryan and Reinhardt 1988; Mantgem *et al.* 2003; Hood *et al.* 2007). Unfortunately, most studies have failed to link fire behaviour with post-fire vegetation response (Smith *et al.* 2016). This is illustrated in Table 1, which shows widely differing *Pinus ponderosa* growth and physiology responses despite similar treatments, tree sizes and ages, and post-fire sampling times. Research that has tried to link heat transfer with vegetation response has mainly focused on localised cell death, such as through stem girdling and cell deformation (Bova and

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Table 1. Summary of previous research on *Pinus ponderosa* growth and physiological responses to fire

Fire behaviour metrics include: I, fireline intensity; FL, flame length. Growth or other physiological metrics include: DBH, diameter at breast height; BAI, basal area increment; A, photosynthesis; pre-dawn Ψ, pre-dawn water potential. Notation: ns, non-significant. State acronyms include: Colorado, CO; Oregon, OR; Arizona, AZ; Montana, MT; Idaho, ID; Utah, UT

Location	Approx. age	Approx. DBH (cm)	Treatments	Fire behaviour	Growth or physiological metric	Increase (+), decrease (−)	Sampling Time (year post-fire)	Reference
Growth metrics								
Rocky Mountains, CO	–	21–34	Burn (fall (autumn)), no burn, control	Avg. I: 20 kW m^{-1}	Fascicle length, bud size	+	1	Wyant *et al.* 1983
Central OR	45	25	Burn (high fuel consumption), burn (moderate fuel consumption), control	FL (m): 0.3–0.5 (mod.), 0.6–1.0 (high) ROS (m min^{-1}): 2–4.6 (mod.), 0.3–0.6 (high)	Needle mass, foliar nitrogen, tree height, basal area	–	1, 4	Landsberg *et al.* 1984
Central AZ	50–190	20–40	Burn (fall), control	FL < 0.4 m	BAI	– ns	<2 8	Sutherland *et al.* 1991
Central AZ	115–423	16–41	Thin, thin + burn (fall), control	FL: 0.15 m (0.6 m max.)	A, BAI Pre-dawn Ψ	+ –	1, 2	Feeney *et al.* 1998
South-central OR	–	–	Burn (spring), control	I: 4.2–48 kW m^{-1}, FL: 0.15–0.46 m	Basal area, crown length	–	2–4	Busse *et al.* 2000
Central AZ	–	26 ± 1.1	Thin + burn (spring)	FL: 0.3–0.6 m (2.5 m max.)	A, pre-dawn Ψ	+	<1	Wallin *et al.* 2003
Bitterroot Mountains, MT	70	25–31	Thin, thin + burn (spring and fall), control	–	A, radial wood growth	ns	9	Sala *et al.* 2005
Bitterroot Mountains, MT	20–250	–	Thin, thin + burn (spring), control	–	BAI	+	10	Fajardo *et al.* 2007
Blue Mountains, OR	80–100	–	Burn (spring), burn (fall), control	FL: 0.6 m	BAI	ns	1–2	Hatten *et al.* 2012
North-central ID	34	23 ± 0.6	Thin + burn (fall), thin control	FL: 0.2–1.1 m, I: 83–2712 kW m^{-1}	Relative wood growth	–	1.5	Present study
Resin metrics								
Central AZ	115–423	16–41	Thin, thin + burn (fall), control	FL: 0.15 m (0.6 m max.)	Resin flow	+	1, 2	Feeney *et al.* 1998
Central AZ	–	26 ± 1.1	Thin + burn (spring)	FL: 0.3–0.6 m (2.5 m max.)	Resin production	–	<1	Wallin *et al.* 2003
Crater Lake NP, OR	–	94 ± 22.4	Burn (spring), burn (fall), control	FL: 0.18–0.6 m (spring), 0.3–0.9 m (fall)	Resin flow	+	1, 2	Perrakis and Agee 2006
Western MT	–	>25	Thin, thin + burn (spring), burn (spring), control	FL: 0.2–2.7 m	Resin flow	+	1, 2 months	Six and Skov 2009
MT, ID	–	21.5–46.6	Wildfire (fall), burn (spring)	–	Resin flow	+	0.25–3	Davis *et al.* 2012
MT, UT	–	29.5	Wildfires	–	Resin duct size and area	+	1, 2	Hood *et al.* 2015
North-central ID	34	23 ± 0.6	Thin + burn (fall), thin control	FL: 0.2–1.1 m, I: 83–2712 kW m^{-1}	Resin duct size and area	+	1.5	Present study

Dickinson 2005; Michaletz *et al.* 2012). For instance, Michaletz *et al.* (2012) observed heat-induced xylem conduit wall deformation and cavitation, which they hypothesised could lead to reduced xylem conductivity and tree mortality. Other studies have applied hot water baths to excised branch segments as a proxy for fire (West *et al.* 2016). However, these studies are limited in their inference because they do not replicate natural fire conditions where large sections of plants are exposed to heat (Smith *et al.* 2016). Further, the constant heat flux created by the application of a heater, controlled flame or water bath is limited in relevance to the sporadic short-duration heat pulses that are experienced in a wildland fire (Kremens *et al.* 2010). Physiologically, the application of heat to a plant module or portion of the stem provides insight into cellular and molecular processes, but may miss both compensatory responses that allow plants to maintain physiological function at an organismal scale (Trifilò *et al.* 2011) and potential synergistic effects that could result from damage to multiple portions of the plant.

Fire damage to boles and crowns can reduce photosynthetic potential and phloem transport and increase immediate (within 2 years post-fire) *Pinus ponderosa* vulnerability to secondary mortality agents, such as *Dendroctonus ponderosae* (mountain pine beetle) (Davis *et al.* 2012). Primary tree defence to bark beetle attacks consists of resin duct systems that can transport resin vertically through axial ducts in the sapwood and radially through ducts in the sapwood and phloem (Lieutier 2002; Hood *et al.* 2015). In pines, resin ducts are crucial during beetle attack and serve as physical barriers that are toxic to both the beetles and the symbiotic fungi introduced by the beetles (Lieutier 2002; Hood *et al.* 2015). Resin duct systems can be classified as defences that are either constitutive, which are preformed before damage, or induced, which are activated by injury or pest colonisation (Lieutier 2002). There is growing evidence that trees with greater resin duct defences (i.e. resin duct size and proportional area of growth ring) have a greater chance of surviving beetle attack than trees with lesser defences (Kane and Kolb 2010; Ferrenberg *et al.* 2014; Hood *et al.* 2015*a*). Resin duct properties have been demonstrated to be more important than growth for predicting tree survival (Kane and Kolb 2010; Hood and Sala 2015).

Low-intensity surface fires have been observed to increase the size and production of resin ducts and enhance resin flow in *Pinus ponderosa* (Feeney *et al.* 1998; Perrakis and Agee 2006; Davis *et al.* 2012; Hood *et al.* 2015*a*). This increase in resin duct defence can persist for years post-fire, increasing constitutive defences and long-term resistance to pest attack (Hood *et al.* 2015*a*). Hood *et al.* (2015*a*) hypothesised that non-lethal fire damage could serve as a cue for trees to increase defence capacity in preparation for beetle attacks that are common post-fire (Hood and Bentz 2007; Davis *et al.* 2012). In the studies we have identified (Table 1), the induction of increased resin duct defence in *Pinus ponderosa* following wildfire is fairly universal. However, none of these studies related spatial variation in fire behaviour to differences in resin duct formation, leaving relationships between fire intensity and post-fire changes in tree defences largely unknown.

Recent studies have highlighted the utility of using radiative heat flux metrics that quantify fire energy as a route to characterise fire behaviour and predict post-fire tree mortality, growth and physiological function. Radiation typically represents only ~11–17% of the total heat flux (Freeborn *et al.* 2008; Kremens *et al.* 2012; Smith *et al.* 2013); however, it is fairly easy to measure (Kremens *et al.* 2010) and is strongly correlated with other heat flux components (Freeborn *et al.* 2008). Kremens *et al.* (2012) and Hudak *et al.* (2016) used fire radiative power per unit area, hereafter referred to as fire radiative flux density (FRFD: W m^{-2}) to characterise fire behaviour in oak woodland and longleaf pine forests respectively. Satellite-derived fire radiative power (FRP: W) has been used to predict changes in burn severity spectral indices at landscape scales (Heward *et al.* 2013) and FRP products derived from the Moderate Resolution Imaging Spectrometer (MODIS) are widely used in the assessment of fire regimes (Giglio 2007; Roberts *et al.* 2009; Archibald *et al.* 2010; Andela *et al.* 2015) and regional and global fire emissions (Mebust *et al.* 2011; Kaiser *et al.* 2012; Konovalov *et al.* 2014). Recent studies have observed dose–response relationships in *Pinus contorta* (lodgepole pine) and *Larix occidentalis* (western larch) seedlings to increasing doses of fire radiative energy per unit area, hereafter referred to as fire radiative energy density (FRED: J m^{-2}). Specifically, under controlled nursery and laboratory conditions, increasing FRED dose resulted in decreasing photosynthesis and diameter at root collar in surviving trees (Smith *et al.* 2017) and increased mortality at extended temporal scales (Sparks *et al.* 2016). These studies indicate that there is a strong link between measures of radiative heat flux and vegetation response and mortality. However, there is a need to investigate such linkages on larger trees and under field burning conditions. In larger trees, we would expect that defensive traits, such as crown base height and bark thickness, would result in reduced impacts of heat flux dose on the post-fire recovery and mortality (Wade 1993). Trees burning within the natural environment (not within a laboratory) would also be expected to be more resistant given they have adapted to environmental conditions and variability. Consequently, in the present study, we sought to answer the following questions:

(1) Is there a dose–response relationship between metrics of fire intensity and radiative flux and the post-fire mature tree growth? If yes, are the radiative heat flux metrics the same as those observed to produce dose–response relationships in seedlings and if not, why?
(2) Is there a dose–response relationship between metrics of fire intensity and fire radiative flux and mature tree defences?

Methods

Site description and experimental design

The University of Idaho Experimental Forest (UIEF) is located on the Palouse Range, ~20 km north-east of Moscow, Idaho. The UIEF is characterised by a mixed-conifer temperate forest. Dominant tree species within the UIEF include *Pseudotsuga menziesii* (Douglas-fir), *Abies grandis* (grand fir), *Thuja plicata* (western red cedar) and *Pinus ponderosa* (ponderosa pine). Mean summer temperature over the 1981–2010 time period was 16.4°C and mean summer precipitation was 97.5 mm (annual precipitation was 658.1 mm) (Arguez *et al.* 2010).

Three even-aged *Pinus ponderosa*-dominated stands were chosen for the present study, ranging in elevation from ~880 to

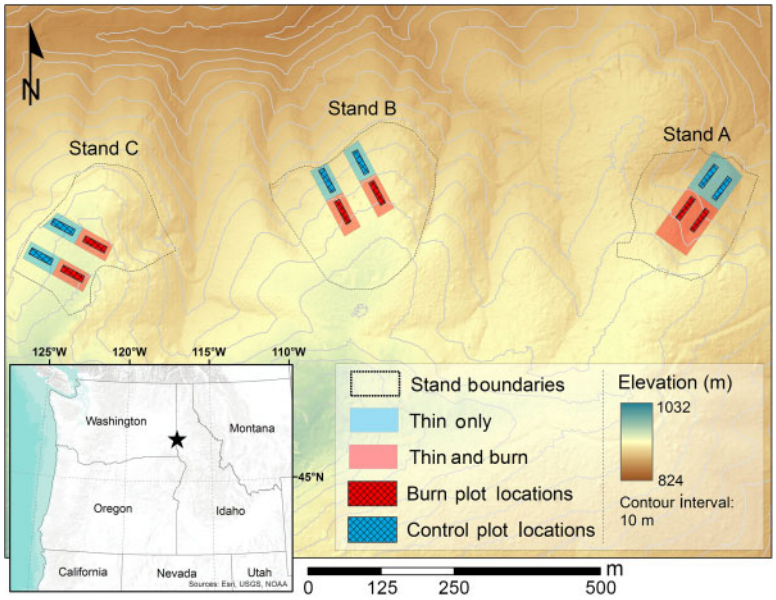

Fig. 1. Location of the treatment units and plot locations within the three *Pinus ponderosa* stands at the University of Idaho Experimental Forest near Moscow, Idaho. (For colour figure, see online version available at http://www.publish.csiro.au/nid/17.htm.)

950 m (Fig. 1). The three stands were planted in 1982 following clear-cut and broadcast burn treatments and have understories dominated by *Physocarpus malvaceus* (ninebark) and *Symphoricarpos albus* (snowberry). In June 2014, approximately 2 ha of each stand was mechanically thinned using a boom-mounted brushing head on a CAT 320B excavator (Caterpillar Inc.). All understorey shrubs were chipped and the overstorey *Pinus ponderosa* was thinned to a target spacing of 6 m and chipped (see Fig. 2 for pre-burn conditions). The thinning decreased basal area (m^2 ha^{-1}) of trees >5 cm diameter at breast height (DBH) by an average of 12.1 m^2 ha^{-1} across all three stands (Table 2). Likewise, stand density (tree ha^{-1}) of trees >5 cm DBH was reduced by an average of 655 trees ha^{-1} across all three stands (Table 2).

Prescribed burns were conducted on two consecutive days in late October 2014 in one-half of each stand to reduce surface fuel loadings. Prior to the prescribed burns, nine 5 × 7-m rectangular plots were selected from a 60-plot grid established as part of an ongoing study (Fig. 3). The nine plots were deliberately selected to exhibit a wide variability of slopes, aspects, fuel loading and moisture content to facilitate a large range of potential fire behaviour conditions. Temperature during burning operations on both days ranged from 16 to 20°C, with the highest temperature occurring at the start of operations and the lowest temperature occurring at the end of operations. Likewise, relative humidity ranged from 26 to 52% both days. Surface winds were 1.6–4.8 km h^{-1} during burning operations. Plots were ignited with a drip torch on the downhill side to establish a uniform head fire flaming front, with ignition lines separated by ~8 m.

Fire behaviour and fuel consumption

Fireline intensity was calculated using the low heat of combustion for *Pinus ponderosa* chipped woody material and needles. To calculate the heat yield of the fuel consumed in each plot, we followed the calculations presented in Van Wagner (1972) for woody fuels and subtracted the heat loss due to bound and free water. Specifically, a deduction of 1264 kJ kg^{-1} was made from high heat of combustion estimates obtained through bomb calorimetry. Fuel depth and loading of fine and coarse woody debris (1-, 10-, 100-, 1000-h fuels), duff and litter were obtained through destructive quadrat (0.5 by 0.5 m) sampling in the four corners of each plot. Following collection, the fuels were sorted and oven-dried to obtain dry fuel loading (detailed in Table 3). Litter and 1-, 10- and 100-h fuel samples ($n = 5$) were collected immediately before plot ignition just outside each plot, sealed in plastic bags and oven-dried to obtain fuel moisture content. Ignition operation logistics did not permit the collection of litter and 1-h fuel moisture samples in plots 1 and 2. Consumption was estimated following Kreye *et al.* (2013). Specifically, a systematic grid of nine steel pins was installed in each instrumented plot in order to measure the average depth of pin exposed post-fire. This method was used as there were strong linear relationships ($r^2 = 0.66$, s.e. = 3.52 kg m^{-2}, $P < 0.001$) between woody fuel depth and total fuel load derived from 62 individual quadrats. These relationships have also been observed in similar chipped fuelbeds (Reiner *et al.* 2009). To enable the calculation of rate of spread, video cameras (Samsung HMX-F90 HD Camcorder, Samsung Electronics America Inc.) were positioned at each of the plots such that the plot corner pin flags and centre of the plot were visible. The average rate of spread for each plot was calculated by analysing the time to travel between different sets of reference points ($n = 10$). As all of the plots had some slope and were ignited from the bottom, the direction of spread was predominately uphill and in line with reference points.

We used the definition of flame length described by Johnson (1992) owing to its ease of use and interpretation, where flame length is the distance from the centre of the burning bed on the

Fig. 2. Fuelbed conditions pre-burn, during and post-burn for plots with fire radiative energy density (FRED) ranging from minimum observed values (bottom row) to maximum observed values (top row).

Table 2. Stand characteristics pre- and post-thinning (mean ± s.e.)
DBH, diameter at breast height

Timeframe	Stand	DBH (cm)		Height (m)		Basal area (m^2 ha^{-1})		Density (trees ha^{-1})	
Pre-thinning	A	14.9	± 0.7	9.4	± 0.4	24.6	± 1.4	1325.0	± 89.7
	B	17.6	± 0.6	10.9	± 0.2	32.8	± 2.6	1208.3	± 79.3
	C	19.0	± 1.4	10.6	± 0.9	24.0	± 3.5	700.0	± 56.4
Post-thinning	A	18.2	± 0.9	11.0	± 0.5	10.6	± 1.1	383.3	± 20.7
	B	21.8	± 0.9	12.9	± 0.4	14.6	± 1.5	391.7	± 45.2
	C	21.7	± 1.4	11.8	± 0.8	20.0	± 3.5	491.7	± 62.1

surface to the tip of the continuous flame in the direction of the travelling fire front. The centre towers were marked with graduated height intervals to create reference points to aid in the assessment of flame length. Flame lengths were observed and recorded by field observers and were validated through examination of still-frame video data, analysed at 10-s intervals. Flame residence time was derived from the video data and was calculated as the total time that plots maintained continuous flaming combustion (Cheney 1990). Smouldering time was estimated to be the difference between the total duration of radiometer signal above average pre-fire values and flame residence time.

Fire radiative flux density (W m^{-2}) was calculated using observations from dual-band infrared radiometers and methodology detailed in Kremens *et al.* (2012). The dual-band infrared radiometers were affixed on instrument towers 5.2 m above the centre of each plot and recorded data at 0.1 Hz from pre-ignition to fire extinction. The size of the burning plot exceeded the radiometer field of view, thus minimising edge effects.

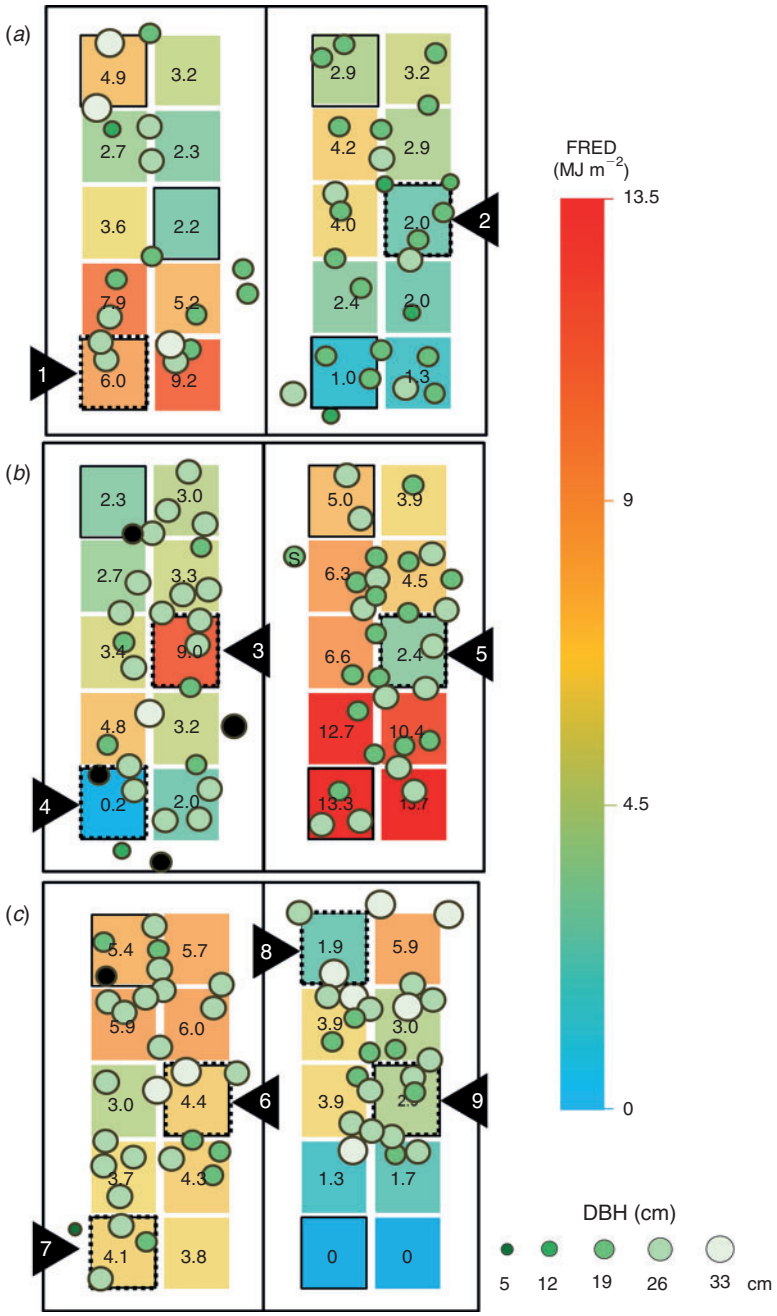

Fig. 3. Stem map of *Pinus ponderosa* by diameter at breast height (DBH) class with observed and modelled fire radiative energy density (FRED) (stands (*a*)–(*c*)). Numbered plots (1–9) with dotted outlines indicate where consumption and fire radiative flux density (FRFD) were measured. Solid plot outlines indicate plots where fuel consumption was measured and FRED was modelled. Consumption and FRED were modelled for plots with no outlines. Trees outside the plots but within 2 m are shown for illustrative purposes. Black and 's' trees indicate dead and stressed trees respectively.

We calculated FRED (J m^{-2}) as the time integral of FRFD observations for each plot. For non-instrumented plots, FRED was modelled using the combustion factor (kg J^{-1}) derived from linear regression analysis between observed FRED and fuel consumption ($r^2 = 0.92$, s.e. = 0.991 kg m^{-2}, $P < 0.001$). Effects of variable FRED dose duration (J m^{-2} h^{-1}) are not well researched (Smith *et al.* 2016) and so we also calculated FRED normalised by total burn duration for each plot (average FRFD per

Table 3. Pre-fire fuel characteristics and fire behaviour, consumption and radiative flux metrics derived from videography and infrared radiometers

FL, flame length; ROS, rate of spread; I, fireline intensity; $FRFD_{peak}$, peak fire radiative flux density; FRED, fire radiative energy density; $FRFD_{\mu}$, average fire radiative flux density

Plot	Fuel load (kg m^{-2})			Fuel moisture content (%)			Litter + duff depth (cm)	Total consumption (kg m^{-2})	FL (m)	ROS (m min^{-1})	I (kW m^{-1})	Flame residence time (h)	Smouldering time (h)	$FRFD_{peak}$ (kW m^{-2})	FRED (MJ m^{-2})	$FRFD_{\mu}$ (MJ m^{-2} h^{-1})
	Litter	Duff	Wood	Litter	1-h	10-h	100-h									
1	0.8	1.6	3.9	–	–	9	15	7.9	4.2	0.30	0.50	734	0.37	6.52	5.96	6.00	0.87
2	1.2	4.4	2.8	–	–	12	18	8.4	2.2	0.23	0.45	324	0.15	17.68	3.62	1.99	0.11
3	2.3	5.1	14.5	13	23	28	41	5.7	6.6	0.30	0.37	637	0.34	14.16	2.16	9.75	0.68
4	0.3	8.3	2.8	40	26	26	53	7.3	1.6	0.30	0.27	83	0.12	1.24	1.69	0.17	0.15
5	1.0	1.0	5.8	22	22	23	22	8.1	3.0	0.79	0.55	346	0.25	10.47	3.81	2.41	0.22
6	1.4	4.2	3.9	20	26	27	57	5.2	4.7	1.07	2.22	2516	0.14	8.78	11.74	4.36	0.49
7	0.3	1.3	1.5	16	18	19	28	4.7	1.8	1.02	6.00	2712	0.08	22.03	16.27	4.09	0.19
8	0.2	2.2	2.9	14	16	19	37	8.4	2.3	0.61	0.80	460	0.13	11.87	2.79	1.94	0.04
9	0.4	2.4	2.4	14	19	27	54	7.8	1.7	0.61	2.40	1099	0.20	12.35	5.70	2.94	0.23

unit time: $FRFD_{\mu}$). $FRFD_{\mu}$ was obtained by dividing FRED by the total duration of radiometer signal above average pre-fire values.

Tree growth and resin ducts

In March 2016, a mortality and tree health survey was conducted in all prescribed-burned stands. Live or dead status, DBH and overall stem and crown condition were recorded for each tree. Additionally, we collected 5-mm increment cores at ~1.37 m above the ground from all ($n = 31$) trees within the nine 5 × 7-m study plots. Additional cores ($n = 31$) were also collected from trees in randomly selected control plots of the unburned half of each stand (see Fig. 1 for control plot locations). Cores were prepared for cross-dating following standard methodology (Speer 2010). Ring widths were measured to the nearest 1 μm using a Nikon SMZ800 microscope (Nikon Instruments Inc.) equipped with a Velmex micrometer and Metronics digital readout (Velmex Inc.). Ring widths were used to calculate relative growth (% deviation from mean 3-year pre-fire growth), calculated as $[(Growth_{year_x} - Growth_{avgPrefire})/Growth_{avgPrefire}]$. Images of each core were obtained using a SPOT Idea 5 MP camera and *SPOT Imaging Microscopy Imaging Software version 5.2* (Diagnostic Instruments, Inc.). Images were acquired at a resolution (0.741 pixels μm^{-1}) where individual earlywood and latewood tracheid cells were clearly visible. This resolution was considered adequate as the resin ducts in this study were, on average, 30 and 90 times greater in size compared with earlywood and latewood cells respectively. Axial resin duct size was obtained using *ImageJ 1.50b* (US National Institutes of Health) following methodology presented in Hood *et al.* (2015*a*).

Statistics

Growth and resin duct metric differences between burned and control trees were compared with ANOVA, and if significant, a Tukey's Honest Significant Difference test ($\alpha = 0.05$) was employed. Growth and resin duct metric differences were also analysed by peak FRFD, FRED and $FRFD_{\mu}$ class to determine if there was a dose–response relationship. Data were organised into classes using equal-width bins for each radiative energy flux metric. Distributional assumptions required for ANOVA were graphically assessed and homogeneity of variances were verified using the 'Bartlett Test of Homogeneity of Variances' (Bartlett 1937). Relationship 'goodness of fit' between dependent and independent variables was assessed using the coefficient of determination (r^2) and standard error of the estimate (s.e.) from regression analysis.

Results

Fire behaviour, consumption and radiative flux measurements for each plot are summarised in Table 3 and typical fire behaviour is shown in Fig. 2. Although some plots displayed very active fire behaviour (high rate of spread and long flame length), most plots were dominated by smouldering combustion. On average, smouldering-dominated combustion represented 97.3% of the total burn duration. Similar to studies in other ecosystems (Kremens *et al.* 2012), we observed linear relationships between peak FRFD and fireline intensity. Peak FRFD was linearly related with both fireline intensity ($r^2 = 0.96$, s.e. = 284.6, $P < 0.001$) and fireline intensity derived from

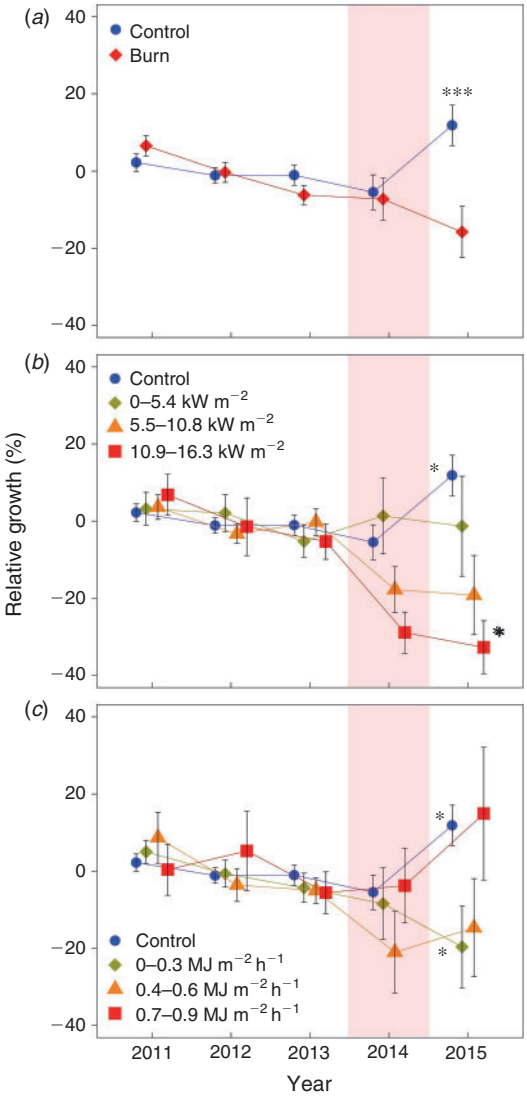

Fig. 4. *Pinus ponderosa* relative radial growth (mean ± s.e.) by treatment (*a*); peak fire radiative flux density (FRFD) class (*b*); and normalised average fire radiative flux density ($FRFD_{\mu}$) class (*c*). Relative radial growth is calculated as $[(Growth_{yearx} - Growth_{avgPrefire})/Growth_{avgPrefire}]$. Highlight indicates year that prescribed fires were conducted. Asterisks indicate significant differences: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

flame length ($r^2 = 0.86$, s.e. = 59.7, $P < 0.001$). Two trees died within the plots, one with 17.8-cm DBH and one with 22.1-cm DBH. These trees died in plots with FRED ranging from 0.2 to 5.4 MJ m^{-2} and had no obvious signs of bark beetle attack (e.g. pitch tubes, beetle larvae galleries) ~1.5 years after the burns. Owing to the fact that only two trees died within the burn plot boundaries during the study period (Fig. 3), we had little statistical power to detect a relationship between fire behaviour and tree mortality.

There were no significant differences in pre-fire relative growth between burned and control trees. Relative growth was lower for burned trees compared with control trees 1 year post-fire (Fig. 4*a*). Additionally, there was a clear dose–response between peak FRFD and 1-year post-fire relative growth (Fig. 4*b*). There were no significant differences between pre-fire peak FRFD groups and only control and high peak FRFD groups were significantly different from each other in 2015. Generally, trees exposed to higher doses of peak FRFD experienced lower relative growth compared with those exposed to lower peak FRFD dose and control trees. There was a weak linear relationship between relative growth and peak FRFD ($r^2 = 0.23$, s.e. = 29.7, $P < 0.001$). There were no obvious dose–response relationships between $FRFD_{\mu}$ or FRED and relative growth. Only relative growth for control (11.5 ± 5.2%) and low (−20.8 ± 9.3%) FRED groups and control (11.9 ± 5.2%) and low (−19.7 ± 10.7%) $FRFD_{\mu}$ groups were significantly different from each other (Fig. 4*c*). There were no significant linear relationships between relative growth and FRED or $FRFD_{\mu}$.

The only significant differences in duct metrics pre-fire were between control (1.7 ± 0.25 ducts $year^{-1}$) and high (1 ± 0.0 ducts $year^{-1}$) FRED duct production groups and control (0.013 ± 0.0008 mm^2) and high (0.024 ± 0.0092 mm^2) FRED total duct area groups in 2011. Unlike relative growth, there were differences in resin duct metrics in 2014 but not 2015 (Fig. 5). Duct production (ducts $year^{-1}$), mean duct size (mm^2 $duct^{-1}$) and total duct area (mm^2) in 2014 were higher in burned trees compared with control trees (Fig. 5*a–c*). Unlike relative growth, there were no apparent dose–response relationships between peak FRFD, FRED or $FRFD_{\mu}$ and any of the duct metrics. In 2014, duct production and total duct area were lower in the control group than in the low $FRFD_{\mu}$ groups (Fig. 5*d*, *f*). Mean duct size was lower in the control group than in the low and moderate $FRFD_{\mu}$ groups in 2014 (Fig. 5*e*). There were no significant effects of burn status (control, burn) or radiative heat metrics on resin duct size, production or area in 2015.

Discussion

Sources of variability in post-fire Pinus ponderosa growth

There is considerable variability in reported fire effects on *Pinus ponderosa* growth metrics (Table 1). This variation even occurs across research conducted in the same region and with trees of similar size and age. For example, in central Arizona, basal area increment has been observed to both decrease (Sutherland *et al.* 1991) and increase (Feeney *et al.* 1998) relative to control trees ~1–2 years post-fire. Likewise, in the Bitterroot Mountains in western Montana, radial wood growth has been observed to increase (Fajardo *et al.* 2007) or not be significantly different (Sala *et al.* 2005) relative to control trees ~9–10 years post-fire. Variability in growth metrics could be due to differences in water availability and other environmental factors between studies. Our findings suggest that this variability could be attributed to fine-scale spatial variability in fire intensity. It is clear that both FRED and FRFD can vary by many orders of magnitude in low-intensity wild- and prescribed fires. The peak FRFD data observed in the current study were within the typical range observed in past studies. Specifically, peak FRFD in prescribed fires have been observed to range from ~4 to 20 kW m^{-2} in mixed oak forests (Kremens *et al.* 2012), 0 to 15 kW m^{-2} in longleaf pine forests (Hudak *et al.* 2016), 13.5 to 48.6 kW m^{-2} in hardwood and loblolly pine forests (Cannon *et al.* 2014), and 1.7 to 16.3 kW m^{-2} in chipped ponderosa pine forests (present study). Although most studies in Table 1 recorded an 'average'

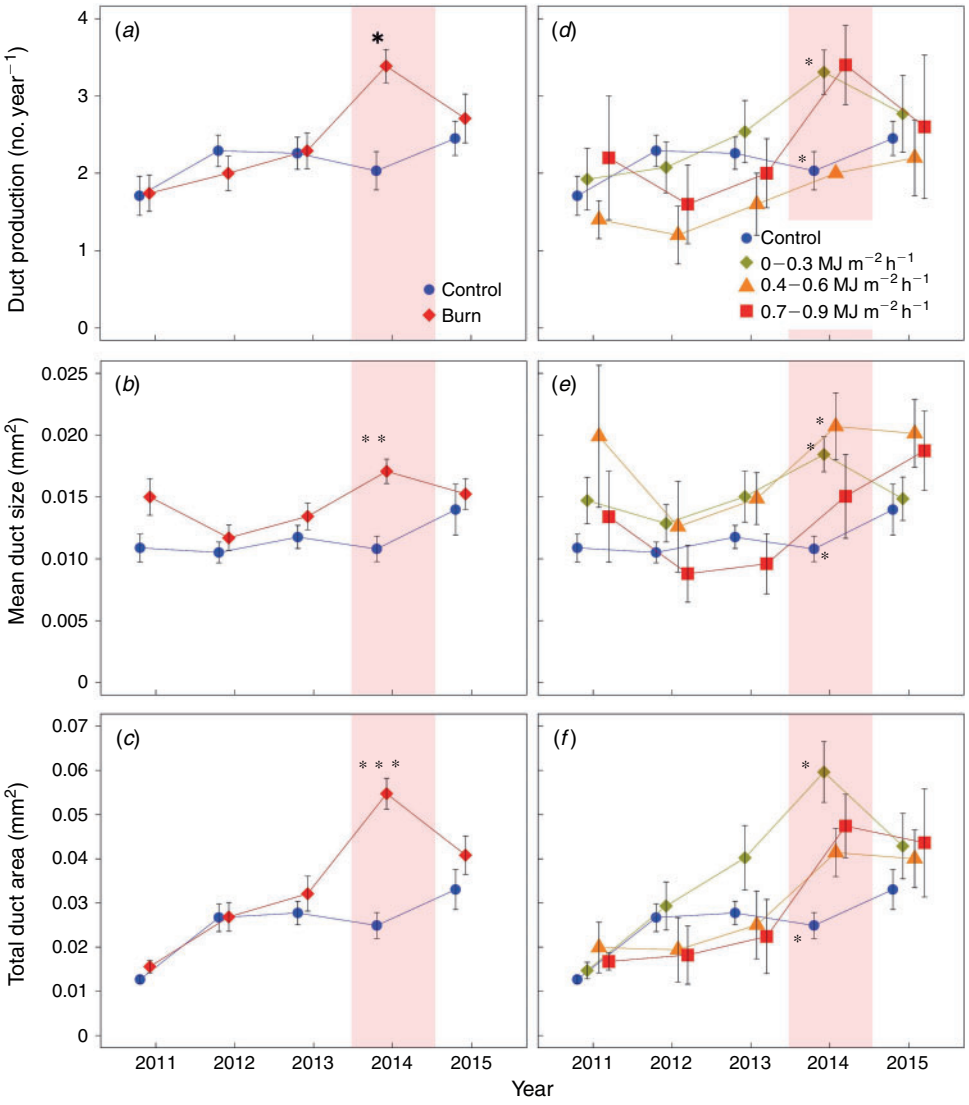

Fig. 5. *Pinus ponderosa* resin duct production (mean ± s.e.) by treatment (*a*), and normalised average fire radiative flux density ($FRFD_\mu$) class (*d*); mean resin duct size by treatment (*b*), and $FRFD_\mu$ class (*e*); and total resin duct area by treatment (*c*), and $FRFD_\mu$ class (*f*). Highlight indicates year that prescribed fires were conducted. Asterisks indicate significant differences: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

fire intensity metric for the entire burn, none quantified fire intensity spatially, and thus they could not link within-study variation in post-fire tree response to differences in fire intensity experienced by the trees. Smith *et al.* (2016) used a dose–response methodology with *Pinus contorta* seedlings and found strong relationships between FRED dose and photosynthesis. As FRED dose increased, there was a linear decrease in photosynthesis 4 weeks post-fire. Likewise, they observed decreasing tree diameter at root collar with increasing FRED.

Heat transfer mode and dose–response

Unlike Smith *et al.* (2017), we did not observe a dose–response between FRED and changes in post-fire diameter growth in these mature *Pinus ponderosa* trees. There are several factors that could account for this disparity, including: (i) variability in microsite environmental conditions; (ii) the trees in our study were much larger and had more fire-resistant traits (thicker bark, higher crown base height); and (iii) compared with the flaming-dominated combustion in the other study, combustion in these burns was smouldering-dominated.

Variability in microsite environmental conditions such as water and light availability could be the result of differences in slope position. These conditions could influence the radial growth and mask any dose–response relationships like those seen in prior studies. These differences could also have led to variation in the degree of heat exposure around the boles and the degree to which flames interacted vertically with each tree (i.e. bole scorch on leeward sides).

Diameter and bark thickness have been observed to be strong predictors of post-fire conifer survival, with larger diameter and

greater bark thickness increasing the probability of survival (Ryan and Reinhardt 1988; Stephens and Finney 2002). Whereas the previous dose–response studies used seedlings with thin bark and low crown base height (<0.2 m) and observed crown scorch from 40 to 100% (Sparks *et al.* 2016), the *Pinus ponderosa* trees in our study ranged from 13.2 to 33.0 cm in DBH and had an average crown base height of 6.4 ± 0.3 m.

Relative to the controlled laboratory burns conducted by Smith *et al.* (2016) and Sparks *et al.* (2016), the burns in our study produced larger FRED values (up to 13.7 MJ m^{-2}). However, compared with the artificially constructed fuelbeds in the laboratory burns, combustion of the chipped fuelbeds was much more dominated by smouldering (>97% of total burn duration on average) and occurred over a much longer period of time (11.9 h on average). Distributing the FRED dose over a longer duration may have reduced the amount of damage caused by the fires. However, the smouldering-dominated combustion could have led to below-ground damage of tree root systems and damage to fine roots, which could result in reduced growth (Swezy and Agee 1991). The dose–response relationship between peak FRFD and relative growth (Fig. 4*b*) may be indicative of damage to the tree crowns caused by convective heat fluxes. Similarly, the past studies of FRED doses on seedlings (Smith *et al.* 2017) involved flames in contact with the entire plant, leaving it open to speculation as to what mode of heat transfer was responsible for the observed effects. In these studies, FRED was only used owing to its ease of repeatability and the radiative heat flux itself was not assumed to necessarily be the cause of the observed effects. In the current study, although flames did not conduct heat to foliage through direct contact, maximum flame lengths reached >1.5 m in several of the plots, which could deliver substantial convective heat flux to the crown via high-temperature gases rising above the flames. These heat fluxes could cause necrosis in foliage and buds (Michaletz and Johnson 2007) and extreme drops in vapour pressure, which could lead to structural deformation in xylem cell walls (Michaletz *et al.* 2012), cavitation in foliage (Kavanagh *et al.* 2010), and consequently decrease tree growth.

Vulnerability to secondary mortality agents

The data from our study and others (Table 1) suggest that low-intensity fires serve as a cue for *Pinus ponderosa* to increase their resin duct defences. The majority of studies surveyed observed post-fire increases in resin duct defences (Feeney *et al.* 1998; Perrakis and Agee 2006; Davis *et al.* 2012; Hood *et al.* 2015*a*) despite an enormous range of reported fire intensity. Likewise, we observed no dose–response relationship between radiative heat transfer metrics (peak FRFD, FRED, $FRFD_{\mu}$) and resin duct metrics. The increase in resin duct production that occurs after fire could be a direct physiological response to fire or it could be indirect response to fire induced by changes in resource (light, water, nutrient) availability that are associated with fire. Other studies have hypothesised that smoke exposure could serve as a cue for increased production of defensive compounds (Calder *et al.* 2010). Although Calder *et al.* (2010) found decreases in photosynthesis, they did not find significant differences in defensive compound production between trees exposed to 20 min of smoke and control trees. The control trees in our stands were in close proximity (~20–55 m) to the burn plots and could have received some smoke exposure; however, we do not have sufficient data to conclude that the smoke exposure experienced by the burned and control trees increased or decreased resin duct metrics. In addition to direct fire effects, other studies have found that resin duct area in *Pinus ponderosa* increases under higher temperature and precipitation (Hood *et al.* 2015*a*). For our study area, mean summer temperatures increased from 2011 to 2015; however, precipitation decreased over this period. Average departure in mean summer (June, July, August) temperature from the 30-year normal (1981–2010) (Arguez *et al.* 2010) was +1.9°C in the 3 years before the burn experiments and +3.5°C in the 2 years after. The percentage of normal summer precipitation averaged 19% in the 3 years before the burn experiments and 11% in the 2 years after. In our study, the increase in all resin duct metrics in the burn treatments could also be due to the pulse of nutrients that typically follows combustion of surface fuels (Certini 2005).

Limitations and future work

We acknowledge that our study has some limitations. First, we have relatively small sample sizes for higher doses of peak FRFD, FRED and $FRFD_{\mu}$ compared with lower doses and control samples. Future studies could manipulate surface fuel loading and moisture content so that even sample sizes are maintained. Second, in an attempt to create a wide range of fire intensities, our plots were set up on slightly different slopes and aspects, creating increased potential for different growing conditions between the sampled trees pre- and post-fire. Studies continuing this research should strive for more uniform stand conditions to help control for environmental variation.

Conclusions

Our study demonstrates that quantification of fine-scale fire behaviour (e.g. flaming versus smouldering combustion) are crucial components for quantifying post-fire tree growth. These results highlight the utility of peak FRFD for characterising post-fire growth in *Pinus ponderosa* and its potential for landscape-scale application (e.g. MODIS derived FRP). More research is needed to test the applicability of this dose–response relationship in different age classes and species. This study also highlights the need for more research into heat flux dose duration (e.g. vegetation response to large dose distributed over a long time versus large dose distributed over a short time). Our observations also suggest that non-lethal surface fires, regardless of intensity, have potential to significantly increase resin duct defences of *Pinus ponderosa* post-fire. This study extended the prior dose–response studies on seedlings (Sparks *et al.* 2016; Smith *et al.* 2016) through investigating whether radiative heat flux doses lead to predictable responses in post-fire growth and vulnerability to secondary mortality agents. Ultimately, this research furthers the argument to advance fire severity research through connecting doses of the fire heat flux to plant ecophysiology responses.

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