Fire-injured ponderosa pine provide a pulsed resource for bark beetles

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Abstract: Bark beetles can cause substantial mortality of trees that would otherwise survive fire injuries. Resin response of fire-injured northern Rocky Mountain ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) and specific injuries that contribute to increased bark beetle attack susceptibility and brood production are unknown. We monitored ponderosa pine mortality and resin flow and bark beetle colonization and reproduction following a prescribed fire in Idaho and a wildfire in Montana. The level of fire-caused tree injury differed between the two sites, and the level of tree injury most susceptible to bark beetle attack and colonization also differed. Strip-attacked trees alive 3 years post-fire had lower levels of bole and crown injury than trees mass attacked and killed by bark beetles, suggesting that fire-injured trees were less well defended. Brood production of western pine beetle (*Dendroctonus brevicomis* LeConte) did not differ between fire-injured and uninjured trees, although mountain pine beetle (*Dendroctonus ponderosae* Hopkins) brood production was low in both tree types, potentially due to competition with faster developing bark beetle species that also colonized trees. Despite a large number of live trees remaining at both sites, bark beetle response to fire-injured trees pulsed and receded within 2 years post-fire, potentially due to a limited number of trees that could be easily colonized.

Résumé : Les scolytes peuvent tuer beaucoup d'arbres qui pourraient autrement survivre aux blessures causées par le feu. La production de résine chez les pins ponderosa (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) dans le nord des montagnes Rocheuses en réaction aux blessures causées par le feu ainsi que les blessures spécifiques qui contribuent à l'augmentation de la susceptibilité aux attaques des scolytes et à la production de nouvelles générations d'insectes n'ont pas été étudiées. Nous avons suivi la mortalité et l'écoulement de résine chez le pin ponderosa, ainsi que la colonisation et la reproduction des scolytes à la suite d'un brûlage dirigé en Idaho et d'un feu de forêt au Montana. La quantité de blessures causées par le feu était différente dans les deux stations et la quantité de blessures sur arbres les plus susceptibles d'être attaqués et colonisés par les scolytes était également différente. Les arbres qui avaient subi une attaque localisée et qui étaient vivants 3 ans après le passage du feu avaient moins de blessures au tronc et dans la cime que les arbres qui avaient subi une attaque massive et avaient été tués par les scolytes; ce qui implique que les arbres blessés par le feu s'étaient moins bien défendus. La production de nouvelles générations de dendroctone occidental du pin (*Dendroctonus brevicomis* LeConte) n'était pas différente que les arbres aient été blessés ou non par le feu, mais la production de nouvelles générations de dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins) était faible chez les deux types d'arbre, possiblement à cause de la compétition d'espèces de scolyte dont la croissance était plus rapide et qui colonisaient aussi les arbres. Malgré le grand nombre d'arbres vivants encore présents dans les deux stations, la réponse des scolytes aux arbres blessés par le feu a bondi et s'est résorbée en moins de 2 ans après le feu, possiblement à cause du nombre restreint d'arbres qui pouvaient facilement être colonisés.

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Introduction

Fire can kill conifers directly from a combination of injuries to foliage, buds, cambium, and roots (Ryan 1982) or indirectly by bark beetles (Coleoptera: Curculionidae, Scolytinae) that exploit a period of reduced host tree defenses following fire (Lombardero et al. 2006). Individual tree resistance to fire-caused mortality depends on morphological characteristics that protect vascular and meristematic tissue from heat injury and a physiological capacity for recovery from the fire injury (Butler and Dickinson 2010). Adaptation to frequent fires, for

example, has resulted in thick bark, a morphological trait that increases ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) post-fire survival probability (Schwilk and Ackerly 2001). Some conifers that survive fire injury, however, are subsequently killed by bark beetles that may respond to volatiles emitted by fire-injured trees (Kelsey and Joseph 2003), causing substantial mortality of trees that may otherwise have survived fire injury alone (Hood and Bentz 2007).

Ponderosa pine is widespread across montane regions of the western United States, Canada, and Mexico (Conkle and Critchfield 1988) and can be a host to a variety of native bark

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beetle species (Wood 1982). Climatic conditions, specifically warm springs followed by warm and dry summers, have been important synchronizers of regional-scale fires for the past several centuries in ponderosa pine dominated forests of the northern Rocky Mountains (Heyerdahl et al. 2008). Human influences, including fire suppression and logging, have also likely played a role in fire activity and will continue to add to the complexity of future fire management in western forest ecosystems (Falk et al. 2010; Naficy et al. 2010). As knowledge of fire regimes and their importance to functioning forest ecosystems becomes more widespread, restoration efforts to enhance resistance of ponderosa pine forests in the northern Rocky Mountains increasingly rely on the use of prescribed fire (Harrington 1993; Fiedler et al. 2010). For restoration efforts to be successful, we must understand the secondary effects of fire injury on tree survival and bark beetle population dynamics, particularly in forest types such as ponderosa pine that frequently experience low- to mixed-severity fires.

Mixed-severity fires can result in a mosaic of fire-killed, fire-injured, and uninjured ponderosa pine across a landscape, and studies conducted in multiple regions have investigated specific fire-related injuries and their role in post-fire ponderosa pine mortality (Regelbrugge and Conard 1993; Sieg et al. 2006; Thies et al. 2006; Hood et al. 2010). In all cases, an interaction among factors including tree size and degree of crown and bole damage was found to be important for predicting post-fire delayed mortality of ponderosa pine. Bark beetles are also recognized as significant contributors to post-fire ponderosa pine mortality. Significantly more bark beetle attacked ponderosa pine were found on prescribed burned sites than on associated unburned sites in California (Schwilk et al. 2006; Fettig et al. 2008, 2010; Maloney et al. 2008) and inclusion of bark beetle presence improved the accuracy of models developed to predict post-fire delayed ponderosa pine mortality in Arizona (McHugh et al. 2003; Sieg et al. 2006; Breece et al. 2008). Bark beetle attacks have also been observed following wild and prescribed fire in ponderosa pine forests in the northern Rocky Mountains (Miller and Patterson 1927; Perrakis and Agee 2006; Six and Skov 2009; Youngblood et al. 2009), although the relationship between attack and tree-level fire injury has not been quantified. In these studies, several bark beetle species, including western pine beetle (*Dendroctonus brevicomis* LeConte), mountain pine beetle (*Dendroctonus ponderosae* Hopkins), pine engraver (*Ips pini* Say), and red turpentine beetle (*Dendroctonus valens* LeConte), were found attacking fire-injured ponderosa pine (variety *ponderosa*). These species were also found attacking fire-injured ponderosa pine (variety *bracyptera*), although several additional bark beetle species can be active in fire-affected ponderosa pine stands in the southwestern United States including *Dendroctonus adjunctus* (Blanford), *Dendroctonus approximatus* (Dietz), *Dendroctonus frontalis* (Zimmermann), and several *Ips* spp. (Sánchez-Martínez and Wagner 2002). The distribution of these additional species does not currently extend into ponderosa pine in the northern Rocky Mountains (Wood 1982).

The mechanisms driving bark beetle attraction to fire-injured trees and specific injuries that contribute to increased susceptibility to attack are unclear. Pines more resistant to bark beetle attack tend to have greater overall constitutive and induced resin flow (Raffa and Berryman 1983; Boone et al. 2011). Although a temporary reduction in resin defenses occurs immediately following fire injury (Lombardero et al. 2006), sustained resin flow of conifers has repeatedly been shown to increase within a year following fire injury (Feeney et al. 1998; Knebel and Wentworth 2007) and remain at elevated for levels for up to 4 years post-fire (Perrakis et al. 2011). Even though increased resin flow can positively influence tree defense against bark beetle attack, in fire-injured trees, it may also play a role in preferential attack by bark beetles (Perrakis and Agee 2006). The level of injury may be a significant factor in mediating bark beetle attraction to a fire-injured tree and the potential for successful colonization (Wallin et al. 2003). Once a tree has been successfully colonized, fire injury may also play a role in bark beetle reproductive success. Thermal stress that results in increased resin flow could also cause substantial damage to the inner cambium. In these cases, heavily injured trees could be attractive to beetles, but poor for brood production. Conversely, nonlethal physiological injuries to crowns that result in increased resin flow could result in little damage to internal tissues that bark beetles feed on, especially in thick-barked trees such as ponderosa pine. Little is known about bark beetle brood production in fire-injured ponderosa pine, and data on resin response in northern Rocky Mountain ponderosa pine are lacking. When coupled, this information will provide a greater understanding of fire injury levels that result in good, adequate, or poor resources for bark beetle population success and potential expansion.

Our goal was to describe the influence of fire on the relationship between ponderosa pine and associated bark beetle population dynamics in northern Rocky Mountain ecosystems. We chose a wildfire and a prescribed fire site with varying levels of fire injury and stand structure to examine the relationships. Specifically, our objectives were to (1) describe post-fire ponderosa pine mortality as a function of morphological and fire injury characteristics, (2) evaluate bark beetle host selection and brood production as they relate to morphological and fire injury characteristics, and (3) investigate the influence of specific bole and crown fire injuries on ponderosa pine resin flow volume.

Methods

Study areas

The Lolo study area, located approximately 8 km southwest of Missoula, Montana, is within the boundary of the August 2003 Black Mountain 2 wildfire (Table 1). Hereafter referred to as the wildfire site, the ~100 ha (1 km^2) study site is characterized by a mix of second-growth ponderosa pine and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The Payette study area is located on the Payette National Forest, Idaho (Table 1). Within the Payette study area, there was a ~300 ha (3 km^2) treatment site that was prescribed burned in May 2004 (hereafter referred to as the prescribed fire site) and a ~300 ha (3 km^2) unburned control area (hereafter referred to as the unburned site). The prescribed fire and unburned sites were 12.8 km apart and are mixed old-growth ponderosa pine and Douglas-fir forests. Bark beetle caused tree mortality was not detected in aerial detection surveys (US Forest Service, Forest Health Protection, http://www.foresthealth.info/portal) within the wildfire, prescribed fire, or unburned site boundaries in 2003, and thus, we considered populations at both sites to be at endemic levels in 2004.

Table 1. Site and stand information for the three study areas.

Site	Location	Number of plots (0.04 ha)	All tree species		Ponderosa pine	
			Trees/ha	Basal area (m²/ha)	Trees/ha	Basal area (m²/ha)
Wildfire	Black Mountain 2 Fire, Lolo National Forest, Montana, Missoula Ranger District, 46°0.49′40.44″, –114°9′33.69″, elevation 1371–1677 m	15	640	29.83	502	21.89
Prescribed fire	Payette National Forest, Idaho, Krassel Ranger District, 44°57′35.64″, –115°31′33.64″, elevation 1097–1768 m	21	281	44.76	221	34.2
Unburned	Payette National Forest, Idaho, Krassel Ranger District, 44°56′56.04″, –115°15 25.2″, elevation 1097–1768 m	20	233	40.02	144	28.67

Note: All tree species includes ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*).

Table 2. Tree morphological and fire injury variables measured for each tree.

Variable	Abbreviation	Description
Tree status	TS	Tree living or dead (0, 1)
Diameter at breast height	DBH	Tree circumference at 1.3 m above ground level (cm)
Tree height	TH	Height of tree from ground level (m)[a]
Crown base height	CBH	Pre-fire height of lowest canopy above ground level (m)[a]
Live crown length	LCL	TH–CBH (m)[a]
Crown volume scorched	CVS	Percentage of the crown volume heat scorched[b]
Percent bud volume killed	PBK	Percentage of the crown bud volume heat killed; this measurement does not include foliage with only scorched needles[b]
Scorch height	SH	Height of the highest visible heat damage, on bole or canopy, from ground level (m)[a]
Percent crown scorch length	PSL	SH–TH[a]
Percent circumference of tree bole charred	PCC	Percent circumference of the tree bole with visible charring at ground level
Bark char severity index	BCI	A visual estimate of the quadrant-level bark char codes averaged for each tree (Ryan 1982)
Cambium kill rating	CKR	A direct measurement of the number of quadrants with dead cambium

Note: See Fowler and Sieg (2004) and Hood et al. (2007) for details.
[a]Heights measured to 0.5 m using a laser hypsometer (Opti-Logic Corporation, Tullahoma, Tennessee).
[b]Scorch percentages were visual estimates made in 10% increments from 10% to 90% and in 5% increments from 0% to 10% and from 90% to 100%.

Ponderosa pine fire injury and mortality

We established 0.04 ha plots at each site the summer of 2004, 12 months following the fall wildfire in Montana and 3 months following the spring prescribed fire in Idaho (Table 1). In Idaho, the prescribed fire and unburned sites within the Payette study area were within the boundary of a study investigating effects of prescribed fire on avian populations (Saab et al. 2006). Plots for the avian study were established on a grid throughout each site, and our plots were located in a random direction 61 m from plot centers used by the avian project. At the wildfire site, we established plots in areas where bark beetle attacked trees were located during general site surveys. All trees ≥9.9 cm diameter at breast height (DBH) within each plot were permanently tagged and the species recorded. All morphological variables were measured post-burn, but were estimated as pre-burn measurements, and measurements of all fire injury variables, described in Table 2, followed

existing methodology (Fowler and Sieg 2004; Hood et al. 2007). To test if a single variable that describes both crown and bole injury can predict tree mortality or bark beetle attack, we developed a fire injury categorical variable with five levels: (1) unburned: no crown or bole injury, (2) low: CKR = 0, 1, or 2 and PBK or CVS < 70, (3) moderate: CKR = 3 or 4 and PBK or CVS < 70, (4) high: CKR = 0, 1, or 2 and PBK or CVS > 70, and (5) severe: CKR = 3 or 4 and PBK or CVS > 70. DBH was also categorized into classes for some analyses: DBH class1 = <30 cm, DBH class2 = 30–39 cm, DBH class3 = 40–49 cm, and DBH class 4 = >49 cm. Following establishment, all plots were revisited annually for two consecutive years (2005 and 2006) to monitor tree mortality and bark beetle activity. We assessed 236 trees (i.e., Douglas-fir and ponderosa pine) at the prescribed fire site, 185 trees at the unburned site, and 384 trees at the wildfire site.

Bark beetle attack preference and brood production

All trees were examined for bark beetle attack by visually assessing the entire bole circumference up to 8 m above ground. Although attacks of some species may be restricted to higher on the bole, species that attack from the ground level to 8 m are the major contributors to ponderosa pine mortality and were the target of this study. Because *Ips* spp. and western pine beetle can have more than one generation a year at our sites, trees were assessed in early summer and early fall. We assessed attack status, colonization success, and attacking species by presence of pitch tubes, beetle frass in bark fissures and on the ground, gallery patterns underneath the outer bark, and identification of adult beetle samples (Wood 1982). All trees with successful attacks by any bark beetle species on the entire bole circumference (i.e., successful entrance into the tree leading to gallery construction and oviposition) were recorded as mass attacked. Trees with less than the entire bole circumference showing signs of attack were recorded as strip attacked, and trees with no sign of attack or only a few pitch tubes were recorded as unattacked. Attack status for each tree was verified in the subsequent year survey. Preference of bark beetles attacking charred versus uncharred bole areas was measured in each bole quadrant.

We measured bark beetle brood production by recording adults that emerged into cages placed on beetle-infested burned and unburned ponderosa pine at each study site. Cages (30 cm × 60 cm) were placed on trees that were located on plots, in addition to beetle-attacked trees randomly located within the study area boundary (prescribed fire site: 31 emergence cages on 16 trees; wildfire site: 38 cages on 19 trees). Adult beetle emergence was monitored on a weekly basis during the summer in 2005 and 2006. All beetles collected from cages were returned to the laboratory in Logan, Utah, and frozen for subsequent species identification (Wood 1982). Additionally, we cut four beetle-infested trees with a range of fire injuries and two unburned trees from within and near the boundary (0.4 km) of the wildfire site in April 2005. Limitations at the prescribed fire and unburned sites prevented us from cutting trees at these sites. We brought bolts from these trees to Logan, Utah, and kept them in rearing cans at room temperature (~21 °C) until all adults emerged. Surface area of the bolts was calculated as $SA = 2(\pi r^2) + h(2\pi r)$, where r is radius and h is bole height, and then standardized to 1858 cm^2 (the sample area of emergence cages on trees in the field) for analysis.

Resin flow

We sampled constitutive resin flow, defined as the resin volume exuded (millilitres) from an unwounded tree (Ruel et al. 1998) that occurred after fire, but before beetle attack (Wallin and Raffa 2001). Sample trees at each site were randomly selected from within established plots, with an attempt to sample an equal number of trees in each fire injury category. Although we monitored trees ≥9.9 cm DBH for tree mortality and bark beetle attack at each plot, resin volume was only sampled on ponderosa pine 20–56 cm DBH. Resin flow was sampled on a burned and unburned side of each fire-injured sample tree (when possible) at 1.3 m from the ground. A 2.54 cm diameter arch punch was used to remove a circular section of phloem and bark down to the xylem layer, but not into the xylem. Funnels were constructed using clear silicon

caulking placed 3–5 mm directly below the bottom of the excised phloem directing resin into a 50 mL plastic graduated test tube (Nalgene Corp., Rochester, New York). Samples were collected after 24 h (±2 h). Santoro et al. (2001) found that red pine (*Pinus resinosa* Aiton) resin flow quantity did not change significantly between 6 and 24 h after tapping. Resin flow volume was measured ocularly to the nearest 0.5 mL.

To investigate natural within-tree variation in resin flow (Roberds and Strom 2006), we collected resin samples on four bole aspects (north, east, south, and west) of five unburned trees in June, July, and August 2005 at the wildfire and unburned sites (15 trees total per site). We repeated this sampling again in 2006 at both sites, although a wildfire at the Payette site (our prescribed fire site) in August 2006 prevented resin sampling that month. At the wildfire site, we measured the first resin flow samples on fire-injured trees in June 2005, 20 months following the August 2003 fire, and in June 2005 at the prescribed fire site, 13 months following the May 2004 fire. At the wildfire site, resin flow was sampled on two bole aspects (one charred and one uncharred) of 12 fire-injured trees in June, July, and August 2005 (12 total trees) and 18 fire-injured trees in 2006 (18 trees total). Five uninjured trees were sampled at the same time periods in 2006. At the prescribed fire site, resin flow was sampled on two bole aspects (one charred and one uncharred) of 15 fire-injured trees in June, July, and August 2005 and 18 fire-injured trees in June and July 2006. At the unburned site in 2006, 10 uninjured trees were sampled at the same times as fire-injured trees were sampled in June and July 2006. Measurements on trees used for multiple inductions were made a minimum of 3 cm to the right or left of the previous wound to minimize confounding of mechanically induced resin production (Lombardero et al. 2006).

Data analyses

All analyses were conducted using SAS version 9.2 (SAS Institute Inc., Cary, North Carolina) and all statistical tests were conducted using $\alpha = 0.05$. Our goal was to describe the effects of fire injury and tree morphological variables on ponderosa pine mortality and resin flow and on bark beetle attack frequency and brood production. We used mixed-model analyses (GLIMMIX) to test the effect of fire injury on mortality, with a binomial error distribution and logit link function. Trees that were living 3 years post-fire were assigned a code of 0, and dead trees were assigned a code of 1. Study sites were analyzed separately and plot was included as a random effect. We initially used a univariate logistic regression analysis (LOGISTIC) to identify candidate independent variables of tree size, fire injury, and bark beetle attack that best described ponderosa pine post-fire mortality (Hosmer and Lemeshow 2000) (Table 2).

Mixed models were also used to analyze the effect of tree size and fire injury on bark beetle attack. Analyses were conducted separately for the wildfire and prescribed fire data and for trees attacked by mountain pine beetle and western pine beetle and trees with only attacks by pine engraver and emarginate ips. Trees attacked by mountain pine beetle and western pine beetle within 3 years following each fire were assigned a code of 1, otherwise 0, and plot was included as a random effect and a binomial response distribution was used. Mixed-model analysis was also used to investigate the effect of tree size and fire injury on total number of bark beetles emerged

Table 3. Mean (±SE) and range of tree and fire injury variables of ponderosa pine (*Pinus ponderosa*) measured within the boundary of a fall 2003 wildfire (Lolo National Forest, Montana), a spring 2004 prescribed fire (Payette National Forest, Idaho), and an unburned site (Payette National Forest).

Variable	Wildfire ($N = 312$)	Prescribed fire ($N = 186$)	Unburned ($N = 114$)
Diameter at breast height (DBH)	21.50 (0.60) a	43.18 (1.50) b	46.59 (1.54) b
	7.6–69.3	7.9–120.1	13.2–98.0
Tree height (TH)	13.47 (0.27) a	23.58 (0.60) b	21.10 (0.76) c
	3.1–27.7	4.3–43.3	4.0–42.7
Crown base height (CBH)	5.62 (0.15) a	8.57 (0.34) b	9.25 (0.47) b
	0.0–15.2	0–21.4	0.9–24.7
Live crown length (LCL)	7.87 (0.24) a	15.01 (0.49) b	11.85 (0.24) b
	0.9–21.6	2.1–31.1	2.1–31.0
Crown volume scorched (CVS)	64.23 (2.02) a	28.38 (2.35) b	na
	0.0–100.0	0.0–100.0	
Percent bud kill (PBK)	52.62 (2.15) a	17.17 (1.92) b	na
	0.0–100.0		
Scorch height (SH)	9.38 (0.22) a	8.43 (0.57) a	na
	0.0–23.2		
Percent crown scorch length (PSL)	0.74 (0.15) a	0.37 (0.23) b	na
	0.0–1.0	0.0–1.0	
Percent circumference of tree bole charred (PCC)	60.31 (2.24) a	25.26 (2.43) b	na
	0.0–100.0	0.0–100.0	
Bole char severity index (BCI)	1.92 (0.03) a	1.81 (0.03) b	na
	0.0–3.0	0.0–2.75	
Cambium kill rating (CKR)	2.47 (0.08) a	1.13 (0.09) b	na
	0.0–4.0	0.0–4.0	

Note: N is the number of ponderosa pine measured at each site. See Table 2 for variable descriptions. Means in the same row with different letters are significantly different (adjusted $p < 0.05$). na, not applicable.

using a Poisson response distribution, with plot and tree included as random effects. Contingency table analysis using a χ^2 test for significance was used to test for differences in the binary response variable, beetle attack absence–presence, between charred and uncharred areas of fire-injured tree boles.

The significance of tree and fire injury variables in explaining resin flow was also analyzed using mixed models. For errors to meet the assumption of normality and homoskedasticity, resin flow data were transformed using a cube root function. Untransformed data are reported in the results. Differences among tree bole aspects of unburned trees sampled once in June, July, or August in 2005 and 2006 were tested using the random effects plot, year, tree, and tree bole aspect to account for subsampling error. We used repeated-measures analysis for trees sampled repeatedly in consecutive months, using plot, year, and tree bole aspect as random effects to account for subsampling error. Bole aspect was not significant and subsequent analyses were conducted on resin volume mean per tree. Pairwise differences in categorical variables were tested using a Tukey–Kramer Honestly Significant Differences multiple comparison test.
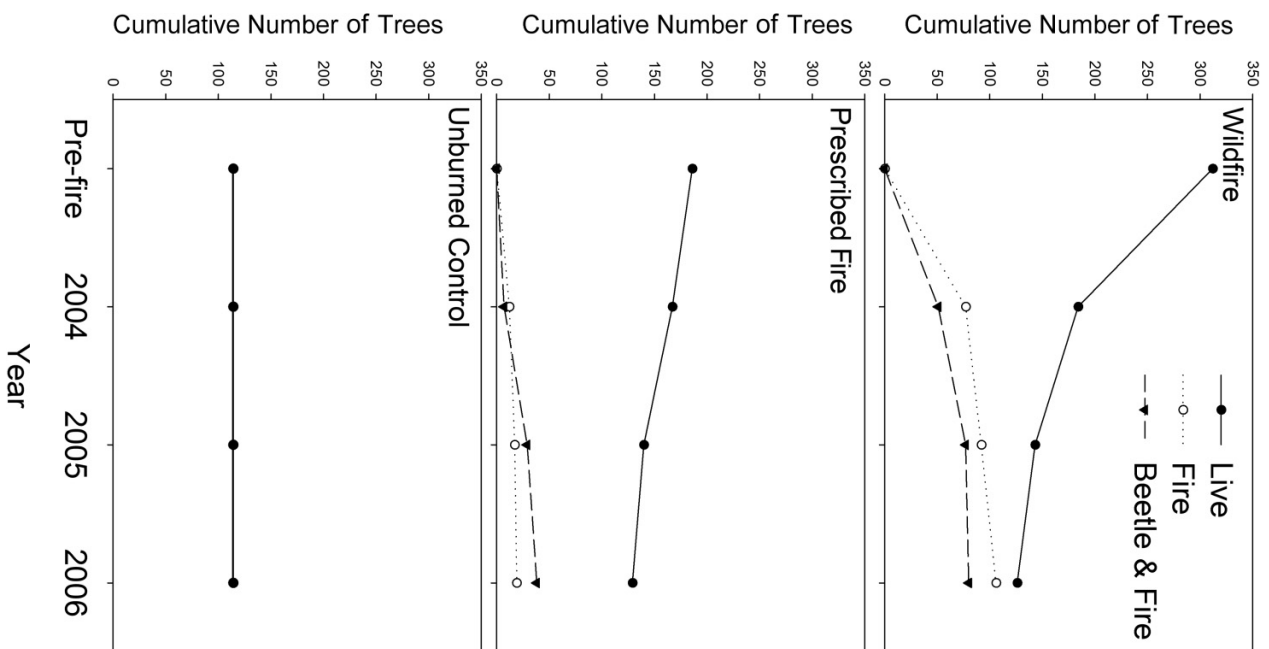
Results

Ponderosa pine fire injury and mortality

At the prescribed fire and nearby unburned site, ponderosa pine morphological characteristics were similar and only TH was significantly different (Table 2). However, all measured tree and fire injury characteristics, except SH, differed significantly ($p < 0.05$) between the wildfire and prescribed fire

sites (Table 3). Trees at the wildfire site were smaller and had greater levels of fire injury than trees at the prescribed fire site (Table 3), and a larger percentage were killed by a combination of fire injuries alone (34%) and fire injuries and bark beetle attacks (26%). At the prescribed fire site, 10% of the ponderosa pine were killed by fire alone and an additional 20% were dead due to a combination of fire injury and bark beetle attacks (Fig. 1). The majority of ponderosa pine sampled died within the first year following the August wildfire. At the prescribed fire site, most trees died the year following the spring burn (i.e., 2005, the second post-fire year) (Fig. 1). At the wildfire site, DBH, CVS, PBK, PSL, PCC, and CKR were significantly different between trees that were live unattacked or live fire injured and trees killed by either fire alone or fire and bark beetle attack (Table 4; Fig. 2). In all cases, smaller trees with greater fire injury to the bole and crown were killed by fire alone. At the prescribed fire site, CVS, PBK, PCC, and CKR were greater in trees killed by fire alone or fire and bark beetles than in live trees (Table 4). Trees killed by fire alone had significantly greater CKR and PCC and were generally smaller than trees that remained alive or were attacked by bark beetles. DBH, LCL, and TH were highly correlated at both sites (prescribed fire: DBH–LCL $\rho = 0.6814$, TH–LCL $\rho = 0.8206$, DBH–TH $\rho = 0.7349$; wildfire: DBH–LCL $\rho = 0.8147$, TH–LCL $\rho = 0.8269$, DBH–TH $\rho = 0.8390$). PBK and CSV were also highly correlated (prescribed fire: $\rho = 0.82696$; wildfire: $\rho = 0.9114$). All ponderosa pine on plots at the unburned control site were uninjured and alive at the end of the study.

Davis et al.

Fig. 1. Cumulative number of ponderosa pine (*Pinus ponderosa*) that were live, killed by fire alone, and killed by bark beetles and fire before (pre-fire) and following a fall 2003 wildfire (Lolo National Forest, Montana), a spring 2004 prescribed fire (Payette National Forest, Idaho), and an unburned control site (Payette National Forest).

At the wildfire, DBH, PBK, CKR, and DBH × ATK best explained post-fire ponderosa pine mortality (Table 5). In an independent model, CVS, rather than PBK, was also significant ($F_{[1,183.3]} = 14.57$, $p = 0.0002$) and both models had similar overall fits based on the Residual Log Pseudo-Likelihood. At the prescribed fire site, the same variables (PBK, CKR, and DBH × ATK) best explained post-fire ponderosa pine mortality, although DBH alone was not significant (Table 5). The categorical fire injury class variable, a single variable that includes a measure of both crown and bole injury, was not significant at either site. At both sites combined, 2572

At the wildfire site, DBH, PBK, CKR, and DBH × ATK best explained post-fire ponderosa pine mortality ...

Table 4. Mean (±SE) of morphological and fire injury variables of live and dead ponderosa pine (*Pinus ponderosa*) (within 3 years post-fire) located within the boundary of a wildfire (Lolo National Forest, Montana) and a prescribed fire (Payette National Forest, Idaho).

	Wildfire				Prescribed fire			
	Live (N = 126)		Dead (N = 186)		Live (N = 133)		Dead (N = 53)	
Variable	Not attacked	Fire, attacked	Fire, attacked	Fire	Not attacked	Fire, attacked	Fire, attacked	Fire
Diameter at breast height (DBH)	28.76 (1.23) a	26.68 (1.32) a	22.55 (1.11) b	13.73 (0.49) c	45.83 (1.77) a	43.31 (4.34) a	46.85 (3.64) a	19.90 (2.34) b
Tree height (TH)	15.69 (0.46) a	16.43 (0.62) a	15.07 (0.53) a	10.00 (0.33) b	25.47 (0.60) a	25.50 (3.02) a	23.40 (1.48) a	11.02 (1.39) b
Crown base height (CBH)	5.71 (0.27) a	6.52 (0.37) a	6.52 (0.38) a	4.53 (0.23) b	9.22 (0.39) a	9.65 (1.27) a	9.03 (0.82) a	3.40 (0.85) b
Live crown length (LCL)	9.98 (0.44) a	9.89 (0.58) a	8.55 (0.50) a	5.49 (0.32) b	16.25 (0.55) a	15.85 (2.23) a	14.37 (1.19) a	7.60 (1.34) b
Crown volume scorched (CVS)	37.41 (3.14) a	47.22 (4.9) a	69.45 (3.89) b	88.98 (2.24) c	22.14 (2.44) a	18.33 (9.0) a	44.69 (5.49) b	42.89 (10.63) bc
Percent bud kill (PBK)	21.78 (2.34) a	32.78 (3.99) a	58.20 (4.09) b	81.82 (2.93) c	9.03 (1.38) a	11.67 (7.8) a	35.00 (4.69) b	39.75 (10.38) b
Scorch height (SH)	8.20 (0.43) a	10.96 (0.66) b	10.65 (0.59) b	9.05 (0.31) a	8.57 (0.71) a	6.76 (2.42) a	11.09 (1.38) a	3.79 (0.95) a
Percent crown scorch length (PSL)	0.53 (0.24) a	0.67 (0.03) a	0.75 (0.03) b	0.92 (0.02) c	0.34 (0.03) a	0.29 (0.11) a	0.50 (0.51) a	0.41 (0.10) a
Percent bole circumference charred (PCC)	30.72 (3.26) a	34.03 (4.41) a	70.32 (4.62) b	85.34 (2.79) c	15.31 (1.82) a	23.33 (13.02) a	39.74 (8.24) ab	73.95 (8.78) c
Bark char severity index (BCI)	1.77 (0.04) a	1.92 (0.04) ab	1.83 (0.08) ab	2.07 (0.05) bc	1.76 (0.04) a	2.08 (0.05) a	1.97 (0.07) a	1.87 (0.12) a
Cambium kill rating (CKR)	1.30 (0.13) a	1.47 (0.19) a	2.83 (0.18) b	3.43 (0.11) c	0.67 (0.08) a	1.00 (0.51) a	1.73 (0.22) ab	3.00 (0.34) c

Note: *N* is the number of trees measured. Live includes trees that were not attacked and trees that were strip attacked by bark beetles. Dead includes ponderosa pine mortality due to fire injuries alone and a combination of fire injuries and bark beetle attack. See Table 2 for variable descriptions. Variable means within a site with different letters are significantly different between live and dead trees (adjusted $p < 0.05$).

Fig. 2. Diameter at breast height (DBH) (cm), percent fire-caused bud kill (PBK), and cambium kill rating (CKR) of live not attacked trees, fire-injured trees strip attacked by bark beetles that remained alive, fire-injured trees mass attacked by bark beetles and killed, and trees killed by fire alone 3 years post-fire at a wildfire and prescribed-fire site. Shown are the 5th and 95th percentiles, interquartile range, mean (broken line), and median (solid line). Pairwise differences determined by the Tukey–Kramer Honestly Significant Difference test are indicated by letters.
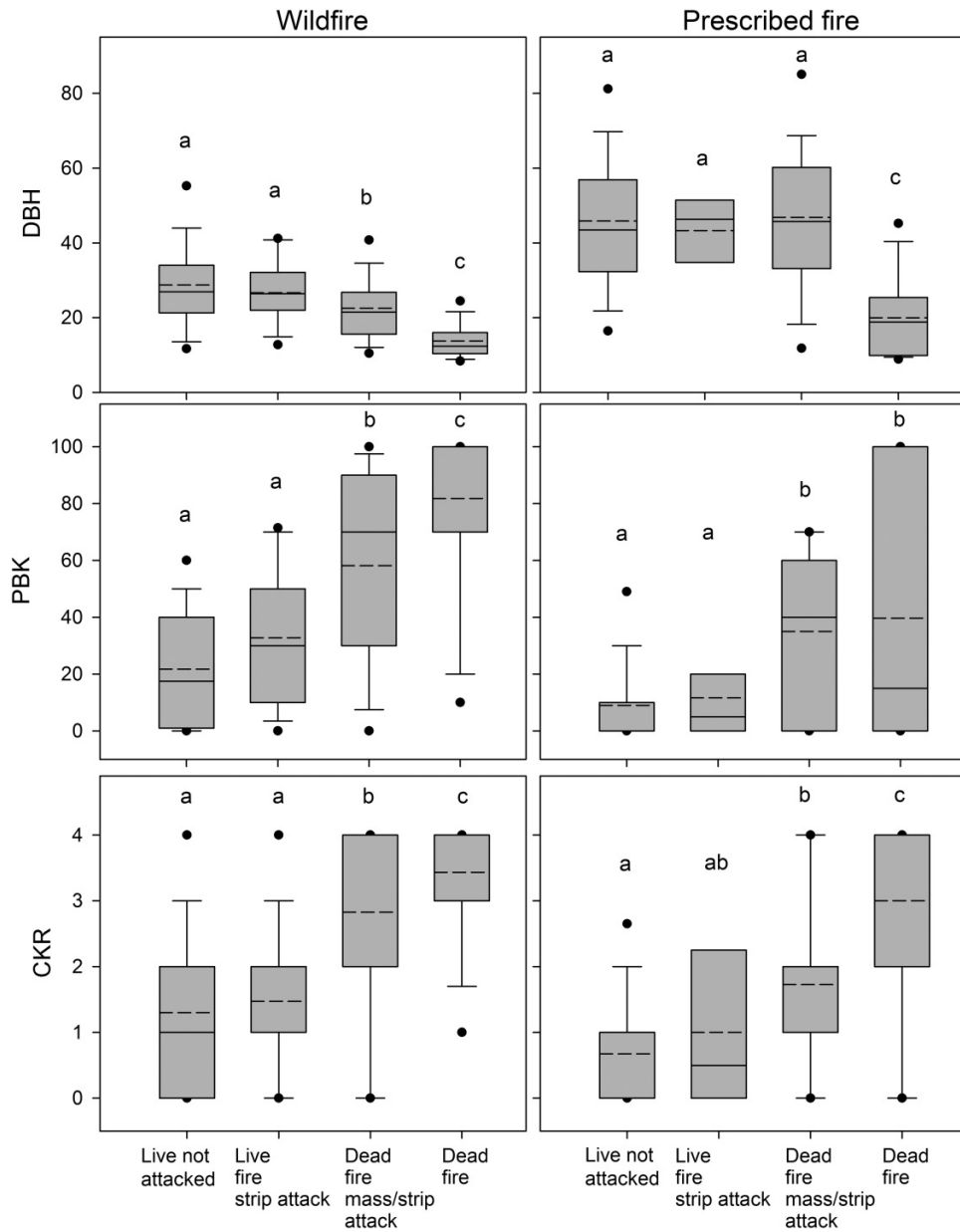

Table 5. Fire injury variables found most significant in describing ponderosa pine (*Pinus ponderosa*) mortality 3 years post-fire at a wildfire and a prescribed burn site based on logistic regression.

Variable	Wildfire	Prescribed fire
Diameter at breast height (DBH)	$F_{[1,299]} = 6.27, p = 0.0128$	$F_{[1,170]} = 0.62, p = 0.4328$
Percent bud kill (PBK)	$F_{[1,266.1]} = 17.53, p < 0.0001$	$F_{[1,170]} = 5.65, p = 0.0186$
Cambium kill rating (CKR)	$F_{[1,299]} = 6.27, p < 0.0001$	$F_{[4,170]} = 2.98, p = 0.0207$
Bark beetle attack (ATK)	$F_{[1,299]} = 1.07, p = 0.3011$	$F_{[1,170]} = 0.86, p = 0.3564$
DBH × ATK	$F_{[1,299]} = 5.08, p = 0.0249$	$F_{[1,170]} = 5.91, p = 0.0161$

Note: ATK is a class variable with 2 levels: 0 = unattacked by western pine beetle and mountain pine beetle and 1 = attacked. See Table 2 for variable descriptions.

Fig. 3. Proportion of all bark beetle attacks by species, attack type, and postfire year following a wildfire that burned in fall 2003 (BM2, Lolo National Forest, Montana) and a prescribed fire that burned in spring 2004 (Parks, Payette National Forest, Idaho). The arrow approximates the timing of fire at each site. Bark beetle species are mountain pine beetle (MPB), western pine beetle (WPB), emarginate ips and engraver ips (IPS), and some mix of the four species (MIX). No bark beetle attacked trees were observed at the unburned site on the Payette National Forest.
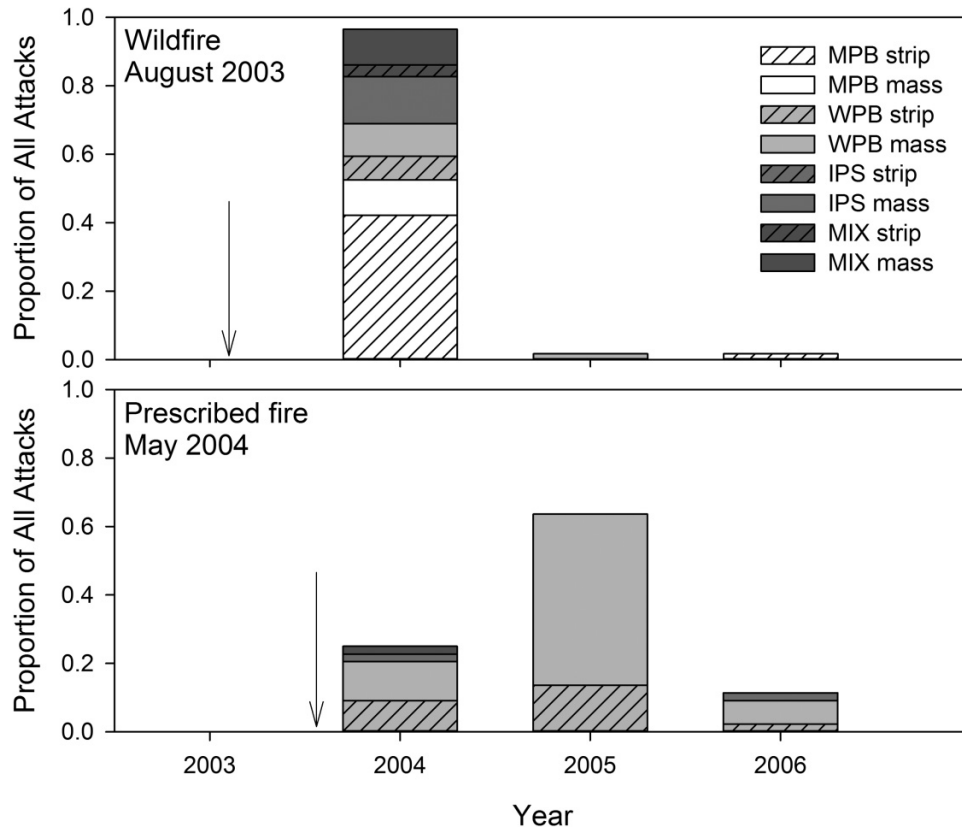
quadrant-level samples were taken for cambium status (dead or alive) and assigned a visual bark char severity rating (deep, moderate, light, and unburned). Quadrants with a deep char rating ($N = 275$) had the highest percent dead cambium (91.64%), quadrants rated as low ($N = 306$) had 12.09% dead cambium, and samples from quadrants rated as unburned ($N = 148$) had the lowest percent dead cambium (10.14%). The majority of samples were rated moderate ($N = 1843$), and 48.62% of these samples had dead cambium.

Bark beetle attack preference and brood production

Mountain pine beetle, western pine beetle, pine engraver (IPS), emarginate ips (IPS), and a combination of the species (MIX) attacked trees at the wildfire site. At the prescribed fire site, only western pine beetle, IPS, and MIX were observed. Western pine beetle and IPS attacked trees in the early and late summer and these trees were summed by year in the analyses. More than 98% of attacks on plots at the wildfire site occurred the summer following the August 2003 wildfire (Fig. 3). The prescribed fire occurred May 2004 and the highest percentage of bark beetle attacks on trees within the fire boundary did not occur until the summer of 2005. When data for both sites were combined, 87 (15%) trees were mass attacked and 74 (13%) trees were strip attacked within 3 years post-fire. The majority of strip attacks were caused by mountain pine beetle and were at the wildfire site (Fig. 3). More than 50% of these trees were

alive 3 years post-fire. No unburned, attacked trees were observed on plots at the wildfire site. At the prescribed fire site, only two ponderosa pine on established plots lacked signs of bole or crown fire injury, and these trees were not attacked by bark beetles. Significantly more trees were attacked at the prescribed fire site compared with the adjacent unburned control site ($\chi^2 = 57.9360$, $p < 0.0001$). No bark beetle attacked ponderosa pine were observed on plots at the unburned control site. Woodpecker foraging was high on attacked trees throughout both study areas. Red turpentine beetle attacks were found on 97 (21%) of burned trees at both sites, and wood-boring beetles (e.g., Cerambycidae and Buprestidae) were also found in large numbers on fire-injured trees, although not quantified.

At both sites, ponderosa pine with greater fire injury were attacked, colonized, and killed by bark beetles compared with trees that were strip attacked by bark beetles and survived 3 years post-fire. The variables that best described the differences, however, varied between the sites (Table 4). At the wildfire site, trees that were attacked by bark beetles and subsequently died were significantly smaller, with significantly higher PSL, CVS, PBK, CKR, and PCC, than trees that were attacked but remained alive 3 years post-fire (Table 4). At the prescribed fire site, trees attacked and killed by bark beetles had significantly higher PBK and CVS than trees that were attacked but remained alive 3 years post-fire (Table 4;

Table 6. Mean (±SE) diameter at breast height (cm) of ponderosa pine (*Pinus ponderosa*) attacked by IPS (pine engraver and emarginate ips), MPB (mountain pine beetle), WPB (western pine beetle), and MIX (some combination of the four species) at wildfire and prescribed fire sites.

	IPS	MPB	WPB	MIX
Wildfire	13.5 (3.8) a	24.2 (7.9) b	20.76 (7.2) b	27.53 (12.1) b
	$N = 16$	$N = 63$	$N = 21$	$N = 16$
Prescribed fire	36.7 (11.7)	na	45.92 (19.3)	35.3
	$N = 2$		$N = 41$	$N = 1$

Note: Means within a row (i.e., within a site) with different letters are significantly different at $p < 0.05$. na, not applicable.

Fig. 2). At the wildfire site when only bark beetle attacks that resulted in tree death were included, PBK ($F_{[1,284]} = 7.02$, $p = 0.0085$), PBK × DBH ($F_{[1,284]} = 11.34$, $p = 0.0009$), and CKR ($F_{[4,285]} = 4.31$, $p = 0.0021$) were significant predictors of bark beetle attacks on individual ponderosa pine. At the prescribed fire site, PBK ($F_{[1,182]} = 5.34$, $p = 0.0219$) and CVS ($F_{[1,182]} = 4.93$, $p = 0.0276$) both explained if a tree was attacked and subsequently killed by bark beetles in independent models, although the model using PBK was slightly more significant based on the Residual Log Pseudo-Likelihood. The categorical variable fire injury did not explain attacks at either site.

At the wildfire site, trees attacked by IPS were significantly smaller than trees attacked by mountain pine beetle, western pine beetle, or MIX ($F_{[3,110]} = 10.53$, $p < 0.0001$), although no differences in DBH were found among bark beetle attacked trees at the prescribed fire site, where fewer trees were attacked by IPS (Table 6). Based on trees at both sites, significantly more bark beetle attacks were located within charred areas of tree boles than within uncharred areas ($\chi^2 = 20.8$, $p < 0.0001$). Mountain pine beetle only attacked and colonized trees at the wildfire site. Of the trees monitored that had some level of mountain pine beetle attack, mountain pine beetles only emerged from trees that were also attacked by western pine beetle and (or) IPS. More western pine beetle emerged from fire-injured trees than did mountain pine beetle or IPS at the wildfire site, and western pine beetle emergence from fire-injured trees was also greater than IPS emergence at the prescribed fire site (Fig. 4). Mountain pine beetle and western pine beetle emergence was not significantly different between fire-injured and unburned trees at either site, although significantly more IPS emerged from uninjured compared with fire-injured trees at the wildfire site ($F_{[1,12.42]} = 10.46$, $p = 0.0069$). None of the fire injury or tree variables tested explained western pine beetle, mountain pine beetle, or IPS brood emergence at either site.

Resin flow

In post-fire years 2005 and 2006, a total of 634 resin flow volume (millilitres) samples were collected from 139 total trees, 66 burned and 73 unburned. Resin flow did not differ significantly among unburned tree bole aspects at either site. At the prescribed fire site, resin flow volume of unburned trees differed significantly by sample month ($F_{[2,78.87]} = 5.97$, $p = 0.0038$) and DBH class ($F_{[3,81.02]} = 3.55$, $p = 0.0180$). Resin volume was greater in July than in June ($t_{75.03} = 3.46$, adjusted $p = 0.0025$), and unburned trees in the largest DBH

class, 4, had greater resin volume flow than trees in DBH classes 2 and 3 (class 4 versus class 3: $t_{64.57} = -3.03$, $p = 0.0170$; class 4 versus class 2: $t_{82.52} = -3.06$, $p = 0.0158$). Resin volume of unburned trees also differed by month at the wildfire site ($F_{[2,102]} = 5.73$, $p = 0.0044$) and was greater in August and July than in June (August versus June: $t_{102} = 3.09$, adjusted $p = 0.0071$; July versus June: $t_{102} = 2.77$, adjusted $p = 0.0183$). The year × month interaction was also significant ($F_{[2,102]} = 3.17$, $p = 0.0462$), and June 2005 was greater than June 2006 ($t_{101} = -3.26$, $p = 0.0186$). Resin flow was positively correlated with LCL, and unburned trees with greater LCL had higher flow ($F_{[1,102]} = 4.08$, $p = 0.0459$).

Resin flow volume did not differ among tree bole aspects of fire-injured trees or on charred versus uncharred bole aspects of fire-injured trees. Fire-injured trees had greater mean resin flow volume than uninjured trees, although the difference was not significant at either site (prescribed fire: $F_{[1,15.85]} = 2.67$, $p = 0.1219$; wildfire: $F_{[1,10.89]} = 0.61$, $p = 0.4531$) (Fig. 5). DBH and LCL were highly correlated at both sites (see above), and in separate models, fire-injured trees with greater LCL and DBH had the greatest mean resin volume of all tree classes. Based on model Akaike information criterion values, LCL was the best predictor of resin flow volume of fire-injured trees at both sites (prescribed fire: $F_{[28,54.04]} = 7.50$, $p < 0.0001$; wildfire: $F_{[30,35.12]} = 2.03$, $p = 0.0227$). Month was significant in explaining resin flow of burned trees sampled repeatedly only at the wildfire site ($F_{[2,73.52]} = 7.68$, $p = 0.0009$), and August and July were both significantly greater than June (August versus June: $t_{73.68} = 3.85$, adjusted $p = 0.0007$; July versus June: $t_{73.68} = 2.81$, adjusted $p = 0.0173$).

Discussion

Bark beetles attacked significantly more ponderosa pine in a prescribed burned area, when compared with a nearby unburned control area, and a large number of fire-injured trees were attacked at a wildfire site. These results provide additional evidence that fire-injured trees are attractive to multiple bark beetle species (Hood and Bentz 2007; Jenkins et al. 2008; Fettig et al. 2010; Powell et al. 2012). Western pine beetle, emarginate ips, and pine engraver attacked trees at the prescribed fire site, often co-colonizing individual fire-injured trees. Mountain pine beetle, in addition to the other beetle species, only attacked ponderosa pine at the wildfire site, also co-colonizing trees with the other beetle species. The percentage of trees that died due to a combination of fire and bark beetle attacks was much higher at the wildfire site (60%),

Fig. 4. Mean (±SE) emergence of mountain pine beetle (MPB), western pine beetle (WPB), and *Ips* spp. (IPS) from fire-injured and uninjured trees at the wildfire and prescribed fire sites. IPS and MPB only emerged from trees that also contained as least one other bark beetle species. MPB was not found at the prescribed fire site. *N* is the number of emergence samples (standardized to 1858 cm² sample area) containing a particular species. Shown are the mean (dotted line), interquartile range, median (solid line), and 5th and 95th percentiles.
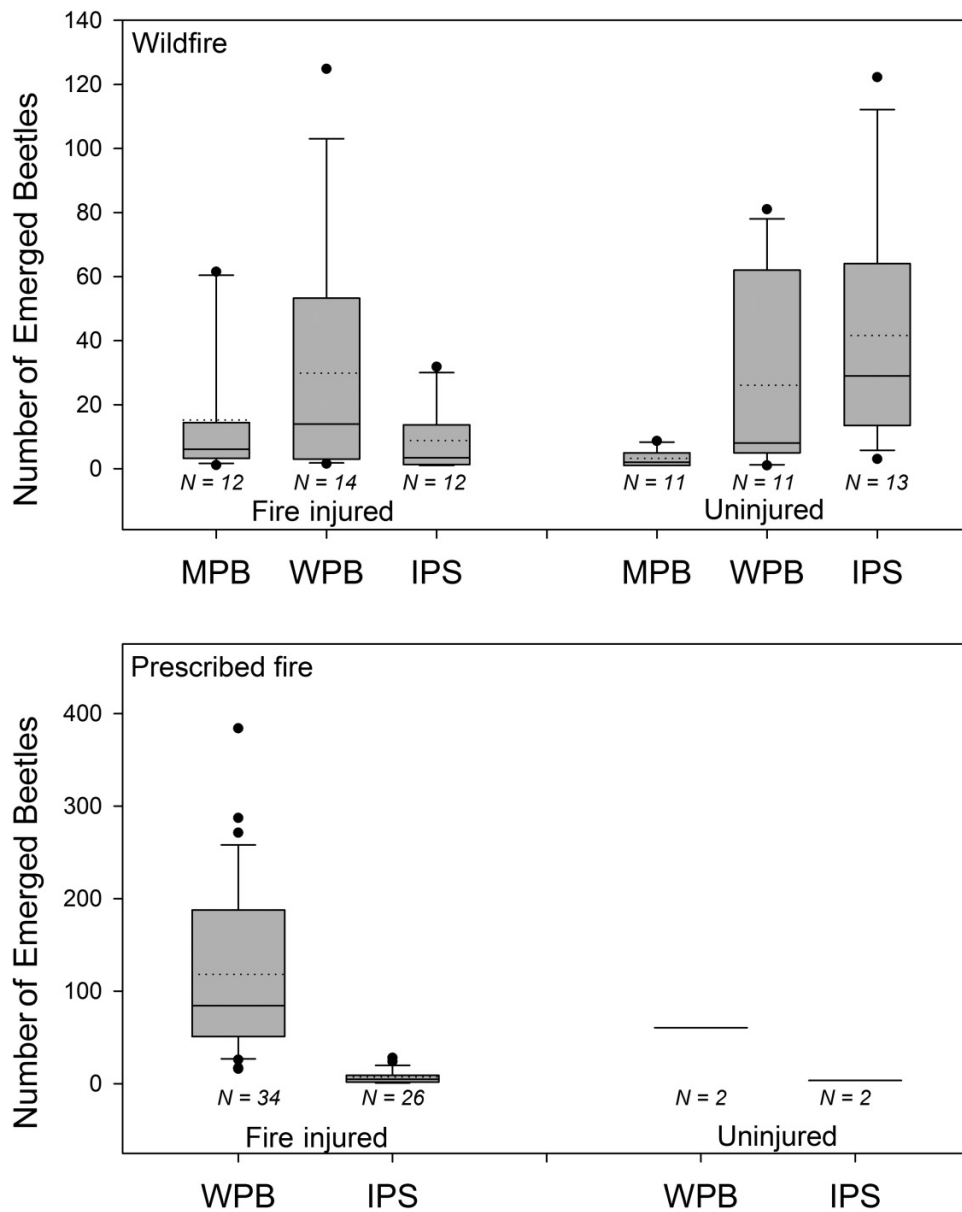

where all beetle species were observed and trees were smaller with higher levels of fire-caused injury, than at the prescribed fire site (30%). Only 15% of brood emergence samples from infested trees at both the prescribed fire and wildfire sites contained a single beetle species, and that species was most often western pine beetle. These results are congruent with observations on ponderosa pine in California (Fettig et al. 2008) and Arizona (Breece et al. 2008).

Historically, mountain pine beetle was not considered a major contributor to post-fire pine mortality (Geiszler et al. 1984; Rasmussen et al. 1996). More recently, however, mountain pine beetle attacks have been reported on both fire-injured ponderosa pine (Fettig et al. 2008, 2010) and fire-injured

lodgepole pine (*Pinus contorta* Douglas ex Loudon) (Powell et al. 2012). In our study, mountain pine beetle attacks were only observed at the wildfire site, and western pine beetle was the dominant bark beetle species observed mass attacking ponderosa pine at both sites. Mountain pine beetle attacks were most likely not observed at our prescribed fire site because there was not an active pre-fire mountain pine beetle population available for immediate response to the pulse of fire-injured trees. Our results add to the growing literature base documenting mountain pine beetle attacks on fire-injured pines.

Tree size is often a major contributor to bark beetle attack, and similar to other studies (Rasmussen et al. 1996; McHugh et al. 2003; Hood and Bentz 2007), we found that *Dendroctonus*

Fig. 5. Mean resin volume per tree of fire-injured and uninjured ponderosa pine (*Pinus ponderosa*) by sample month. Data shown include samples collected in 2005 and 2006. Differences in resin flow between fire-injured and uninjured trees were not significant at either site. Resin volume was not sampled in August 2006 at the prescribed-fire site. Shown are the mean (dotted line), interquartile range, median (solid line), and 5th and 95th percentiles.
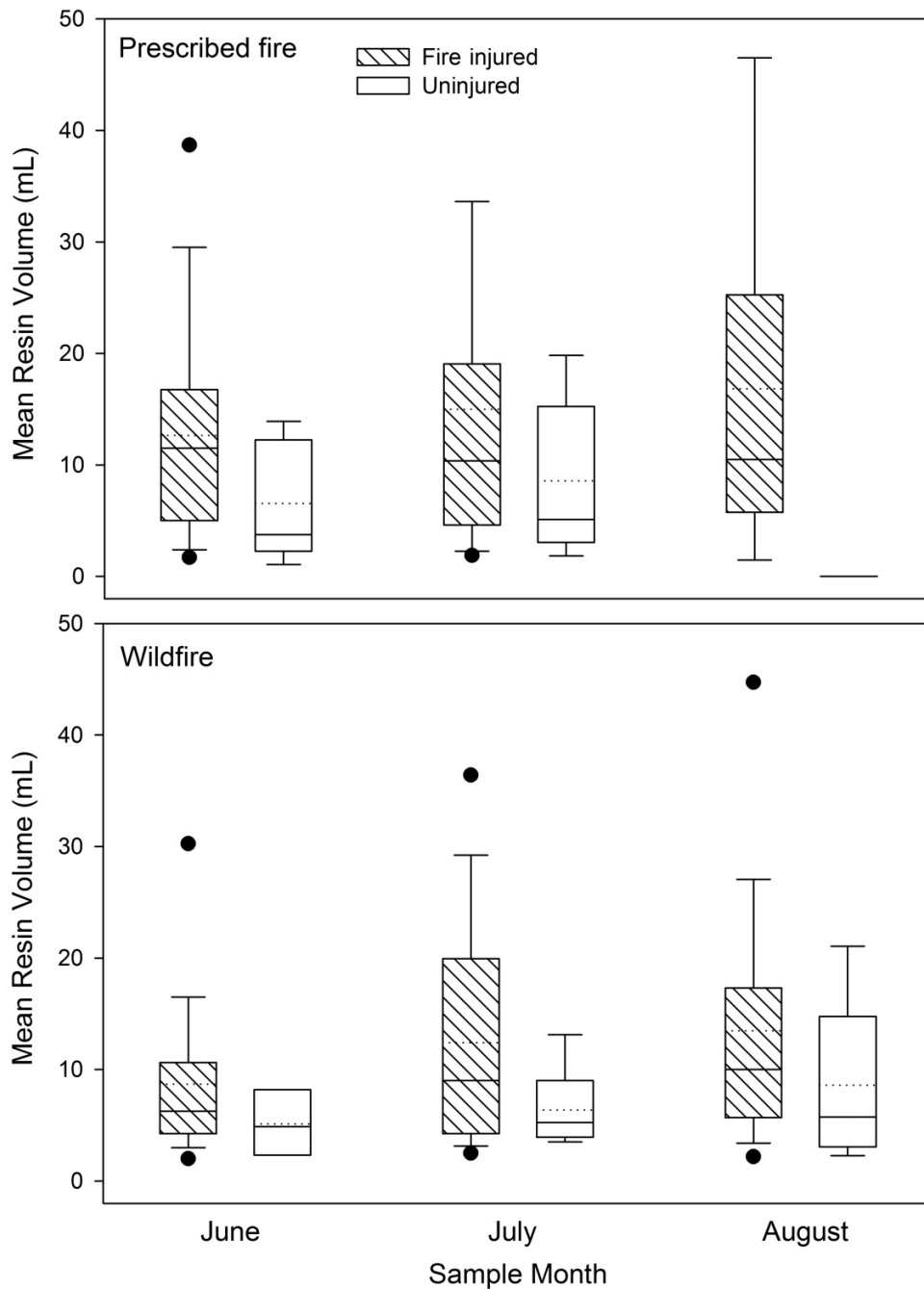
spp. (i.e., mountain pine beetle and western pine beetle) attacked larger fire-injured trees than did *Ips* spp. Tree size alone, however, was not significant in predicting attacks on fire-injured ponderosa pine at either site. At both sites, trees with greater bole and crown fire injury were attacked and killed by bark beetles compared with trees that were strip attacked by bark beetles and remained alive 3 years post-fire. We did not find, however, that a single categorical variable describing a mix of bole and crown injury (i.e., unburned, low,

moderate, high, or severe) was sufficient to explain if a tree was attacked and killed. Powell et al. (2012) found that mountain pine beetle preferentially attacked moderately injured lodgepole pine with 0%–50% bole injury, 0%–10% crown injury, and CKR = 1, 2, or 3. At our wildfire site, mountain pine beetle and western pine beetle mass attacked ponderosa pine with high levels of crown (mean PBK = 58%) and bole (mean CKR = 2.8) injury, although trees with extreme crown (mean PBK > 82%) and bole (mean CKR > 3.4) injury were

not attacked. At the prescribed fire site where injury levels were lower, the upper limit of fire injury suitable for attack was also lower (mean PBK > 40% and mean CKR > 3.0). The thick bark and protected buds of ponderosa pine may provide an adequate resource for bark beetles even when fire injuries are high, relative to lodgepole pine. Both crown and bole injury play an important role in bark beetle attacks on fire-injured trees, although the range of fire injuries suitable and attractive to bark beetles will be specific to host tree species and mediated by the range of fire-injured trees available in an area.

We found no significant differences in brood production of bark beetles (measured as total adult emergence) in fire-injured ponderosa pine compared with uninjured trees at the same site, except for the two *Ips* spp. At the wildfire site, significantly more *Ips* spp. emerged from unburned trees. In the year following fire (when >90% of attacks occurred), fire-injured trees were therefore potentially a sink for *Ips* spp. and mountain pine beetle, although mountain pine beetle brood production was poor in both fire-injured and uninjured trees. Poor mountain pine beetle brood production in burned and unburned trees could potentially be due to competition with other bark beetle species. Mountain pine beetle emergence was only observed in trees with either western pine beetle or *Ips* spp. or both. Mountain pine beetle has a univoltine life cycle, whereas both western pine beetle and *Ips* spp. can complete at least two generations in a single year at our study sites. Therefore, because western pine beetle and *Ips* spp. colonize trees earlier in the growing season, they can consume the phloem resource in advance of mountain pine beetle, resulting in reduced mountain pine beetle brood production (Safranyik et al. 1999). Fire-injured trees did not appear to be a sink for western pine beetle, as brood production was not significantly different between fire-injured and uninjured trees at the wildfire site. Moreover, total adult emergence of western pine beetle was significantly greater than that of mountain pine beetle at the wildfire site where both species were found.

None of the fire injury variables measured at either site were significant in explaining the number of brood emerged. At both sites, the majority of attacks occurred the summer following each fire, and by post-fire year 3, few attacks were observed (Fig. 3). At the end of the study, 40% of all ponderosa pine at the wildfire site and 70% of all ponderosa pine at the prescribed site were still alive, although 99% of the trees had some level of fire injury. These results suggest that fire-injured ponderosa pine may provide a short-term resource, within the first year following fire, for bark beetles when population levels prior to fire are at endemic levels, concurrent with the results in Powell et al. (2012). Trees alive 3 years post-fire had significantly less fire injury than trees either attacked and killed by bark beetles or killed by fire alone (Fig. 2). For western pine beetle in particular, however, a reduction in attacked trees through time does not appear to be caused by reduced brood production in fire-injured trees and is more likely due to a limited number of trees in fire injury categories that can be easily colonized (i.e., those with higher crown and bole injury).

Constitutive resin flow did not differ between the sample years or among tree bole aspects, but each year, flow increased through the summer from June to August in both burned and unburned trees, a result congruent with previous research

(Callaham 1955; Perrakis and Agee 2006; Gaylord et al. 2007). Resin flow of unburned trees was greatest in trees with the largest DBH at the prescribed fire site and greatest in trees with the highest pre-fire live crown length at the wildfire site, findings similar to Davis et al. (2011). LCL, which was highly correlated with DBH, also explained the most variance in resin flow of fire-injured trees. Larger trees likely have greater access to water, nutrients, and light, giving them more resources for post-fire secondary metabolism (Wilkens et al. 1998). In addition to increased resin flow in large trees, Perrakis et al. (2011) observed that fire-injured ponderosa pine had greater resin flow relative to uninjured trees. In our study, fire-injured trees exuded almost 50% more resin in July, on average, than uninjured trees. Although trees with greater resin flow are presumed to have greater resin defenses (Hodges et al. 1979; Lombardero et al. 2000; Strom et al. 2002), Powell and Raffa (2011) found that fire injury can reduce the ability of lodgepole pine to manufacture induced volatile monoterpenes important in defense against bark beetle attack. Fire injury also caused changes in the proportion of some individual compounds that could favor mountain pine beetle attack success in trees with higher injury (Powell and Raffa 2011). We did not measure resin composition, but the increased levels of resin flow that we observed in fire-injured trees may be mediated by reduced capacity for an induced volatile response to beetle attack. Our result that trees with strip attacks by mountain pine beetle and western pine beetle had lower levels of fire injury than trees that were mass attacked and killed suggests that trees with less fire injury were potentially better defended.

Similar to other studies (McHugh and Kolb 2003; Sieg et al. 2006; Hood et al. 2010), we found that separate measures of crown damage, to the buds (PBK) or needles (CVS), were important predictors of ponderosa pine mortality, particularly at the wildfire site where trees were smaller. Ponderosa pine buds are large and protected, enabling them to survive high levels of scorch. Measuring bud kill, rather than needle kill alone (needles are more susceptible to heat), can provide a more detailed description of fire-related injury and the tree's ability to recover and produce new needles (Wagener 1961; Dieterich 1979; Hood et al. 2010). At both sites, the interaction of DBH and attack by western pine beetle and (or) mountain pine beetle was significant in predicting mortality within 3 years post-fire. Smaller trees were killed by fire alone, a finding similar to others (Harrington 1993; Regelbrugge and Conard 1993; Thies et al. 2006), and larger trees either survived or were attacked by beetles. In agreement with previous studies conducted on Douglas-fir (Ryan and Reinhardt 1988; Hood and Bentz 2007) and ponderosa pine (Ryan and Frandsen 1991; Hood et al. 2010), we found that a direct measure of cambium death (CKR) was also an important predictor of tree mortality following fire at both sites. Although a direct measurement of cambium death, such as CKR, can be time consuming, we found that a visual measurement was not an accurate measure of cambial death, particularly for moderate bark char, the most commonly assigned rating (Breece et al. 2008; Hood et al. 2008). For practical field application, char ratings unburned, low, and deep can estimate cambium status fairly accurately, but if moderate-rated quadrants are encountered, cambium coring to determine status is advised.

In summary, we found that bark beetle attraction to fire-injured ponderosa pine was related to increased levels of fire

injury that affected both the crown and the bole. Results from our study show that when populations of bark beetles are present in areas prior to prescribed or wildland fire, they can contribute significantly to post-fire mortality in ponderosa pine, although the effects at both our sites were short term. Bark beetle response to fire-injured trees within the fire boundary pulsed and receded within 2 years post-burn. These results agree with studies conducted in lodgepole pine (Powell et al. 2012) and Douglas-fir (Hood and Bentz 2007) and suggest that fire-affected forests do not generate sustainable outbreak bark beetle populations with potential spread to adjacent, unburned areas, particularly when populations are endemic. We did not, however, monitor unburned areas immediately surrounding the study areas. Fire-injured trees were not a sink for western pine beetle brood production. Conversely, mountain pine beetle brood production was poor in both fire-injured and uninjured trees, potentially due to competition with faster developing bark beetle species present in the same trees. The potential for greater secondary defenses in unburned and low fire injury level trees, relative to trees with greater fire injuries (Powell and Raffa 2011), was supported by our result that strip-attacked trees that remained alive 3 years post-fire had lower levels of crown injury than trees attacked by beetles and killed. The underlying mechanisms responsible for post-fire tree susceptibility and attraction to bark beetles and the role of constitutive and secondary host resin defenses remain unclear, warranting further investigation. The level of fire-caused ponderosa pine injury that was attractive to bark beetles differed at our two sites and was potentially due to site differences in tree size, stand structure, and fire behavior. Predicting bark beetle attacks as a function of fire injury, even for a single host tree species, will depend on pre-fire stand conditions, fire behavior, and the resulting range of fire-injured trees available for attack.

Acknowledgements

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