

Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties

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Abstract: This study examined the effects of spring and fall restoration burning in an old-growth mixed-conifer – ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) forest in southern Oregon. Variables measured include fuel loads, forest structure indices, mortality of large ponderosa pines, and pine resin defenses. One year after treatment, reductions in surface fuel loads and changes to forest structure parameters suggested that burning treatments could meet restoration objectives, with fall burns being somewhat more effective than spring burns. However, mortality of pre-settlement pines was significantly higher in fall burns than in spring burns, and both were higher than in unburned controls. Bark beetles (Coleoptera: Scolytidae) were important mortality agents within 2 years after burning. Resin defenses (pressure and flow) were variable over the 2 years of postburn study but showed no evidence of decrease in burned trees; rather, resin defenses were significantly higher in burned trees than in controls at several measurement dates. While increased beetle attacks have previously been documented following burning, there has been much less research on resin responses to fire. These findings suggest that current models of beetle–host interactions do not properly explain the effects of prescribed fire in ponderosa pine forests.

Résumé : Cet article examine les effets d'un brûlage de restauration au printemps ou à l'automne dans une forêt ancienne mélangée composée de conifères et de pin ponderosa (*Pinus ponderosa* Dougl. ex P. & C. Laws.) dans le sud de l'Oregon. Les variables mesurées incluent : la quantité de combustibles, des indices de structure de la forêt, la mortalité parmi les gros pins ponderosa et la production de résine comme mécanisme de défense des pins. Un an après le traitement, la réduction des quantités de combustibles et les changements dans les paramètres de la structure de la forêt indiquaient que le brûlage permettait d'atteindre les objectifs de restauration et qu'il était un peu plus efficace à l'automne qu'au printemps. Cependant, la mortalité chez les pins présents avant la colonisation était significativement plus élevée lorsque le brûlage avait lieu à l'automne plutôt qu'au printemps et plus élevée dans les deux cas que dans les parcelles témoins non brûlées. Les scolytes (Coléoptères : Scolytidae) étaient des causes importantes de mortalité pendant les deux années qui ont suivi le brûlage. Les réactions de défense impliquant la production de résine (pression et écoulement) étaient variables pendant les deux années qui ont suivi le brûlage mais n'ont montré aucun indice de diminution chez les arbres brûlés. Au contraire, les mécanismes de défense impliquant la production de résine étaient significativement plus importants chez les arbres brûlés que chez les arbres témoins à plusieurs dates où des mesures ont été prises. Bien qu'une augmentation des attaques de scolytes ait déjà été rapportée à la suite d'un feu, il y a eu beaucoup moins d'études sur la production de résine en réaction au feu. Ces résultats indiquent que les modèles actuels d'interaction entre les scolytes et leurs hôtes n'expliquent pas correctement les effets du brûlage dirigé dans les forêts de pin ponderosa.

[Traduit par la Rédaction]

Introduction

Fire exclusion during the 20th century is recognized to have caused long-lasting and profound effects on many forests of the western United States. In ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) forests, these effects include increases in fuel loading and changes to forest structure that have contributed to conversions from low- to high-severity fire regimes (sensu Agee 1993) and a modern crown fire hazard that has reached crisis condition in many areas (Covington and Moore 1994; Anonymous 1999; Carle 2002).

During the mid to late 20th century, mounting evidence linked fire exclusion to increased fire hazard, prompting calls for reintroducing fire for purposes of ecological restoration and public safety (Carle 2002).

The National Park Service was one of the earliest agencies to embrace the new paradigm, adopting policies of prescribed burning and wildland fire use as early as the 1960s (Butts 1985). Prescribed burning at Crater Lake National Park in southern Oregon began in the mid-1970s in the park's ponderosa pine dominated mixed-conifer stands, forests similar in structure and disturbance history to widely distributed mixed-conifer types in western states. These communities have historic regimes of low- to mixed-severity fire, although suppression efforts have effectively excluded fire since 1902 when the park was created (McNeil and Zobel 1980). Typical stands are currently in declining health owing to vigorous growth of shade-tolerant species in the understory, especially white fir (*Abies concolor* (Gordon and Glend.) Lindl.) (McNeil and Zobel 1980).

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Following a decade of experimental burning at Crater Lake, early fire effects studies identified problems with the treatment effectiveness. Specifically, higher mortality was occurring among the largest size classes of ponderosa pines in burn units compared with control areas. Many trees appeared to survive the immediate effects of the fires but later succumbed to attacks from bark beetles (especially western pine beetle (*Dendroctonus brevicomis* LeConte)), sometimes several years after the burns took place (Thomas and Agee 1986). Subsequent research at Crater Lake confirmed this mortality pattern (Swezy and Agee 1991; Agee 2003a), and the interaction between fire and bark beetles emerged as a critical topic in the management of this ecosystem. The discovery of a positive correlation between prescribed fire and elevated insect presence in these forests complicates the restoration issue considerably from both scientific and management perspectives. As postfire mortality of large ponderosa pines continues, the use of prescribed fire as the sole restoration treatment in this ecosystem is being questioned (Agee 2003a). Following where earlier studies left off, this project sought to evaluate a series of spring and fall prescribed burns at Crater Lake by analyzing the effects of prescribed burning treatments on three related components: fuels and forest structure, ponderosa pine mortality, and ponderosa pine resin defenses.

Fuel reduction to limit wildfire hazard is probably the most common objective of management burning programs (Biswell et al. 1973; Martin 1990). In Pacific Northwest ponderosa pine forests, the link between fire exclusion, fuels buildup, and increased fire hazard has been recognized for decades from early work in central Oregon (Weaver 1959) to later studies at Crater Lake and in northern California. Thomas and Agee (1986) measured an immediate fuel mass reduction of 67% following summer burning, although postfire additions to the fuel bed limited the treatment effectiveness to a 29% reduction by the second year. Spring burning in ponderosa pine stands on the nearby Fremont National Forest, Oregon, reduced preburn loads by 41% (Busse et al. 2000). In the southwestern United States, fuel reduction percentages from restoration burns have typically been higher (e.g., Sackett 1980; Harrington 1981; Fulé et al. 2002), although reduction in absolute fuel mass is typically lower in southwestern stands than in mixed-conifer stands owing to lower total fuel loads in the former. While treatment effects may be short-lived and quantitative data on fuel reduction effectiveness are often lacking (Fernandes and Botelho 2003), emerging studies suggest that prescribed burning can be effective in reducing subsequent wildfire severity in ponderosa pine forests (van Wagtenonk 1995; Stephens 1998; Pollet and Omi 2002).

In addition to fuel reduction, objectives of restoration burns often include forest structure prescriptions. In ponderosa pine forests, these typically involve killing small trees, reducing overall forest density, and favoring fire-exclusion vegetation (Biswell et al. 1973; Fulé et al. 2002; Waltz et al. 2003). At Crater Lake, prescribed burning successfully reduced understory tree density, although sometimes with the unintended effect of overstory mortality as well (Thomas and Agee 1986).

Ponderosa pine was historically the dominant species in Crater Lake's mixed-conifer forests (McNeil and Zobel 1980), and avoiding adverse effects on the population has always been of great concern during burn planning. While ponderosa

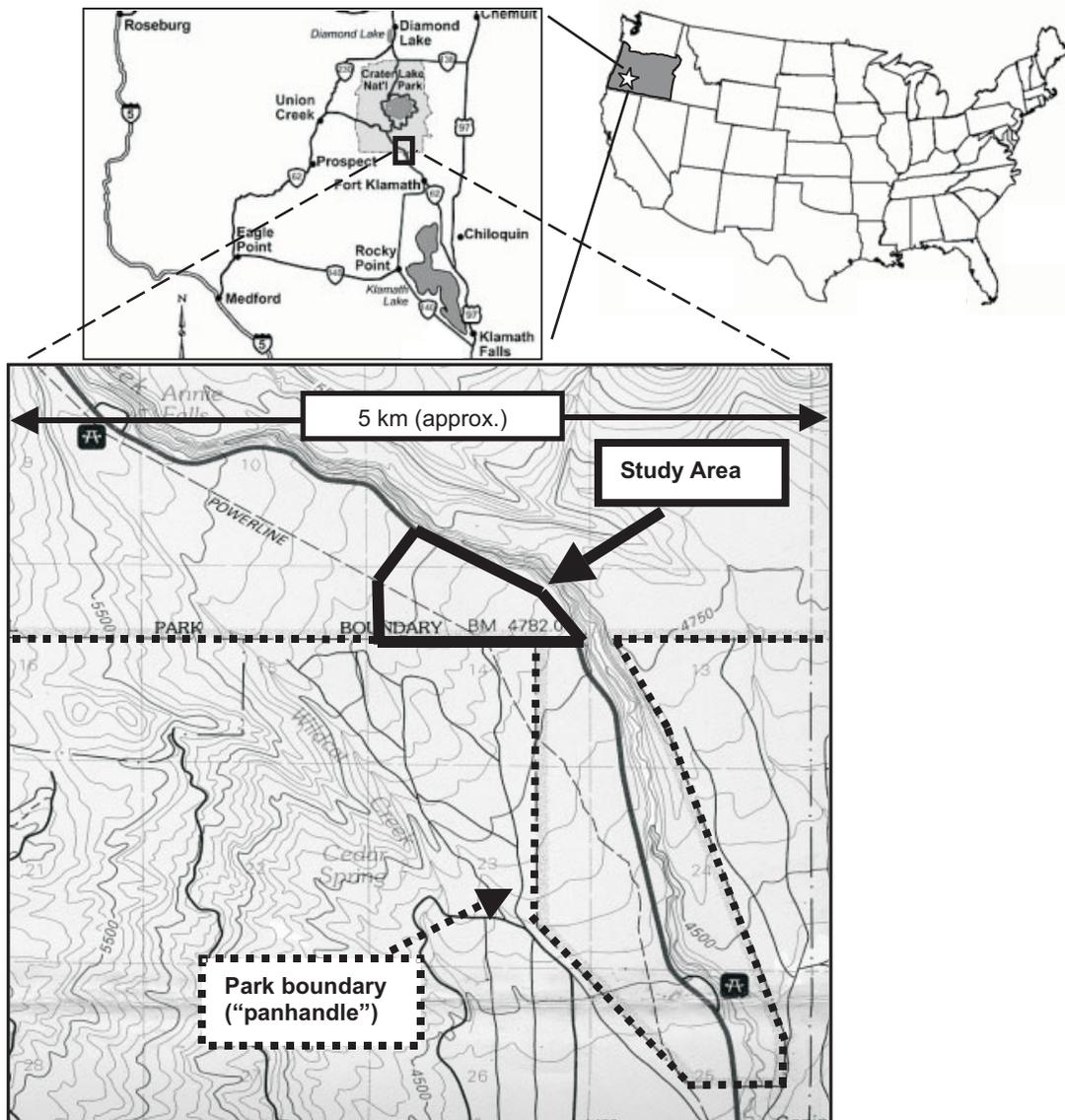
pine are known to be highly resistant to low-intensity fire (Biswell et al. 1973; Agee 1993) and ponderosa pine dominance in these forests is clearly dependent on frequent fires (McNeil and Zobel 1980), the largest size classes occasionally suffer high mortality following prescribed fires (Swezy and Agee 1991; Sackett and Haase 1998; McHugh and Kolb 2003). Postburn ponderosa pine mortality has been found to be higher in early season burns than in late-season burns or controls (Swezy and Agee 1991; Harrington 1993) and significantly related to damage indices such as crown scorch, bark char, and root heating (Dieterich 1979; Swezy and Agee 1991; McHugh and Kolb 2003). While much of the large pine mortality in early Crater Lake burns took place in the first year after burning (Thomas and Agee 1986), additional mortality continued for several years afterwards, with attacks from bark beetles apparently playing an increasingly important role in posttreatment years (Swezy and Agee 1991; Agee 2003a).

Primary attraction in bark beetle – host relationships refers to the attraction of dispersing beetles to kairomones (Wood 1982) in potential host trees (Moeck et al. 1981) and is a confirmed host selection mechanism for some Scolytids (e.g., Gara et al. 1984; Moeck and Simmons 1991; see Wood 1982 for a review). While some entomologists feel that primary attraction may indeed be a mechanism for western pine beetle host selection (R. Gara, Prof. of Forest Entomology, University of Washington, personal communication; A. Eglitis, Entomologist, USDA Forest Service, Central Oregon Service Center, personal communication), there is little to no experimental evidence for this view (Moeck et al. 1981; Wood 1982; Raffa et al. 1993) except in certain special cases of disease (Cobb et al. 1968; Goheen et al. 1985). The default hypothesis remains that initial host selection in western pine beetles occurs via random dispersal and landing followed by aggregation via pheromone emission (Byers 1996; Wood 1972). While primary attraction (or lack thereof) remains unproven as a host selection mechanism for western pine beetles, postburn increases in western pine beetle attacks might alternatively be related to decreased defenses in host trees.

Pine trees' main defense against insects and many pathogens is provided by resin, or oleoresin, stored in their sapwood canals (Miller and Keen 1960; Phillips and Croteau 1999). Resin acts as a defense against beetle invaders primarily by ejecting or smothering them (Miller and Keen 1960), through chemical toxicity (Smith 1975), or by preventing nesting activities and reproduction (Raffa et al. 1993). More resistant ponderosa pines are thought to have higher overall resin flow volume, resin flows that persist for longer following wounding, higher proportions of certain chemicals (limonene) in their oleoresin (Smith 1975, 2000), and possibly greater resin exudation pressure (Vité and Wood 1961; Barbosa and Wagner 1989; but see Stark 1965; Lorio 1994).

Effects on resin defenses from injury, such as fire, are not well understood. Short-term injury-induced resin production has not been found to be significant in ponderosa pine, with most or all resin being apparently preformed and stored in ducts (Lewisohn et al. 1991; Wallin et al. 2003). The longer term resin response of ponderosa pine to injury has not been studied, however. In other pine species, there is some evidence of increases in resin production several months to >1 year following various forms of physical injury (Bannan 1936;

Fig. 1. Study area location along the southern boundary of Crater Lake National Park, Oregon.



Nebeker and Hodges 1983; Fredericksen et al. 1995; Kozlowski and Pallardy 1997). How such increases affect beetle resistance, however, is not known. That is, could trees be made more beetle resistant, even temporarily, by physical injury?

This study examines the effects of initial restoration burning on surface fuels, forest structure, ponderosa pine survivorship, and ponderosa pine resin defenses following spring and fall fires in Crater Lake mixed-conifer forest. The experiment was designed such that response variables were measured once before treatment and then monitored for several years afterwards. This paper presents interim results after 2 years of postburn study.

Methods

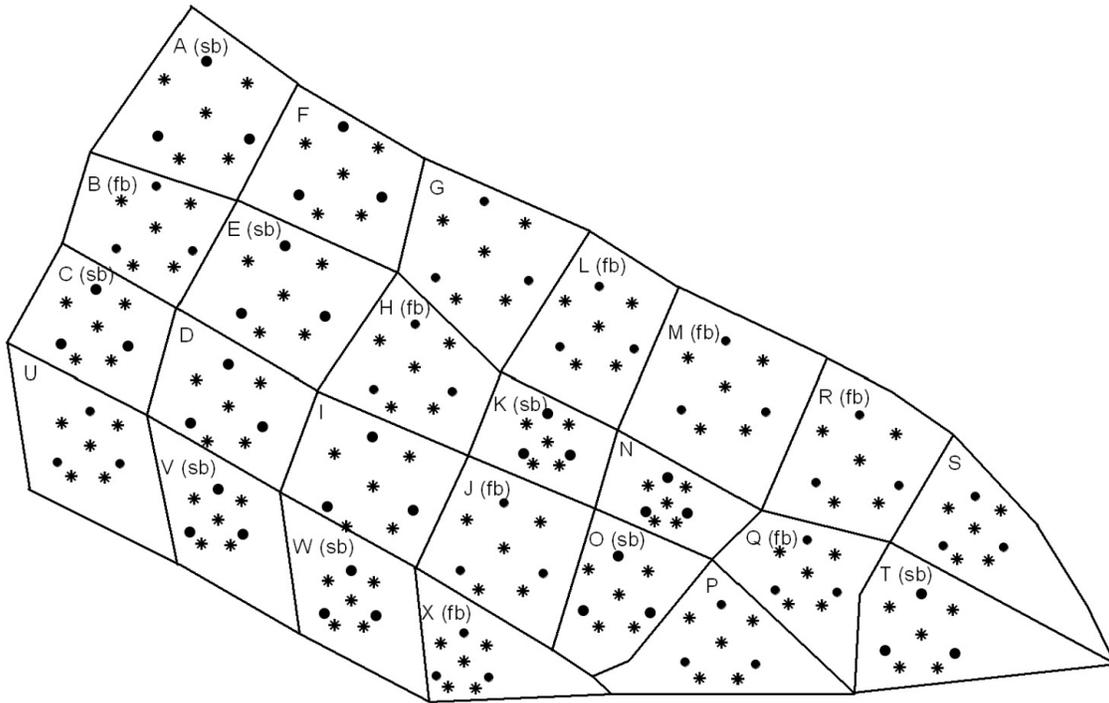
Study area

This study took place in Crater Lake National Park, Oregon. An area protected from fire since 1902 (McNeil and Zobel 1980) of approximately 67 ha was selected at approxi-

mately 42°48'N, 122°05'W along the southern park boundary adjacent to US Highway 62 (Fig. 1). Elevation varied between about 1460 m (4800 ft) and 1550 m (5100 ft), with very gentle topography and no slopes steeper than 5%. Owing to its high elevation and position directly on the Cascade crest, the site receives heavy snowfall in winter, with snow patches usually remaining on the ground until mid- to late June.

Pretreatment forest structure in the study area was typical of fire-excluded stands in the upper elevation mixed-conifer zone (Franklin and Dyrness 1988). Dominant tree species consisted of ponderosa pine, white fir, Shasta red fir (*Abies magnifica* var. *shastensis*), and lodgepole pine (*Pinus contorta* subsp. *murrayana*). Other species present included *Pinus monticola* and *Tsuga mertensiana*, with individuals scattered throughout the stand, as well as small numbers of *Pinus lambertiana*, *Pseudotsuga menziesii*, and *Populus tremuloides*. Woody fuels in the area consisted of a heterogeneous mosaic of fuel models 8, 9, and 10 (from Northern Forest Fire Labo-

Fig. 2. Study area design including locations of fuel transects (asterisks) and vegetation plots (filled circles). Experimental units marked “sb” are spring burns, units marked “fb” are fall burns, and those with neither are controls. For resin monitoring, D, F, I, and N are associated with spring burns and G, P, S, and U are associated with fall burns.



ratory fuel models; Anderson 1982). The area was historically characterized by a low- to mixed-severity fire regime (Agee 1993). Based on fire scar records, fire-return intervals for the study area varied between 12.8 and 40 years, with a mean interval of 21.1 years (calculated from McNeil and Zobel 1980).

Previous studies have identified several bark beetle species occurring near the study area. Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) and western pine beetles were first identified as management concerns at Crater Lake in the early 20th century (Wickman 1990). Thomas and Agee (1986) observed small ponderosa pines killed by *Ips paraconfusus* and white firs killed by *Scolytus ventralis* following fire as well as other unidentified beetle species. Postfire mortality of large ponderosa pines by western pine beetles was identified as a problem by Swezy and Agee (1991) and has been echoed by park managers in recent years.

The study area was subdivided into 24 experimental units with areas between 1.7 and 4.1 ha (mean of 2.8 ha). Since variations in topography and elevation are minor across the study area and no obvious boundaries existed for assigning treatment blocks, treatments were randomly assigned to experimental units. Eight units were selected for each of spring and fall burning, and as controls (Fig. 2).

Prescribed fire treatments

Burn treatments were applied in spring (June) and fall (October) 2002. Fire was applied using drip torches in a strip headfire ignition pattern (Martin 1990). In addition, to ensure that all ponderosa pines were affected by the treatment, the duff mound (Ryan and Frandsen 1991) around

each ponderosa pine was ringed with torch fuel twice, 1–2 m from its bole. Ignitions were completed in approximately 0.5–1 h, and once fire had been applied throughout a unit, it was not reapplied, regardless of burn patchiness. During all burns, on-location weather conditions were measured every 0.5 h by burn personnel.

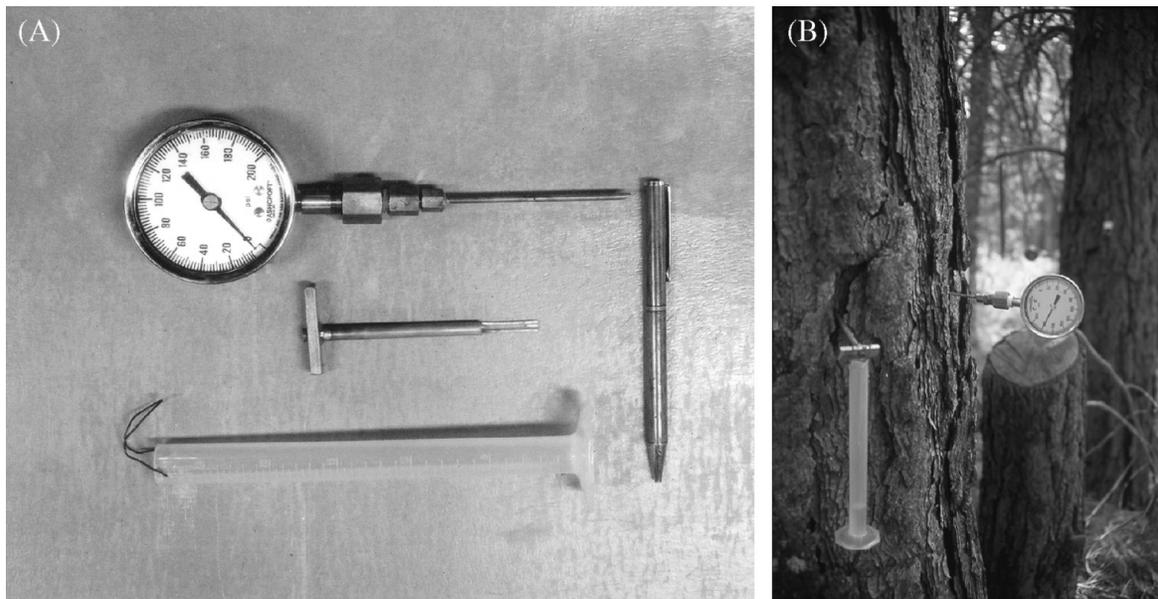
Spring burns were ignited between 20 and 28 June and were allowed to smolder for 7–8 days before being extinguished using water exclusively (no tools). Fall burns were lit on 9 and 10 October and ignited on all eight experimental units sequentially over 2 days owing to operational constraints. Burns smoldered until they were naturally extinguished several weeks later by rain, although most fire activity and fuel consumption took place within few (3–4) days after ignition.

To estimate the proportions of each unit that actually were affected by the fires, we counted foot paces along the length of two diagonal transects, approximately from one corner to its opposite in each unit. Along these transects, the number of paces on burnt and unburnt ground were counted to give an approximate estimate of burn coverage and patchiness.

Forest structure and fuels

In each unit, three vegetation plots (10 m × 20 m, 0.02 ha each) were established in a fixed triangular pattern (Fig. 2) and located on the ground using a hand-held global positioning system device (Garmin AT, Salem, Oregon). Nested 5 m × 5 m and 3 m × 3 m subplots (two of each) were established inside each vegetation plot. Within the area of each whole plot (10 m × 20 m), all trees with a diameter at breast height (DBH) (height = 1.37 m) ≥ 5 cm had their DBH measured, species noted, and crown base height (CBH) estimated. The

Fig. 3. Resin flow and pressure equipment used in this study. (A) From bottom to top: 25 mL cylinder, brass “scoop”, and pressure gauge (with nipple attached). The pen is shown for scale. (B) Oleoresin exudation pressure (OEP) and oleoresin exudation flow (OEF) measurements in a pole-size ponderosa pine (outside the study area) showing ~5 mL of resin and a pressure reading of ~1240 kPa (180 lb/in.²). Note: OEP and OEF were not measured simultaneously in this study as shown in the photograph.



same measures were taken on trees with DBH <5 cm in the 5 m × 5 m subplots, while trees with 0 DBH were counted and noted for species within the 3 m × 3 m subplots. Canopy closure was measured at the northwest corner of each plot using a spherical densiometer and standard sampling protocol (Lemmon 1957), a simple but acceptable means of estimating understory light availability (Jennings et al. 1999). The same person conducted all measurements to minimize operator bias.

Dead and down fuels were measured according to Brown's (1974) planar intersect method with 200 m of line transect per experimental unit. Transects were always more than 90° apart and began 5 m away from the location marker to ensure independence between sampling lines and avoid fuel bed disruption during marking and measurement. In addition to counting woody fuels, litter and duff depths were measured at three locations along each transect. Fuel loads were calculated using constants developed for mixed-conifer forests by van Wagtenonk et al. (1996) (woody fuels) and Agee (1973) (litter and duff).

Fuels and vegetation were measured before burning in summer 2001 (for spring burn units and half of the control units) and summer 2002 (fall burn units and half of the control units) and after burning in summer 2003 (all units). We did not attempt to differentiate between unburned fuels and new fuel additions following burning treatments.

Ponderosa pine mortality and resin monitoring

All large ponderosa pines (DBH >20 cm) were located and tagged and had their DBH measured within each experimental unit. In addition, all ponderosa pines were assessed for vigor according to Keen's (1943) four crown classes: A (full vigor, large crown), B (good to fair vigor, medium to large crown), C (fair to poor vigor, short crown), or D (very poor vigor, sparsely foliated, denuded and declining crown). A subset of these (two class A trees and two class C trees,

randomly determined in each unit) were then selected for resin monitoring. Where a unit contained no class A trees, class B trees were selected instead. One tree of each crown class per unit was subjected to a light raking treatment. Managers and researchers have previously experimented with raking treatments as a way to reduce smoldering intensity and duration (cf. Ryan and Frandsen 1991) at the bases of protected trees to help them survive restoration burns (e.g., Swezy and Agee 1991; Fulé et al. 2002). At Crater Lake, previous experiments with fuel raking down to mineral soil appeared to exacerbate postburn pine mortality, probably because of the thin soils and shallow rooting depth; duff removal likely caused fine root losses (Swezy 1988; Swezy and Agee 1991). In this study, we attempted a light raking approach whereby litter and dead fuels were removed but the fermentation layer was left in place. This treatment was applied to the duff mound area surrounding the boles of treated trees (Ryan and Frandsen 1991) in a 1–2 m radius depending on tree diameter. Raked debris were scattered outside each tree's drip line.

Pretreatment ponderosa pine population sampling was performed in September 2001 (spring burn units, half of the control units) and September 2002 (fall burn units, half of the control units), while posttreatment survival was surveyed on all large ponderosa pines in September 2003 and 2004. During posttreatment monitoring, we assigned a cause of death to each tree based on a short visual survey of the lower (<3 m) bole region. This was not designed to be a thorough autopsy of each dead individual; in most cases, tree mortality is attributable to a number of cumulative stresses that affect resource availability (Waring 1987). Rather, we attempted to identify obvious instances where individuals had been killed outright by fires or bark beetles, these having previously been identified as factors of concern, or from other apparent causes.

Recent studies examining conifer resistance to bark beetles have mostly measured resin yield at the cambial surface.

Lorio (1993) devised a now-popular method (e.g., Feeney et al. 1998; Santoro et al. 2001) that involves removing discs of bark and phloem from tree boles using an arch punch and channeling the exuded resin into vials for collection. While effective for measuring resin volume, this method unfortunately results in wounds to sample trees that are quite large and difficult to seal. This is problematic where multiple measurements over time are needed on individual trees. Furthermore, such wounds can be expected to release resin volatiles into the air until the resin crystallizes, potentially attracting insects and pathogens, such as turpentine beetles (*Dendroctonus valens* LeConte) (Hobson et al. 1993; Erbilgin and Raffa 2000). For this study, we were interested in potentially less-damaging methods, as several measurements were needed on each tree and the trees themselves were old-growth specimens inside a federally protected area.

Resin flow (OEF) was measured using a hybrid method combining aspects from both Lorio (1993) and Cobb et al. (1968): two 5.159 mm (13/64 in.) diameter holes were drilled at breast height on approximately opposite sides of the bole. Holes were drilled at an angle, approximately 30° below horizontal, each to a depth of about 2.5 cm into the sapwood. Funneling “scoops” (Fig. 3A) made of 6.35 mm (1/4 in.) diameter, 0.762 mm (0.030 in.) wall brass tubing (Alaskan Copper and Brass, Seattle, Washington) were inserted into these holes to a shallow depth (not into the phloem or sapwood), which was simple to gauge owing to the trees’ thick bark. Graduated cylinders (25 or 50 mL) were suspended to the ends of the funnels to collect the resin, and resin volume was recorded 24 h (± 1 h) after drilling (Fig. 3B). Following resin collection, holes were plugged with small sections of 6.35 mm (1/4 in.) clean wooden dowel.

Resin pressure (OEP) was measured according to a protocol adapted from Vité (1961). Two 2.381 mm (3/32 in.) diameter holes were drilled horizontally on approximately opposite sides of the bole, each to a depth of 2.5–3.5 cm into the sapwood. Holes were redrilled several times to clean out any woody residue. A piece of 3.175 mm (1/8 in.) diameter steel rod was tapped into each hole after drilling to expand it slightly before inserting the gauge. Pressure gauges used were Ashcroft Duralife models (Dresser Instruments, Stratford, Connecticut) calibrated from 0 to 1379 kPa (0–200 lb/in.²) (Fig. 3A). Nipples were made of 10.5 cm lengths of 3.175 mm (1/8 in.) outside diameter, 0.813 mm (0.032 in.) wall brass tubing (Alaskan Copper and Brass, Seattle, Washington) inserted and soldered to a 9.53 mm (3/8 in.) compression fitting/bell reducer (see Fig. 3A). Nipples were filled with anhydrous glycerin before being attached and tightened to the pressure gauges. A small bead of adhesive caulking was applied to the outside circumference of the nipples approximately 2.5 cm from the tip. The steel rod was removed from each drilled hole immediately prior to inserting the gauge–nipple combination, which was squeezed into the hole hand-tight until the tip of the nipple was about 5 mm from the back of the hole. Gauges were left overnight to stabilize and OEP measurements noted the next day at 1300 (± 1 h) (Fig. 3B). Following measurements, holes were plugged with small sections of 3.175 mm (1/8 in.) clean wooden dowel.

OEF and OEP were measured on different days to avoid confounding factors related to the interconnectedness of resin ducts. Pine resin ducts are organized as either planar or

three-dimensional networks of vertical, radial, and (possibly) tangential canals that can be continuous for several metres (Bannan 1936; Fahn 1979). To avoid simultaneously draining resin at one location (for OEF measurement) and attempting to measure OEP at another location within the same network, the two measures were separated in time. OEF and OEP were measured in trees on spring burn units and controls on six occasions over three seasons as follows. OEF (spring): 6–27 June 2002 (preburn), 1–10 July 2002, 5–14 August 2002, 14–16 July 2003, 19–21 August 2003, and 16–19 August 2004; OEP (spring): 4–25 June 2002 (preburn), 1–10 July 2002, 5–13 August 2002, 7–10 July 2003, 12–15 August 2003, and 9–13 August 2004.

On fall burn units and controls, OEF and OEP were measured on five occasions over three seasons as follows. OEF (fall): 3–12 September 2002 (preburn), 13–19 October 2002, 14–16 July 2003, 19–21 August 2003, and 16–19 August 2004; OEP (fall): 3–12 September 2002 (preburn); 13–18 October 2002, 7–10 July 2003, 12–15 August 2003, and 9–13 August 2004.

Since resin properties in spring and fall burn units were not measured at the same time the first year, control units were randomly split in half by season. Thus, four units were assigned as “spring controls” and four as “fall controls” (see Fig. 2). Trees in control units in each season were measured for OEF and OEP at the same time as trees in burn units.

Data analysis

Burn area coverage was compared among treatments using a *t* test on burnt versus unburnt foot paces. Proportions were arcsine transformed before analysis to stabilize residuals (Zar 1999). Treatment effects on fuel loading were analyzed using two different techniques: (i) one-way fixed factor analysis of variance (ANOVA) on the magnitudes of fuel mass change (posttreatment – pretreatment) and (ii) using a multiplicative regression model incorporating pretreatment fuel loads:

$$[1] \quad \text{post} = f(\text{pre} \times \text{treatment})$$

where post, pre, and treatment represent post- and pre-treatment fuel masses (Mg/ha) and treatment type (spring burning, fall burning, or control, unitless dummy variables), respectively, and *f* signifies a linear function. This model can also be expressed as a log-linear equation:

$$[2] \quad \ln \text{post} = \beta_0 + a \ln \text{pre} + \text{treatment}$$

where *a* (unitless) is fitted for each level of treatment and pre is the covariate (β_0 is the unitless model intercept following statistical convention). Both analyses were done twice: once for total fuel masses and once for fine fuels only (1 and 10 h fuels and litter components).

Forest structure was analyzed by comparing changes in tree density, CBH, and canopy closure measurements between treatments using one-way ANOVA and Student–Newman–Keuls (SNK) multiple comparisons (Zar 1999). Tree densities were compared in two size classes based on diameter: 0–20 and >20 cm DBH. Densities were evaluated in terms of trees per unit (equal plot area in all units) in two size classes: larger trees were evaluated using the sum of >20 cm trees in all three plots, and smaller trees (0–20 cm) were evaluated using the sum of all 5–20 cm trees (three plots) plus the sum

(three plots) of 0–5 cm trees multiplied by 8 (multiplied because of the smaller sampling area (5 m × 5 m) for 0–5 cm DBH trees). Changes in canopy closure, being proportions, were subjected to arcsine transformation after adding a constant to eliminate negative values (Zar 1999). Differences in CBH were log transformed to stabilize sample variances (Zar 1999).

Population characteristics of the ponderosa pines in the study area were assessed using descriptive statistics. Mortality was modeled using logistic regression, an appropriate model when the response variable (survival or death of individual trees) is binary (Neter et al. 1996). The main effects model took the form

$$[3] \quad p = \frac{1}{1 + e^{-(\beta_0 + \beta_1 \times \text{DBH} + \beta_2 \times \text{crown} + \beta_3 \times \text{Trt})}}$$

with p representing the probability of mortality of a given tree and diameter at breast height (DBH), Keen's (1943) crown vigor class (crown), and treatment (Trt) as predictor variables; β_0 , β_1 , β_2 , and β_3 are population coefficients that were estimated for each level of the categorical variables (crown and Trt). Higher fitted model coefficients correspond to a higher probability of mortality. The crown × Trt interaction factor was also initially included in the model. Terms not significant at least at the $\alpha = 0.1$ level based on χ^2 likelihood ratio tests (Neter et al. 1996) were excluded from subsequent regression runs. Logistic regressions were run using S-Plus version 6.1 (Insightful Corp., Seattle, Washington)

OEF values were assessed by comparing the total volume of resin extracted from sample trees across treatment groups at various measurement times. To assemble the model, three-way analysis of covariance was used in a completely randomized split-plot design (Oehlert 2000) with DBH as a covariate. The whole-plot factor was experimental unit, while treatment (burn versus control), raking (raked versus unraked), and crown (high-vigor versus low-vigor crown classes) were included as split-plot factors. All main effect and interaction terms were initially included in the model; terms not significant at the $\alpha = 0.1$ level were subsequently dropped. Resin flow values were square root transformed to correct for moderate heteroscedasticity between groups, as determined by Levene's tests (Neter et al. 1996). Positive values received the $(\text{OEF} + 0.375)^{0.5}$ transformation (Zar 1999), while negative values, the occasional result of subtracting pretreatment values, received the same transformation on the absolute value of the measure: $-(|\text{OEF}| + 0.375)^{0.5}$.

OEP was modeled similarly using the average pressure reading for both gauges as the response variable. Again, the completely randomized split-plot design was used with the split-plot factors treatment, raking, and crown and with DBH as a covariate. Pressure data had more consistent variance than flow data and were therefore not transformed prior to analysis. The relationship between OEF and OEP was also evaluated based on the longstanding debate over the two measures (Vit e 1961; Hodges and Lorio 1971; Lorio 1994) using a simple linear correlation test on individual measurement pairs.

Resin properties (both OEF and OEP) were measured at different times for spring and fall units in the first season, precluding direct comparison between seasons. However, since four control units were measured at the same time as the

trees in each burn season (see Fig. 2), resin response was compared between individual burn treatments and controls. Owing to differences in measurement protocol and personnel between seasons, no quantitative comparisons were possible between measurement times. Because of the inherent high within- and between-tree variability of resin measurements, OEF and OEP were analyzed at the permissive $\alpha = 0.1$ level of significance, with the understanding that this increases the probability of type I errors compared with a stricter (lower) level of α (Zar 1999). Except where specified otherwise, all statistical analyses were run using SPSS 12.0 (SPSS Inc., Chicago, Illinois).

Results

Burn treatments and fire behavior

Spring burn treatments were characterized by cool and uneven fire behavior. Remnant snow patches in the study area finished melting only days before ignition, resulting in moist fuels and low-intensity burns. Weather conditions at time of ignition varied between 19 and 24 °C and between 43% and 29% relative humidity. Winds were light, predominantly from 0 to 3 km/h, with gusts up to 10 km/h. Flame lengths in these burns were mostly between 18 and 60 cm, with occasional flareups to 150 cm in fuel "jackpots". Spring burn coverages were low, ranging between 19% and 57% (37% average) of unit areas visibly charred.

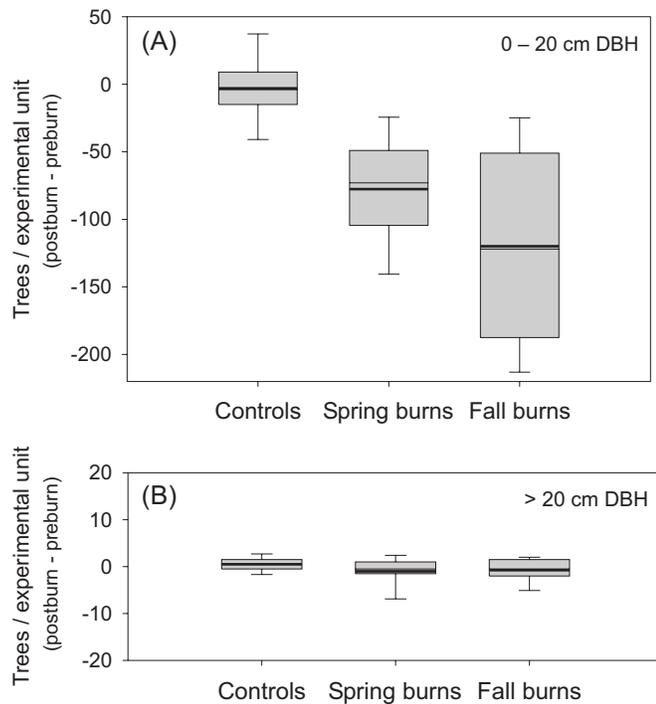
Fall burns were characterized by more intense fire behavior and higher burn coverage than spring burns. Weather at the time of ignition was cool, with a range from 11 to 19 °C and between 49% and 20% relative humidity. Flame lengths were largely between 30 and 90 cm, with localized patches up to 2 m and occasional torching of larger subcanopy trees. Burn coverages in fall units ranged between 64% and 86% (mean of 76%) and were significantly greater than spring burns ($t = 6.876$, $p < 0.0001$).

Forest structure and fuels

Results from forest structure and fuel evaluation reflect conditions from up to 1 year after burning. Following prescribed fire treatments, reductions in small tree (0–20 cm DBH) density were significantly greater in spring and fall burns than in controls (ANOVA: $F = 9.591$, $p = 0.001$) but not significantly different between spring and fall burns (SNK not significant at $\alpha = 0.1$) (Fig. 4A). Changes to large tree (>20 cm DBH) density were not significantly different between treatment groups (ANOVA: $F = 0.680$, $p = 0.517$) (Fig. 4B).

CBH in burn plots was higher following treatment compared with control plots, with net changes in CBH of +0.8, +2.7, and -0.3 m in spring burns, fall burns, and controls, respectively. Changes in CBH (log transformed) were significantly different between all treatments (ANOVA: $F = 21.202$, $p < 0.0001$, SNK significant at $\alpha = 0.05$). Posttreatment reductions in canopy closure were greater in fall burn units (-2.1%) than in spring burn units (+2.1%) or controls (+4.0%), where increased closure was measured ($F = 5.784$, $p = 0.010$, SNK significant at $\alpha = 0.05$); spring burn values were not significantly different from controls (SNK not significant at $\alpha = 0.1$).

Fig. 4. Changes in density of (A) 0–20 cm DBH and (B) >20 cm DBH trees 1 year after spring and fall burning treatments. Thick and thin lines show treatment means and medians, respectively, boxes represent the 25th and 75th percentiles, and whiskers represent the 5th and 95th percentiles.



Spring and fall burns reduced total dead fuels by an average of 17.9% and 51.8%, respectively. Total dead fuels on control units increased by 13.9%, mostly owing to measured increases in litter and duff measurements; these changes probably represent measurement error. The fitted coefficients of the fuel model (eq. 1) are as follows:

$$[4] \quad \text{post} = 4.400\text{pre}^{0.7296} \times 0.7264^S \times 0.4026^F$$

($R^2 = 0.87$), where S and F are dummy variables (0 or 1) representing spring or fall burn treatments, respectively, and the default case, where both S and F are equal to 0, indicates controls. Model terms pre , S , and F were all significantly different from 0 at the $\alpha = 0.01$ level of significance, indicating that proportional changes between treatments were all different from each other.

Absolute changes in dead fuel masses were also tested using one-way ANOVA, in terms of both total fuel masses and fine fuels only (Table 1). Before treatment, total and fine fuel masses were similar between groups (total: $p = 0.397$; fine: $p = 0.829$); after burning, both spring and fall treatments had significantly reduced total fuels compared with controls. Changes in the fine fuel component were also significantly different between groups, with the highest reductions in fall burns, slight reductions in spring burns, and a measured increase in controls (Table 1).

OEF and OEP

Owing to logistical constraints, we were not able to measure OEP or OEF prior to the season of burning (2002). Preburn values for spring treatments were therefore collected

Table 1. Fuel masses before and after burn treatments.

(A) Preburn fuel loads.				
	Treatment	Fuel mass (Mg/ha)	F	p
Fine fuels	Spring burn	38.5±1.643	0.19	0.829
	Fall burn	39.4±2.197		
	Control	37.6±1.985		
Total fuels	Spring burn	155.6±7.402	0.966	0.397
	Fall burn	139.7±10.120		
	Control	159.0±13.072		
(B) Postburn fuel loads.				
	Treatment	Change in fuel mass (Mg/ha)	F	p
Fine fuels	Spring burn	-2.5±2.897a	16.152	<0.0001
	Fall burn	-11.7±2.133b		
	Control	+10.5±3.216c		
Total fuels	Spring burn	-27.0±3.326d	33.135	<0.0001
	Fall burn	-72.8±8.441e		
	Control	+16.8±9.984f		

Note: Pretreatment values represent mean fuel loads, and posttreatment values represent changes from preburn values (post – pre); both are ± 1 SE. Different letters indicate significantly different group means at the $\alpha = 0.05$ level (based on the SNK test; Zar 1999).

in spring (June) 2002 over an extended period of time (20 days) and with a bias between treatments (spring burn units measured first followed by fall burn units and controls). For these reasons, preburn OEF data on spring units cannot be directly compared with postburn data and are shown here for completeness only. See Discussion section for further details.

Initially, OEF was modeled as a function of burn treatment, crown class, raking treatment, and DBH. In the initial model runs, however, only the burn treatment categorical variable was consistently significant ($\alpha = 0.1$). All other terms were then dropped from the model. In spring burn units, OEF increased throughout the summer (2002) and in the two subsequent years (Fig. 5A). After burning, resin flows were higher in burned trees than in controls, although the difference was only significant in August 2004 ($p = 0.036$). In fall burn treatments, preburn OEF was similar between burns and controls (Table 2B.). Immediately after burning (October 2002), resin flows were very low across all treatments and were not significantly different between burns and controls. In subsequent seasons, resin flows in burned trees were consistently higher than in control trees (Table 2B; Fig. 5B).

OEP was also initially modeled as a function of burn treatment, crown class, raking, and DBH. The DBH and raking main effects, as well as all interaction terms, were not statistically significant in initial model runs. Crown class and treatment were both significant at several sampling times. The models were then reanalyzed using only treatment and crown class main effects (Table 3). Spring OEP measurements had the same bias as OEF in preburn data. The treatment factor was significant at most postburn sampling times, with higher resin pressure consistently observed in burned trees (Fig. 6A). High-vigor crown class trees also tended to have higher OEP, although only in earlier postburn sampling (Table 3A). These effects were similar although somewhat

more variable in fall burns, with higher OEP in burned trees appearing in August 2003 and 2004 (Fig. 6B) and higher OEP in higher crown class trees appearing in three of the five sampling periods (Table 3B).

OEF and OEP were positively and significantly correlated ($p < 0.001$, $R^2 = 0.285$ on 432 pairs), although the correlation explains relatively little of the variation between the two indices. Measurements from June and July 2002 were excluded from the correlation owing to the delay between OEP and OEF measurements in these samples.

Ponderosa pine survey and posttreatment mortality

In total, 1725 ponderosa pines were identified and measured for DBH and had their crown class noted (Fig. 7A). Diameters varied between 20.4 and 179.5 cm (Fig. 8), and numbers of trees as well as crown class varied considerably among the 24 experimental units. The greatest numbers of trees had crown vigor in classes B and C, with relatively few trees in classes A or D (Fig. 7A). Before treatment, there were no ponderosa pines < 20 cm inside any units with the exception of a very small number directly beside the highway in units M, R, and S. Ponderosa size classes were approximately normally distributed with a mean of 94.4 cm and standard deviation of 22.4 cm (Fig. 8).

$$[5] \quad p = \frac{1}{1 + e^{-(10.2 + 7.31S + 7.27F + 6.36Cr_C + 7.84Cr_D - 0.110S \times Cr_B + 0.327F \times Cr_B - 6.71S \times Cr_C - 5.37F \times Cr_C - 7.33S \times Cr_D - 5.25F \times Cr_D)}}$$

where S and F are dummy variables (0 or 1) denoting spring or fall burning, respectively, and the Cr variables similarly denote crown classes B through D (the default case is a control treatment and an A class tree). The Cr_B term is excluded because its coefficient (-7.97×10^{-14}) was too small to be deemed useful. Finally, the analysis was run one more time including only the main effects, treatment and crown. Both terms were significant at the 0.01 level, yielding the fitted solution to eq. 3:

$$[6] \quad p = \frac{1}{1 + e^{-(5.12 + 1.14S + 2.24F + 0.404Cr_B + 0.913Cr_C + 2.19Cr_D)}}$$

As eq. 6 shows, mortality generally increased with decreasing crown vigor (increasing class code from A to D) and increased from controls to spring burns to fall burns. The pattern is also evident from Fig. 7B.

Discussion

While prescribed burning research is no longer a new field, fire – bark beetle interactions have not been extensively studied, yet are increasing in importance in forest management. This study attempted to address some of these mechanisms of interactions (burning effects on resin properties) within the context of a straightforward fire effects study (fuels, forest structure, etc.). The overall objective was to further the understanding of fire effects on host tree resistance dynamics while ensuring that the burns were consistent with typical management and research scenarios.

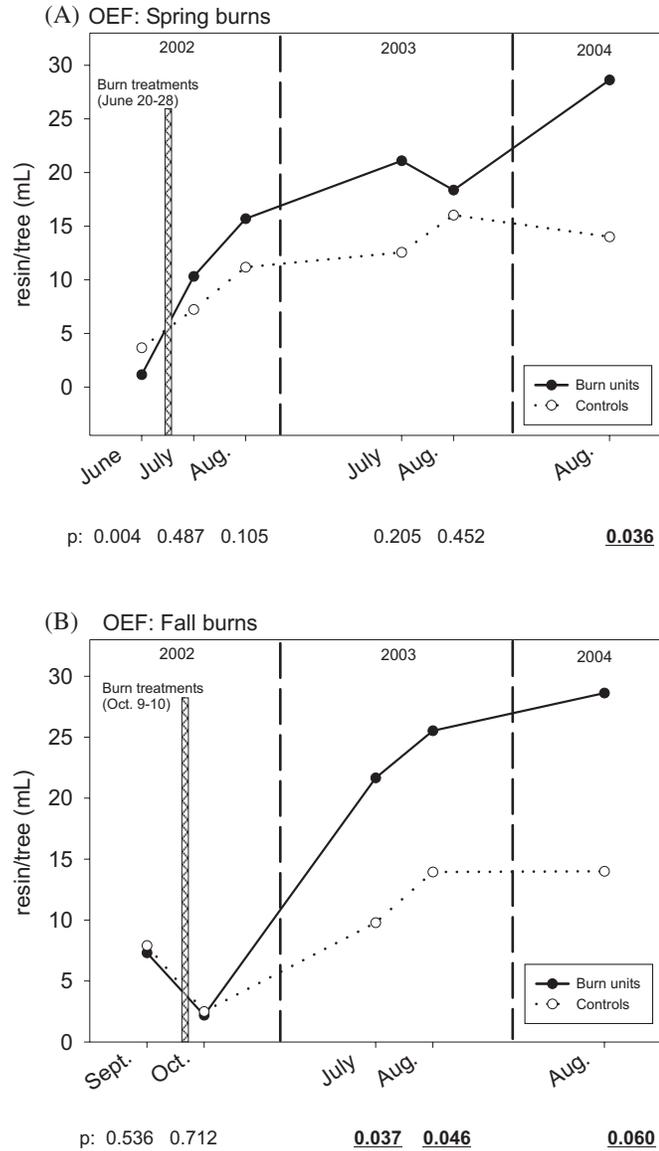
Two years after burning, 90 trees (5.2% of total) had died, with mortality occurring in nearly every treatment – crown class combination (Fig. 7B). Contributing factors leading to mortality appeared to be fire alone (22 trees in burn units), bark beetles alone (six trees in controls), a combination of burning and bark beetles (55 trees in burn units), wind alone (two trees) or after burning (four trees), or other nonapparent causes (one tree). Western pine beetles were assumed to be the bark beetle species of interest on dead trees that showed evidence of frass, woodpecker predation, and exit holes. This assumption was made after we removed bark sections from 10 dead trees with these attributes and found live western pine beetles or their characteristic galleries (Furniss and Johnson 2002) in all of them. Many living trees in burned units (over 200) possessed large basal pitch tubes indicative of red turpentine beetles (Furniss and Johnson 2002), as did some of those killed by western pine beetles. Only three trees in control units had these same basal pitch tubes.

The logistic model sought to expose significant relationships between treatment, crown class, DBH, and subsequent mortality. On the first model run, only the treatment and crown main effects were significant at the 0.1 level as well as the treatment \times crown interaction. The analysis was then computed again including only the terms treatment, crown, and treatment \times crown. All factors were significant at the 0.05 level, yielding the fitted model

Weather conditions during the burns were well within the recommended range for fuel reduction in ponderosa pine (Harrington 1981) or mixed-conifer forests (Haase and Sackett 1998). Since weather was similar between seasons, differences in fire behavior and burn coverage between spring and fall burns were most likely due to fuel moisture; while fuel moistures were not measured in this study, these were undoubtedly higher in spring owing to the recent snowmelt. The main differences between burn seasons were obvious: fall burns were considerably more intense and had much higher coverage than the spring burns. It is likely that many of the apparent differences in fire effects between spring and fall burns are due to the heterogeneous nature of fire in the spring burns and do not represent qualitative differences between treatment types so much as quantitative differences in treatment extent. Thus, spring burning may have been as equally effective as fall burning for accomplishing various objectives (reducing fuels, killing small trees, etc.), but the low proportion of the spring burn units that actually burned limited their overall effectiveness. Criteria for burning effectiveness over large areas in other ecosystems have suggested fuel reductions on at least 50%–75% (Fernandes and Botelho 2003) of treated areas, depending on the objectives of burning. Most spring burns in this study did not meet these thresholds (mean of 37%, six out of eight units below 50%), while most fall burns did (mean of 76%, all units above 50%, five out of eight units above 75%).

Preburn dead fuel loads were comparable with those of previous studies in fire-excluded mixed-conifer forests (Thomas and Agee 1986; Haase and Sackett 1998). Fuel reductions in

Fig. 5. Summary of resin flow (OEF) data. See Table 2 for summary statistics. Underlined values are significantly different between burned units and control units at the $\alpha = 0.1$ level. Error bars are omitted for clarity. Statistical significance between treatment means (mL resin/24 h) is given by the p values. The vertical cross-hatched bars indicate the timing of the burn treatments.



both burn seasons were complicated by postfire fuel inputs. Low-intensity fires will not usually both kill and consume living trees because of the large differences in fuel moisture between live and dead fuels (Huff et al. 1989; Agee 1993). Therefore, much of the vegetation biomass killed by an initial restoration burn in a fire-excluded stand soon becomes surface fuel for the next fire. Although fuel measurements after burning in this study did not differentiate between pre-existing fuels and postburn additions, it was clear that the fires did contribute to the fuel loads. For instance, some of the ponderosa pines killed following burning were observed to have fallen across fuel transects, resulting in large increases on those transects. Measuring fuel reductions 1 year after burning will more accurately reflect long-term condi-

tions than sampling immediately (within days) following a burn but nonetheless excludes fuel additions that can continue for several years (Thomas and Agee 1986; Agee 2003a).

The regression model used preburn fuel loading and season of burn to predict final fuel loads. Since both the spring and fall burning terms were significant in the model, both of these treatments significantly reduced fuels compared with controls, and fall burn fuel reductions were greater than those from spring burns. The difference between pre- and post-treatment values on control units (nearly 14%) suggests a high degree of measurement error, which is probably due to the difficulty of manually measuring forest floor depth.

The average total fuel reduction in the fall burns (52%) as well as the increase in CBH (+2.68 m) suggest that this treatment was equivalent to the simulated treatment of Stephens (1998), a “moderate intensity, moderate consumption prescribed burn”. In that study, the author found that a 50% fuel reduction following prescribed burning in previously fire-excluded mixed-conifer forest was the most effective among several stand manipulations designed to reduce potential wild-fire behavior. The spring burns in our study, with an average of <18% fuel reduction and a very small effect on fine fuels and CBH, would likely be much less effective in mitigating stand-replacing fire hazard (Agee et al. 2000).

Postfire tree mortality can continue for several years following burning, both from the primary fire effects and from insects and pathogens (Thomas and Agee 1986; Harrington 1987; Swezy and Agee 1991; Agee 1993, 2003a; McHugh and Kolb 2003). Two years after burning, certain patterns are nonetheless apparent. Tree densities in the 0–20 cm DBH class were reduced in both spring and fall burns compared with controls. Surprisingly, tree density reductions were not significantly different between spring and fall burns, despite the sparse and patchy nature of burning of the former. We might conclude that lethal burn temperature would be lower in spring than in fall because of differences in bud phenology and low carbohydrate availability early in the growing season (Harrington 1987; Agee 1993; Bond and van Wilgen 1996).

The size class distribution in this study (Fig. 8) shows an aging ponderosa pine stand with little to no recruitment of young individuals to older age classes, with virtually no ponderosa pines in the entire 67 ha study area <20 cm DBH. Ponderosa pine losses in control units are indicative of background mortality levels under the continued absence of fire. Mortality rates of 2.1% and 8.6% (Fig. 8B) of C and D class trees, respectively, in controls during this study suggest that the forest is undergoing conversion to a different dominant species (white fir) in the absence of stand-maintaining disturbances. As Agee (2003b) explained for the eastern Washington Cascades, fire in ponderosa pine forests historically operated as a cyclic process that resulted in equilibrium, rectangular-shaped age class distributions at the forest level. The normal-shaped, unimodal size class distribution representing this study’s ponderosa pine population contains some very large individuals for the species, but many of them are in declining crown vigor classes, stressed, and at risk of dying. While prescribed fire in these stands may generally be successful in achieving structural objectives (opening the canopy and reducing encroaching tree density), the consequences of the fire suppression legacy include a century of

Table 2. Resin flow (OEF) results before and after burning.

(A) Spring treatments.						
	Preburn	Postburn				
	June 2002	July 2002	Aug. 2002	July 2003	Aug. 2003	Aug. 2004
Burn units	1.153±0.421	10.31±1.936	15.69±1.069	21.09±3.106	18.36±3.082	27.087±3.735
Controls	3.662±0.678	7.23±2.823	11.17±2.060	12.55±1.981	16.02±6.626	16.16±3.188
<i>p</i>	0.004	0.487	0.105	0.205	0.452	0.036
(B) Fall treatments.						
	Preburn	Postburn				
	Sept. 2002	Oct. 2002	July 2003	Aug. 2003	Aug. 2004	
Burn units	7.31±1.232	2.19±0.738	21.66±3.213	25.53±3.447	28.63±4.563	
Controls	7.91±0.441	2.49±0.336	9.78±1.689	13.94±3.030	14.00±2.170	
<i>p</i>	0.536	0.712	0.037	0.046	0.060	

Note: Columns show total resin volume extracted from trees (mL/24 h) at each measurement time ± 1 SE of the treatment mean. For burn units, $n = 8$; for controls, $n = 4$. Preburn values on spring units are biased and are shown for completeness only (see Discussion section). Probability values for significantly different group means ($\alpha = 0.1$) are shown in bold.

Table 3. Summary of results from resin pressure (OEP) data.

(A) Spring treatments.						
	Preburn	Postburn				
	June 2002	July 2002	Aug. 2002	July 2003	Aug. 2003	Aug. 2004
Treatment factor						
Burn units	79±33.37	310±64.14	518±25.61	460±24.55	381±51.59	477±45.06
Controls	214±89.38	311±45.72	356±64.34	326±44.05	236±59.04	331±41.96
<i>p</i>	0.174	0.984	0.023	0.048	0.037	0.025
Crown factor						
High vigor	135±39.22	398±68.55	504±37.74	499±44.71	360±42.93	449±51.09
Low vigor	157±52.38	223±57.50	371±53.76	287±51.19	257±53.89	359±57.71
<i>p</i>	0.716	0.071	0.043	0.002	0.141	0.264
(B) Fall treatments.						
	Preburn	Postburn				
	Sept. 2002	Oct. 2002	July 2003	Aug. 2003	Aug. 2004	
Treatment factor						
Burn units	296±62.82	71±23.28	469±36.07	327±47.75	452±37.13	
Controls	245±63.25	121±27.22	374±64.31	201±40.57	321±20.99	
<i>p</i>	0.533	0.271	0.251	0.066	0.046	
Crown factor						
High vigor	368±42.38	125±34.13	493±49.11	278±46.69	439±40.14	
Low vigor	173±55.34	68±25.44	349±59.77	251±44.50	335±44.84	
<i>p</i>	0.008	0.194	0.073	0.673	0.086	

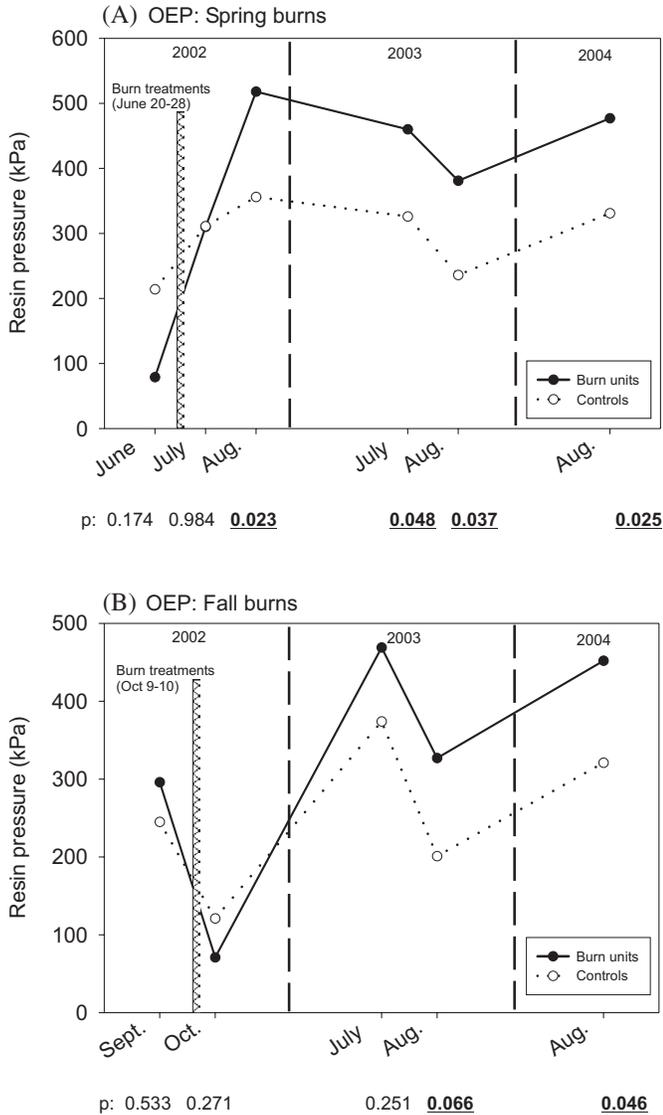
Note: Values shown are mean pressures in kilopascals (kPa) ± 1 SE of the group mean (treatment or crown class). Preburn values on spring units are biased and are shown for completeness only (see Discussion section). Split-plot design accounts for different group sample sizes: burn treatments varied by experimental unit ($k = 24$) and crown class varied by individual tree ($n = 96$). Probability values for significantly different group means ($\alpha = 0.1$) are shown in bold. See Methods section for analysis details.

missing ponderosa pine age class cohorts. These structural elements will remain absent from the stand for decades while the remaining old-growth pines continue to decline.

While ponderosa pine mortality in this study was higher from all causes in fall burns than in spring burns, other studies have reported the opposite trend (Harrington 1987; Swezy and Agee 1991). Ganz et al. (2001) noted that fire intensity cannot be ignored, and an intense fall burn may result in pine mortality equal to or greater than that of a cool spring burn. The current findings in this study support that assertion.

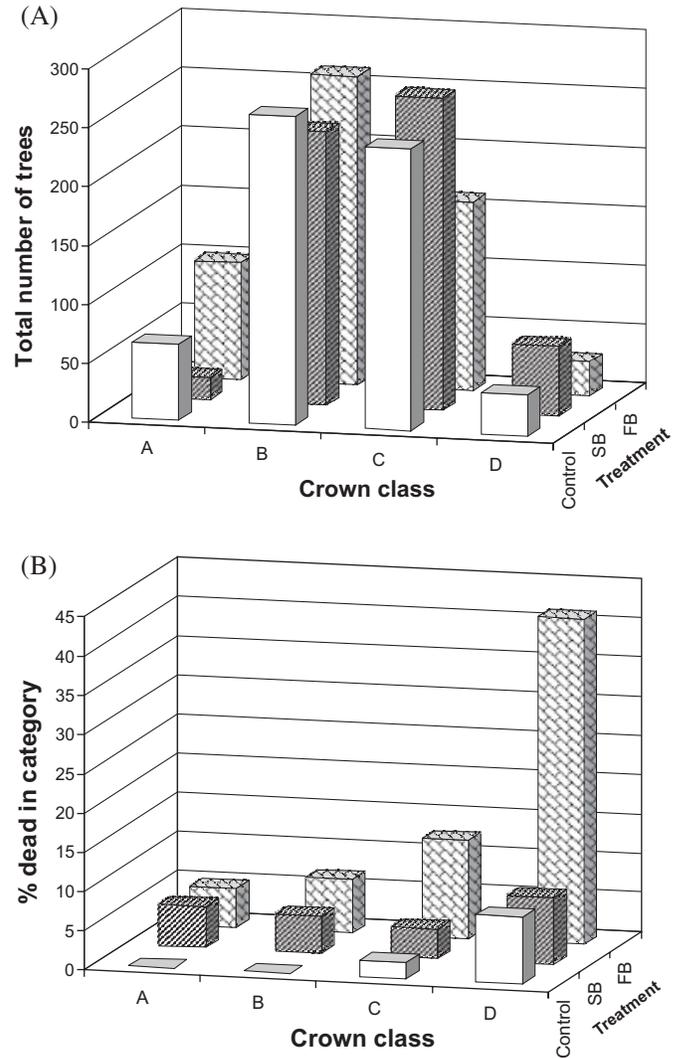
While the objectives of this study did not include a complete survey of insect presence following burning, we did observe some obvious patterns of beetle activity. Visible signs of western pine beetle attacks were strongly associated with dead ponderosa pines, and the largest cause of killed trees was a combination of fire and western pine beetle attacks. Red turpentine beetle signs were also clearly correlated with burning, although not necessarily with mortality (cf. Furniss and Carolin 1977). McHugh et al. (2003) reported a similar pattern following fires in Arizona: trees showing signs of at-

Fig. 6. Summary of resin pressure (OEP) data. See Table 3 for summary statistics. Underlined values are significantly different between burned units and control units at the $\alpha = 0.1$ level. Error bars are omitted for clarity. Statistical significance between treatment means (mL resin/24 h) is given by the p values. The vertical cross-hatched bars indicate the timing of the burn treatments.



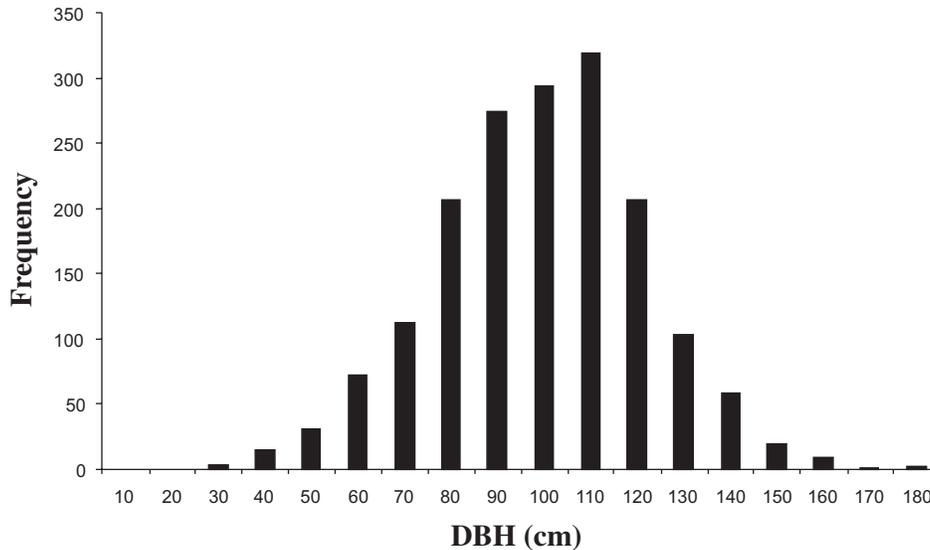
tack by western pine beetles were all killed, while a majority of those attacked by turpentine beetles were still alive after 3 years of monitoring. Other recent studies in the region have also reported heightened presence of *D. valens* following fires, including cases where host trees were killed by the species (Ganz et al. 2001; Bradley and Tueller 2001; Kelsey and Joseph 2003). Many of the trees in fall burns in our study still had green crowns (and were therefore considered alive) while showing heavy turpentine beetle activity by the end of the second season after burning (including 10 trees with >100 visible *D. valens* pitch tubes each). The trees in this study were generally larger than those in previously mentioned reports and may be more tolerant of turpentine beetle presence than smaller trees, but we can likely expect additional mortality among this class in future years.

Fig. 7. Ponderosa pine sample distribution according to crown class and burn treatment by (A) total number of trees and (B) percent dead in each category 1 year after treatment. Crown class letters represent Keen's (1943) crown vigor classes: A, full vigor, large crown; B, good to fair vigor, medium to large crown; C, fair to poor vigor, short crown; D, very poor vigor, sparsely foliated, denuded and declining crown. SB and FB refer to spring burning and fall burning, respectively.



For representing postburn mortality, only the treatment and crown class terms were significant in the regression model. Diameter was not significant, probably because of the large average size and height of most ponderosa pine trees in the study. This observation corresponds to previous postfire modeling efforts in mixed-conifer ponderosa pine: Regelbrugge and Conard (1993) found the best two-variable prediction to be a combination of char height and DBH, with probability of mortality being about zero for trees >80 cm DBH until char heights were very high (>20 m or so). Other ponderosa pine mortality models found crown scorch or damage estimates to be significant postburn mortality predictors (Swezy and Agee 1991; Harrington 1993; McHugh and Kolb 2003). Although scorch height was not measured in this study, high ponderosa pine crown heights relative to short

Fig. 8. Size-class distribution of the ponderosa pines in the study area in all crown classes and treatment groups ($n = 1725$).



flame lengths meant that scorch could only plausibly have occurred in the hottest patches of fall burns. Tree mortality owing to fire alone was highest for the fall burns, although the primary mechanism appeared to be intense burning at the root collar causing stem breakage during or shortly after burning. Bark beetle activity was the largest single factor in ponderosa pine mortality, with 61 trees out of 90 (68%) estimated to have been killed at least partly by bark beetles, with or without fire.

The mortality regression model in this study showed that crown health, as inferred from Keen's (1943) crown classes, can also be indicative of probability of mortality following burning. The combination of hot fall burning and very low vigor (class D) appeared to be particularly lethal, killing 12 of the 29 trees in this group (Fig. 7B). However, the trees in the D class suffered high mortality regardless of treatment, with 5 out of 59 spring burn trees and 3 out of 35 control trees having died within 2 years after treatment. As previously suggested, mortality patterns within control units indicate that the current class D trees could soon be lost even in the absence of burning. In areas yet to be burned, more drastic "fine-filter" management efforts may be needed to protect low-vigor pines, such as mechanical thinning and raking around individual trees with off-site slash disposal followed by a delay of several years before burning to allow trees to recover some foliage. Ponderosa pines in overly dense stands tend to suffer from low vigor and high beetle susceptibility (Sartwell and Stevens 1975; Goyer et al. 1998; Kolb et al. 1998), so a reduction in competition should help improve survivorship. Smith et al. (1981) reported that trees can show improved crown class ratings several years after thinning treatments, while Feeney et al. (1998) and McDowell et al. (2003) both noted increased growth following thinning in old-growth ponderosa pines. Further support for this premise is offered by Kolb et al. (1998), studying northern Arizona ponderosa pine stands maintained at various stand densities; 32 years after initial thinning treatments, lower density plots had higher beetle resistance indices compared with higher density treatments or untreated controls.

Resin data were collected in this study at several different times over 3 years. At each of these times, data collection was approximately synchronous between sample trees (over 3–4 days in most cases), with the notable exception of the preburn OEP and OEF data on spring units, which were collected over 20 days. Furthermore, these data (June 2002 OEP and OEF) were collected with a bias between treatment groups, with data collection completed first on burn units and considerably later on control units. As a result, no comparisons are made between burn units and controls; these data are shown for completeness only. A further problem with this early sampling period is that the time difference between collection of the last "preburn" resin data (27 June 2002) and the first data postburn (1 July 2002) is very short. The accuracy of the July 2002 resin data is therefore also suspect, since resin ducts may not have had sufficient time to refill (Büsgen and Münch 1929). The spring burns were also mopped up using considerable amounts of water, possibly influencing this set of OEP measurements, as OEP is reported to be highly sensitive to changes in available moisture (Vité 1961).

OEP measurements were complicated by high variability between measurement days and different trees and even between the two gauges in a single tree. Differences in OEP on different days and in different trees were expected (Vité 1961) but not between the gauges in one tree at one time. Pine resin ducts have been described as a system of interconnected canals in vertical, radial, and possibly transverse directions throughout the xylem sapwood and phloem (Bannan 1936; Lewisohn et al. 1991; Phillips and Croteau 1999). Resin is both produced and stored in these ducts (Büsgen and Münch 1929) and can be quickly mobilized to a wound or attack sites. The arrangement of resin ducts in ponderosa pine has not been documented, although studies in other pine species describe resin canals as being up to 1 m in length, primarily vertically oriented, wavering, nonparallel, and overlapping such that two vertical ducts may overlap and connect to each other at one or more points (Münch 1919, quoted in Büsgen and Münch 1929; Bannan 1936;

Fahn 1979). Based on this description, the within-tree OEP variability that we observed was unexpected. Some trees also had zero OEP during the entire study. Equipment and method failures might explain some of these cases (e.g., nipple openings blocked by drilling dust, gauges inserted into dead wood), but these problems with OEP measurements are apparently common and not entirely understood (D.L. Wood, Prof. Emeritus, University of California, Berkeley, personal communication; P. Lorio, Emeritus Scientist, USDA Forest Service, Southern Research Station, personal communication).

Our results show OEP generally increasing during the course of the summer, reaching a peak in July or August and dropping rapidly as temperatures decrease in autumn; attempts to collect OEP during colder temperatures resulted in zero-pressure readings. This is the opposite pattern reported by Vité (1961), who studied younger trees at lower elevations and latitude in the Sierra Nevada. Low temperatures are known to be associated with low resin flow (Harper and Wyman 1936; Smith 2000), probably owing to high resin viscosity. Nonetheless, the discrepancy between the seasonal OEP pattern observed in this study and that of previous research remains unexplained. In this study, higher resin pressures were found on trees with higher vigor, in partial agreement with Vité (1961) and Vité and Wood's (1961) much-disputed (Stark 1965; Lorio 1994) original suggestion that OEP was indicative of beetle resistance. OEP was also higher in burned trees than in controls, which conflicts with previous research suggesting that OEP is indicative of moisture relations rather than resin flow (Hodges and Lorio 1971; Lorio 1994). Since prescribed burning in this ecosystem is prone to reducing root mass (Swezy and Agee 1991), and bole heating is reported to cause moisture stress (Ryan 2000), burning seems unlikely to lead to improved water relations in the short term. The weak positive relationship that we found between OEP and OEF does little to resolve the debate, although it does not support the opinion that pressure and flow are entirely independent (cf. Lorio 1994). The only clear conclusion that we can make is that these burning treatments did not reduce OEP in old-growth ponderosa pines, at least in the 3-year duration of this study. OEP measurement and interpretation remain problematic.

Resin flow (OEF) was more predictable than OEP, although still highly variable. In general, mean resin flows were higher in burn treatments than in controls, although this difference was only statistically significant after 2 years postfire in spring burn units. Resin flow in all treatment groups also appeared to increase throughout the summer, with peak flows in July or August, depending on the group, and lower volumes measured in fall. Sampling on a nearby cohort of pole-sized ponderosa pines in 2003 and 2004 also showed the highest resin flows in mid-August (D.D.B. Perrakis, unpublished data), confirming this pattern and further suggesting that OEF is limited by low temperature.

Previous studies have reported increased resin flow in conifers following various types of injury. Wounding does not appear to cause an immediate (<1 week) OEF response in ponderosa pine as it does in *Abies* (Lewisohn et al. 1991; Wallin et al. 2003) or loblolly pine (*Pinus taeda* L.) (Ruel et al. 1998), although laboratory experiments on other *Pinus* species have generally reported increased resin duct formation at longer time scales, i.e., after 3 months or more

(Bannan 1936; Fahn and Zamski 1970), with some evidence that increased resin duct formation was greatest when injury occurred during the growing season and lower when it occurred in dormant periods.

In field settings, variations in resin response have also been seen following various types of stand manipulations. Working on loblolly pine, both Nebeker and Hodges (1983) and Fredericksen et al. (1995) observed increases in resin flows that persisted for 2–3 months after applying various mechanical injury treatments to study trees. In the latter study (Fredericksen et al. 1995), however, resin flows were significantly reduced the following season on stressed trees compared with controls. Unfortunately, fewer studies of the sort have been done on ponderosa pine. Kolb et al. (1998) noted that after 32 years of maintaining various stand densities (via thinning treatments) in a second-growth ponderosa pine forest, OEF was inversely related to stand density and basal area. Similarly, Mason (1971), measuring initial resin flow rate through capillary tubes in young loblolly pine, noted higher resin flow rates in thinned trees (1 year after treatment) compared with unthinned controls. However, Feeney et al. (1998) noted no significant increase in resin flow 1 year after thinning in old-growth ponderosa pine in Arizona. During the second year of study, significant increases in OEF occurred in trees subjected to thinning and a low-intensity prescribed burn as well as significantly higher flows on all trees (Feeney et al. 1998). The burn in that study did not scorch the crowns of the study trees, however. In contrast, Wallin et al. (2003) measured significantly lower resin flow in heavily scorched trees compared with less-affected trees a few months after a moderate-intensity broadcast burn in a young ponderosa pine stand.

These previous findings suggest that resin flow in ponderosa pine appears to reflect overall tree vigor as well as recent injury. It may take more than a few days for resin production to respond to injury and more time yet before increases in resin production can be measured through the rather blunt technique of draining resin canals from bole wounds. These measurement techniques have the added drawback of causing additional physical injury to the trees being examined, potentially confounding the results. The postburn increases observed in this study were likely due to additional resin duct formation brought about by cambial injury (Bannan 1936; Ryan 2000), although growth differentiation principles (Lorio et al. 1990; Herms and Mattson 1992) may also be related. Continued monitoring in future years should help determine if resin flows will decline in burnt trees, as might be expected if trees revert to allocating carbon to root repair and growth at the expense of resin, once the source of injury is removed.

In summary, OEF and OEP were higher in burned trees than in controls after spring and fall prescribed fires. Differences varied over time and were not all statistically significant, but the expected response, reduced resin defenses in burned trees, was not observed in the duration of this study. Reconciling this finding with various observed increases in beetle-related mortality in burned ponderosa pines (Miller and Keen 1960; Swezy and Agee 1991; McHugh et al. 2003; this study) suggests a positive correlation between resin defenses and beetle activity, an observation previously made in another pine ecosystem following prescribed fire (Santoro et

al. 2001) but not adequately explained. Understanding this response may require us to question some previously held beliefs: if basal OEP and OEF do indeed indicate beetle resistance, as several studies suggest they should (Vité and Wood 1961; Smith 1975, 2000; Hodges et al. 1979), then we are left pondering the possibility of primary attraction occurring after all. While Moeck et al. (1981) conducted an extensive study of primary attraction between western pine beetles and ponderosa pine (finding no evidence of attraction to either cut wood samples or weakened trees), their experiments did not examine the effects of fire, which might release different chemical cues into the air than would be emitted in the absence of fire (e.g., Kelsey and Joseph 2003). Further research examining the role of fire in initiating primary attraction and the relative effects of different types or intensities of fire would help answer this question, although there are obvious difficulties associated with designing a conclusive study on the topic. In the meantime, further monitoring of the trees in this study should help identify whether host defenses are reduced over longer periods of time and if this mechanism might explain some of the delayed postburn pine mortality. In the short term, however, we found no evidence for such a mechanism.

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