# Effects of Prescribed Burning on Mortality and Resin Defenses in Old Growth Ponderosa Pine (Crater Lake, Oregon): Four Years of Post-Fire Monitoring

Authors: Perrakis, Daniel D.B., Agee, James K., and Eglitis, Andris

Source: Natural Areas Journal, 31(1) : 14-25

Published By: Natural Areas Association

URL: https://doi.org/10.3375/043.031.0103

RESEARCH ARTICLE

•

# Effects of Prescribed Burning on Mortality and Resin Defenses in Old Growth Ponderosa Pine (Crater Lake, Oregon): Four Years of Post-Fire Monitoring

**Daniel D.B. Perrakis**[1,4]

[1]Fire Ecologist
Western & Northern Service Centre
Parks Canada Agency
635 8th Avenue SW, Suite 1550
Calgary, Alberta, T2P 3M3, Canada

**James K. Agee**[2]
**Andris Eglitis**[3]

[2] Prof. Emeritus
School of Forest Resources
University of Washington
Box 352100
Seattle, Washington 98195

[3]Entomologist, Deschutes National Forest
USDA Forest Service
1230 NE 3rd Street, Suite A-262
Bend, Oregon 97701

•

[4] Corresponding author:
dperrakis@gmail.com

*Natural Areas Journal 31:14–25*

**ABSTRACT**: Forests dominated by old growth ponderosa pine (*Pinus ponderosa* Dougl.) at Crater Lake, Oregon, have been viewed as good candidates for restoration via prescribed burning. Previous burn experiments in this ecosystem observed that ponderosa pine typically survived burning treatments but suffered high post-fire mortality from bark beetle attacks. This paper describes the results of four years of post-fire monitoring of ponderosa pine mortality and resin flow in areas subjected to low intensity spring burning (SB), moderate intensity fall burning (FB), or no burning (unburned controls, UC). Crown vigor estimates, correlated with ring width indices, were also included as a factor in mortality and resin flow analyses. Burn treatment was significant in both ponderosa pine mortality and resin flow, as follows: FB > SB > UC. These results suggest that resin defenses overall did not protect trees from post-fire beetle attacks. Crown vigor was positively related to both survival and resin flow. The relationships between burning, tree vigor, and resin defenses in this study suggest a complex web of interactions. Although some physiological mechanisms are still unconfirmed, these findings suggest that beetles may have been attracted to ponderosa pine following burning, perhaps via the release of volatile resin compounds. Following attraction, resin defenses appear to have been important for protecting trees from beetle attacks, with greater defenses in trees with higher crown vigor and higher growth rates. Management recommendations, including a gradual and incremental approach to fire restoration in these stands, are suggested.

*Index terms:* bark beetles, mixed-conifer, oleoresin, prescribed burning, vigor

## INTRODUCTION

Ponderosa pine (*Pinus ponderosa* Dougl.) forests of the western and southwestern United States present the classic case for fire restoration. Following over one hundred years of fire exclusion, many stands have shown increases in tree density, fuel loading and wildfire severity, and overstory mortality compared to historic conditions (Parsons and DeBenedetti 1979; Agee 1993; Covington and Moore 1994; Sugihara et al. 2006). Consequently, widespread interest exists in restoration treatments that mimic elements of the historic disturbance regime while maintaining the presence of dominant individual pines (Thomas and Agee 1986; Sackett and Haase 1998; Friederici 2003; Kolb et al. 2007). Such treatments, including prescribed burning and mechanical fuel reduction, have shown considerable promise in the short term for reducing post-treatment wildfire intensity or severity (Pollet and Omi 2002; Finney et al. 2005; Raymond and Peterson 2005; Stephens et al. 2009). However, long-term success with this strategy remains uncertain, and successful restoration may involve more than simply lighting prescribed fires, for example, in fire-excluded areas.

Restoring fire in the mixed-conifer forests of Crater Lake National Park, Oregon, has been a mixed success story so far. In these stands, a fire history study suggested that a low severity fire regime (Agee 1993) existed during pre-settlement times (McNeil and Zobel 1980). The regime apparently ended following park establishment in 1902, when fire exclusion and land-use changes suddenly and profoundly reduced the influence of fire on park lands. Prescribed burning began in the late 1970s and was intended to reduce tree density (particularly of post-settlement firs, *Abies* spp.), reduce fuel loading, and maintain larger ponderosa and sugar pine (*Pinus lambertiana* Dougl.) individuals. After the first decade of burning, however, problems with these treatments became apparent. Specifically, canopy-dominant ponderosa and sugar pines were dying in the first few years following these fires, with most post-fire mortality ultimately attributed to bark beetle attacks, particularly from the western pine beetle (*Dendroctonus brevicomis* LeConte, attacking ponderosa pine) and mountain pine beetle (*D. ponderosae* Hopkins, attacking sugar pine) (Thomas and Agee 1986; Swezy and Agee 1991). Further research at Crater Lake and elsewhere confirmed that this response pattern is widespread: beetle attacks and beetle-caused tree mortality in ponderosa pine forests increase significantly following prescribed burns or wildfires (Miller and Keen 1960; Ganz et al. 2003; McHugh et al. 2003; Breece et al. 2008). As fire restoration in these forests is frequently intended to maintain large pine individuals, high post-fire tree mortality has become a critical management issue in many areas

(Kolb et al. 2007; Crater Lake NP staff, pers. comm. 2007).

Much speculation has ensued regarding the mechanism behind increased post-fire beetle attacks. Although many possible interactions could be conceived between fire and subsequent beetle attacks in injured trees, most discussion has focused on conifer resin defenses and bark beetle host selection. (For a review of bark beetle host selection and ecology, particularly concerning D. *brevicomis*, see Miller and Keen (1960), Wood (1972, 1982), Moeck et al. (1981), Raffa et al. (1993); conifer resin defenses, as well as interactions between beetles and resin, have been reviewed by Byers (1995), Phillips and Croteau (1999), Smith (2000), Trapp and Croteau (2001), and Seybold et al. (2000, 2006).

Based on the accumulated body of knowledge on these processes, there appear to be two main possibilities for why western pine beetles might be more successful at killing ponderosa pines following fire: (1) reduced tree defenses (and unchanged number or effectiveness of beetle attacks) or (2) unchanged tree defenses and a greater number of total beetle attacks. The latter possibility implies that fire induces primary attraction to injured trees (Moeck et al. 1981; Wood 1982) or somehow increases the potency of the pheromone mixture emitted by beetles. It is also possible that both compromised defenses and increased attraction occur together.

A recent article on seasonal burning at Crater Lake provided some preliminary results from this project (Perrakis and Agee 2006). For two years after spring and fall burns in Crater Lake mixed-conifer stands, higher mortality of large ponderosa pines was observed in hot fall burns than in cool spring burns or controls; high vigor trees were also significantly more likely to survive than low vigor trees, based on visual assessments of crown vigor. Bark beetle attacks were associated with most large pine mortality, with western pine beetle and possibly red turpentine beetle (*D. valens* LeConte) attacks being the most important species. Part of that study also concerned fire effects on ponderosa pine resin defenses, seeking to identify whether fire might reduce resin flow or pressure. No evidence of such a mechanism was detected, with many burned trees showing higher resin flow than unburned controls up to two years after treatment. These findings suggested some important gaps in the state of knowledge on fire-beetle interactions in this system.

The objective of this study was to continue monitoring resin defenses and mortality in this system for a total of four years following prescribed burning treatments. Specifically, the study was designed to answer the following questions: for how long (up to four years) is the elevated mortality signal detectable after spring and fall burning treatments in this ecosystem, and how does it relate to tree vigor indices and different burning treatments? What is the nature of the post-fire resin flow response in this ecosystem? Does resin flow remain elevated for more than one year after burning, return to the level of unburned control trees, or become reduced compared to controls, within four years after burning treatment? Answering these questions would help provide managers with specific guidance on restoration treatments and policies to conserve these legacy trees in the landscape.

## METHODS

### Study area and burn treatments

Crater Lake National Park is located at the crest of the southern Oregon Cascades. The experimental site consisted of an area of previously unmanaged (except for fire exclusion since 1902) mixed-conifer forest dominated by old-growth ponderosa pines, with a variable-density undergrowth composed of several other conifers: white fir (*Abies concolo*r (Gord. and Glend.) Lindl. ex Hindebr.), Shasta red fir (*Abies magnifica* var. *shastensis* Lemm.), lodgepole pine (*Pinus contorta* var. *murrayana* (Greg. and Balf.) Engelm.), and several other species. The mean diameter at breast height (dbh) of the ponderosa pine population was about 90 cm (Perrakis and Agee 2006), with very few trees smaller than 40 cm dbh; increment cores taken from several samples suggest that the larger trees were 300 to 400 years old (D. Perrakis, unpubl. data). The 67 – ha study area was divided into 24 separate experimental units of approximately 2 – 4 ha each, separated randomly into spring burn (8), fall burn (8), and control (8) treatments.

Prescribed fire treatments were conducted in spring (late June) and fall (early October) 2002. As described previously (Perrakis 2004; Perrakis and Agee 2006), fire behavior and areal coverage in spring burns were somewhat less intense than intended (fire coverage within burn units 19% – 57%), while fall burns were closer to desired prescription values (coverage between 64% – 86%). Spring burn effects were confined to the upper forest floor and understory, with some lower bole charring observed and possible root mortality experienced by most overstory pines, but very little crown scorch or duff consumption. In contrast, fall burn effects included much greater consumption of forest floor layers, extensive bole charring, and occasional scorching of the lower crowns of dominant pines (Perrakis 2004). Thus, season of burn was confounded with fire intensity, and the three treatments in this experiment can, therefore, be described as cool spring burns (SB), hot fall burns (FB), and unburned controls (UC).

### Vigor and mortality monitoring

The ponderosa pine population inside the study area included 1725 individuals. Before treatment, we assessed the crown vigor of these trees using a simple categorical assessment based on the ‘California Pine Risk-Rating System’, as described by F.P. Keen (1943). This method involves a qualitative estimate of overall tree vigor based on crown appearance and approximate age-class, with four classes – A (most vigorous) through D (least vigorous). The entire sample of 1725 trees was monitored annually for mortality during the 2002 – 2006 period, and signs of bark beetle attacks, including pitch tubes, frass, gallery patterns, and feeding by woodpeckers were noted to identify beetle-related mortality. Although tree diameter data was collected, it was non-significant in previous mortality analyses (Perrakis 2004) and so was not included here; this population consisted entirely of mature and old-growth individuals. Likewise, 96 of the trees were subjected to resin flow sampling (see below) and previous resin exudation pressure measurements. These efforts were believed to have had negligible effects on the trees and were not factored into the mortality analysis. In addition, half of the resin flow trees were also treated with a light basal litter raking treatment. Although fuel raking may be a useful technique to reduce the heat affecting a tree's lower bole (Hood 2010), the treatments applied in this study appeared ineffective for this purpose, as considerable smoldering still occurred in the remaining unraked duff (Perrakis 2004). Therefore, the light raking treatments were also omitted from analysis in this study.

Increment cores of the outer xylem rings were collected in summer 2005 from 10 trees per experimental unit. In each unit, cores were taken at breast height (1.4 m) from the north sides of five A- or B-class trees (referring to Keen's crown vigor classes), and from five C- or D-class trees; trees were randomly selected within each unit out of the pool of available A/B and C/D class trees. This sampling strategy resulted in 239 viable cores being collected in total (one core was lost during analysis). On all cores, the number of rings in the outer centimeter was counted and Mahoney's Periodic Growth Ratio (PGR) was calculated. The PGR evaluates the ratio of the most recent five years of growth (ring widths) to those of the previous five years, thereby indicating whether radial growth has been increasing, stable, or decreasing within the past decade (Raffa and Berryman 1982).

### Resin flow monitoring

Resin flow was measured on a subsample of the full study population: 96 large ponderosa pines were monitored on several occasions before and after prescribed fire treatments (Perrakis 2004). This group was split into 48 each of high vigor and low vigor trees, with four of these trees (two high vigor, two low vigor) located in each of the 24 experimental units described above. Trees were selected randomly for resin sampling based on crown vigor classes; the high vigor group consisted of A-class trees (or B-class, when no A-class trees existed) and the low vigor group consisted of C-class trees.

Resin sampling involved drilling angled holes into each tree bole at approximately breast height (1.2 – 1.5 m), with brass funnels directing resin into centrifuge tubes, and resin volumes measured 24 hours after drilling. Two holes were drilled in each tree at each measurement time, on approximately opposite sides of the bole. Pre-treatment resin flow data were collected only from the fall burn experimental units and half of control treatment units. As a result, the full dataset of resin flow values are compared only in terms of total resin volume at each time period; a separate analysis based on differences from pre-burn values was done only for the fall burn units (see Data Analysis below). Pre-treatment sampling on fall treatments (burns and four control units) was conducted in early September 2002. Measurements in 2003 – 2006 were conducted in mid-August of each year for consistency, with all measurements conducted within a few days of stable weather to avoid bias. Although 2002 – 2004 data were previously presented (Perrakis and Agee 2006), results from all years are included for completeness.

### Data Analysis

The mortality analysis used logistic regression on individual tree data (Dalgaard 2002). Treatment (SB, FB, UC) and Keen's crown class (class A, B, C, or D) were the categorical predictor variables. The model was fitted twice: once for the entire sample (N=1725) and once excluding trees that were obviously killed directly by fire (i.e., trees that burned through at the base), windthrow, or other causes (N=1701). The second run was designed to isolate the major factor of interest to this study, that being post-fire attacks by bark beetles and other insects or pathogens.

Increment core data were analyzed using a simple one-way analysis of variance. Mahoney's PGR and the number of rings per outer cm were both evaluated separately as a function of crown vigor class. Post-hoc pairwise differences were evaluated using Tukey's HSD test (Zar 1999) at the $\alpha$ =0.05 level of significance.

The resin flow monitoring data were analyzed using split-plot design linear models (Oehlert 2000; Pinheiro and Bates 2000). Replication (the burn treatments) and tree grouping were at the level of experimental unit, with resin flow measured in the four sample trees per unit. Resin volumes were square-root transformed to stabilize variances before analysis. Categorical predictors included *Crown class* (high or low, based on Keen's classes A/B or C), treatment (UC, SB, FB), and year (2003 – 2006). Fall burn treatment units and four control units were also analyzed separately as differences from pre-treatment resin flow values. For this analysis, pre-treatment values were subtracted in each tree from each year's measured values (post – pre); differences could, therefore, be either positive or negative. Fixed factors (treatment, crown class, and year) and all interactions were initially included in the model; terms were included in the final model based on the $\alpha$=0.05 level of significance.

All analyses described in this study were performed using R version 2.7 (R – Project Collective; available online: http://www.r-project.org), with differences evaluated at the $\alpha$ =0.05 level of significance.

## RESULTS

### Ponderosa pine mortality

By fall 2006, 139 large ponderosa pine individuals had died, representing 8.1% of the original population of 1725. Of those that died, 24 were estimated to have been killed directly by burning or windthrow in 2002 or early 2003. Mortality for the remaining 115 trees out of 1701 (6.8%) was at least partly related to post-treatment insect or pathogen attack. The majority of killed trees occurred in burned treatment units (SB or FB; Table 1).

The main effects logistic regression model was significant at the $\alpha$=0.05 level when run with 1- all trees and 2-only live trees

Table 1. Number (percentage of group total) of dead overstory ponderosa pines by treatment and Keen's crown vigor class, 2003-2006, excluding direct mortality from fire and windthrow. UC, SB and FB refer to Unburned Control, Spring Burn and Fall Burn treatments, respectively.

| Dead ponderosa pines - secondary mortality | | | | | |
|---|---|---|---|---|---|
| Treatment: | UC | SB | FB | Total dead | Total |
| Crown Class: | | | | | |
| A | 0 (0) | 1 (5.3) | 5 (5.1) | 6 | 181 |
| B | 3 (1.1) | 11 (4.8) | 31 (12.3) | 45 | 746 |
| C | 7 (2.9) | 15 (5.7) | 23 (15.0) | 45 | 657 |
| D | 3 (8.8) | 5 (8.8) | 11 (42.3) | 19 | 117 |
| Total dead | 13 | 32 | 70 | 115 | |
| Total | 599 | 572 | 530 | | 1701 |

and those killed by secondary mortality (Table 2). The null model, indicated by the Intercept in Table 2, represents an A-class tree and a control treatment. The treatment factor was significant, with spring burning increasing the probability of mortality and fall burning increasing it further yet. The crown class factor was also significant, with class B, C, and D class trees more likely than class A trees to die during the study, and coefficient estimates (corresponding positively to mortality probabilities) increasing from class A through D. Despite the statistical significance of the independent variables, it should be noted that the predictive power of the logistic regression was low, explaining only 10% – 12 % of observed mortality based on residual deviance (Table 2).

The overall mortality pattern is evident in Figure 1: probability of mortality was inversely proportional to crown vigor (as indicated by the crown classes), and increased by treatment from UC (lowest probability) to SB and FB (highest probability). The apparent exception to this is the higher than expected mortality rate among A-class trees in SB units; this is probably due to a small sample size – only one tree died in that group out of 19, representing 5.3% of the initial group size. The pattern of increased mortality as crown vigor decreases is evident from the remaining crown classes in that treatment group, classes B through D.

Figure 2 summarizes the total proportions of trees killed by year and treatment type. Mortality in spring and fall burn units was clearly highest within the first year after burning, and then dropped off steadily in the following years. By the end of the study, 2.3%, 6.1%, and 16.4% of trees in control, spring burn, and fall burn treatments, respectively, had died.

## Tree vigor

The number of cores sampled from the four crown classes was 16, 97, 110, and 16 from classes A through D, respectively – proportions very similar to the study area population as a whole. Mahoney's PGR was not significantly related to Keen's crown classes ($p = 0.471$). However, the relationship between number of rings per outer centimeter and Keen's crown class was highly significant ($p < 0.001$), with increasing number of rings/cm between classes A to D (along with high variability within groups; Figure 3). As the analysis summary and pairwise contrasts show (Table 3), the A – B class and C – D class ring width differences were not significant, but all other class contrasts were significant

Table 2: Parameters of the logistic regression models. The model form is $\frac{p}{1-p} = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_q x_q)$, where $p$ is the probability of mortality, $x_1$ through $x_q$ are predictor variables, $\beta_0$ is the intercept, and $\beta_1$ through $\beta_q$ are the coefficient estimates. See text for factor descriptions. Factors marked with an asterisk (*) are significant at the $\alpha = 0.05$ level.

| | Total mortality: | | | | Secondary mortality only: | | | |
|---|---|---|---|---|---|---|---|---|
| | Coefficients: | | | | | | | |
| Factor | Estimate | Std.Error | z | p | Estimate | Std.Error | z | p |
| Intercept | -4.933 | 0.477 | -10.349 | <0.001 | -4.923 | 0.506 | -9.739 | <0.001 |
| TrtSB* | 0.841 | 0.325 | 2.588 | 0.010 | 0.839 | 0.337 | 2.490 | 0.013 |
| TrtFB* | 2.233 | 0.298 | 7.493 | <0.001 | 2.046 | 0.312 | 6.562 | <0.001 |
| ClassB* | 0.988 | 0.417 | 2.370 | 0.018 | 0.909 | 0.449 | 2.027 | 0.043 |
| ClassC* | 1.279 | 0.422 | 3.031 | 0.002 | 1.234 | 0.453 | 2.722 | 0.006 |
| ClassD* | 2.470 | 0.467 | 5.290 | <0.001 | 2.261 | 0.504 | 4.488 | <0.001 |
| Null deviance: 966.63 on 1724 degrees of freedom (d.f.) | | | | | Null deviance: 841.67 on 1700 d.f. | | | |
| Residual deviance: 849.52 on 1719 d.f. | | | | | Residual deviance: 759.28 on 1695 d.f. | | | |
| AIC: 861.52 | | | | | AIC: 771.28 | | | |

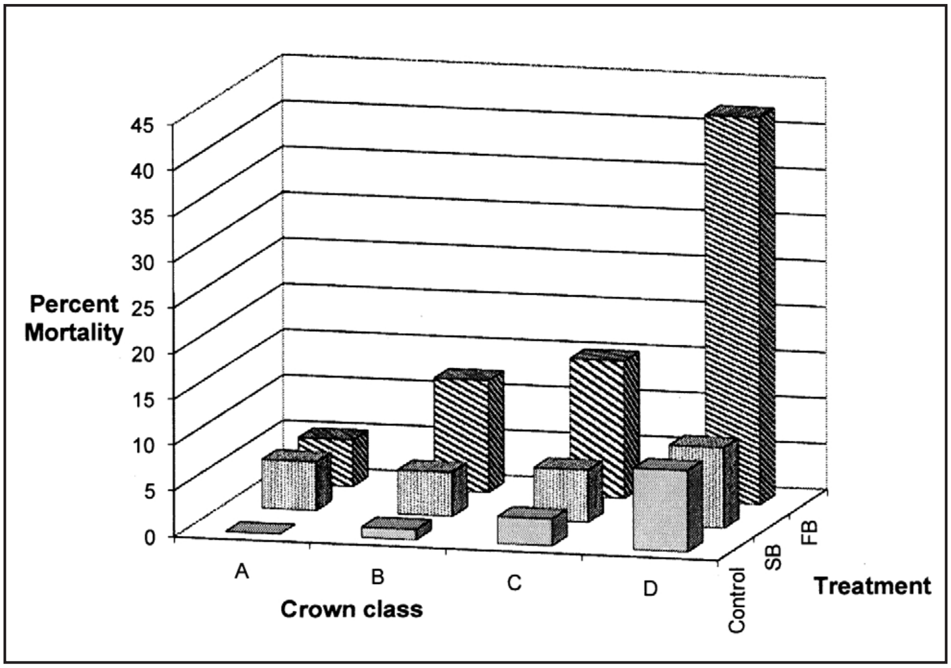


**Figure 1. Post-treatment ponderosa pine mortality, 2003-2006, grouped by Keen's (1943) class (A through D refer to crown vigor classes; see text) and treatment type (Control: unburned; SB: spring burn treatment; FB: fall burn treatment).**

at the $\alpha$=0.05 level. Mean numbers of rings per outer cm (and standard deviations) for the four classes were A: 21.8 (11.9); B: 26.4 (13.2); C: 35.8 (15.3); D: 42.3 (17.4). The grand mean from all samples was 31.5 rings/cm.

## Resin flow

Prior to burning, resin flow was not significantly different between trees in fall burn and control units (Perrakis and Agee 2006). In the first post-treatment year (2003), there were several instances when sampling test tubes overflowed with resin in the highest flow samples. This was noted in seven trees in fall burn treatments (four high, three low vigor), four trees in spring burn treatments (three high, one low vigor), and one tree in control treatments (high vigor). In following years, a switch to larger centrifuge tubes (50 mL) eliminated this problem. Thus, resin flow was slightly higher in 2003 than the values presented, particularly in fall and spring burn treatments.

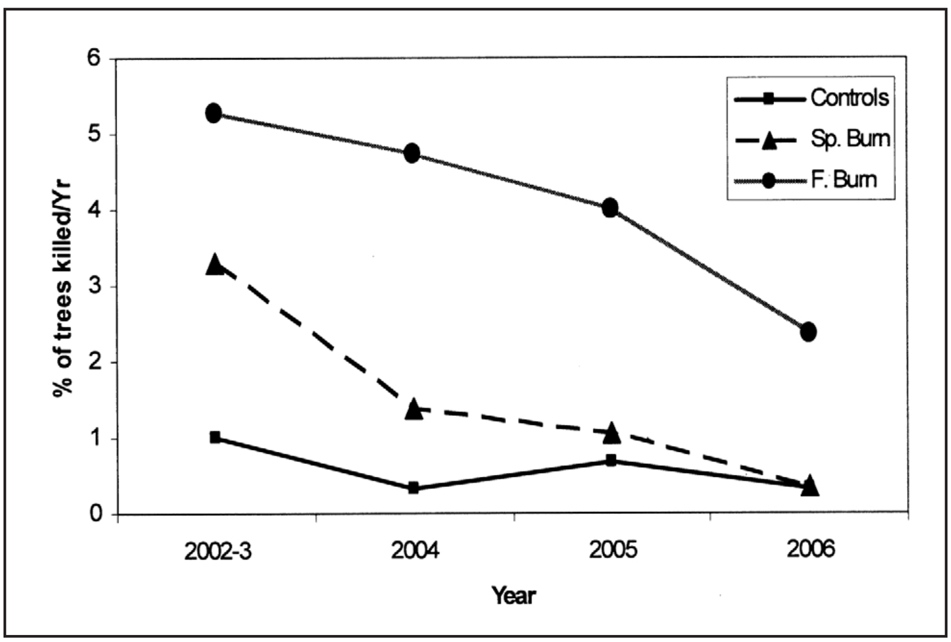


**Figure 2. Percentage of large ponderosa pines killed by year and treatment from all mortality sources (proportion of initial live population).**

Post-treatment analysis results are presented in Tables 4 and 5. *Trt* and *Cclass* refer to treatment type (Control, SB, or FB) and Keen's crown class (high vigor or low vigor) respectively. The intercept represents the default case of a high vigor tree (A class) in a control (unburned) treatment unit. Over the course of the experiment, two of the 96 trees died – both low vigor trees, one in a spring burn unit in 2003, one in a fall burn unit in 2004. Both trees were killed by post-fire western pine beetle attacks.

None of the 2-way or 3-way interaction terms was significant, so these were dropped from subsequent model runs. The non-significance ($p = 0.84$) of the *Trt: Year* term in a full-factorial run (results not shown) suggests that mean treatment effects were not significantly different between the years considered in the study. All fixed-effect factors were significant at the 0.05 level (Table 4). Both the *SB* and *FB* terms were significantly different from zero, suggesting that trees in both spring burn and fall burn treatments had significantly higher resin flow than in controls. Low vigor (*ClassC*) trees had significantly lower resin flow than high vigor trees. The overall *Year* effect is somewhat harder to interpret. Although the fixed factor term was significant, none of the coefficients for individual years was different from zero at the 0.05 level. Year-to-year variation in resin flow likely affected all trees, but these results suggest that they were not a significant factor in any individual year during this experiment.

The separate analysis of resin differences between fall treatments shows similar findings (Table 5). Trees in fall burn units had greater resin flow differences than those in

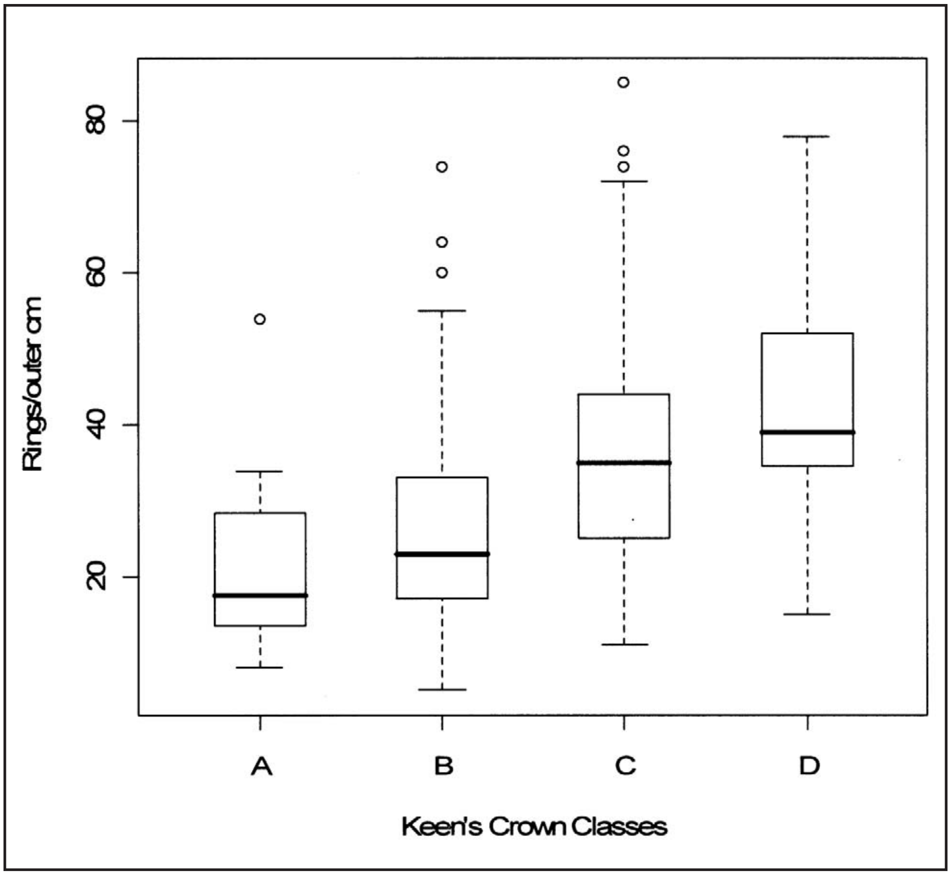


**Figure 3. Boxplots representing number of rings per outer centimeter, grouped by Keen's (1943) crown class. Center lines and boxes represent median and interquartile range values, respectively. Circles represent outlier values in each crown class. Numbers of tree cores analyzed in each class were 16, 97, 110, and 16, for classes A through D, respectively.**

control units, further suggesting a post-fire increase in resin flow. In this analysis, the *Cclass* term was not significant, suggesting that the trees' resin response to burning was similar between the high and low crown vigor classes. The *Year* factor was also not significant in this analysis, indicating that relative resin flow change was constant across the study timeline.

**Table 3. Anova table and Tukey test summary for the increment core analysis (Rings per outer cm as a function of Keen's crown vigor class). 'Contrast' refers to the crown classes being compared, while 'CI' represents Confidence Interval. Factors or contrasts marked with an asterisk (*) are significant at the $\alpha$ = 0.05 level.**

| Factor | DF | Sum Sq | Mean Sq | F | p |
|---|---|---|---|---|---|
| CrClass* | 3 | 7871 | 2624 | 12.618 | <0.001 |
| Residuals | 235 | 48866 | 208 | | |
| Tukey's HSD (0.95): | | | | | |
| Contrast: | difference | CI | p adj | | |
| B-A | 4.69 | -5.38 – 14.76 | 0.624 | | |
| C-A* | 14.01 | 4.03 – 24.00 | 0.002 | | |
| D-A* | 20.56 | 7.37 – 33.75 | <0.001 | | |
| C-B* | 9.32 | 4.12 – 14.52 | <0.001 | | |
| D-B* | 15.87 | 5.80 – 25.94 | <0.001 | | |
| D-C | 6.55 | -3.43 – 16.53 | 0.327 | | |

The overall resin flow trend over the five years of the study is presented in Figure 4 (presented as means of all trees in each treatment group). The post-treatment response of increased resin flow in burned trees is apparent from the figure, with both spring and fall burn treatments apparently peaking in the second year after burning (2004). By 2006, resin flow from spring burn and fall burn treatment groups had declined to levels nearly approaching control treatments.

## DISCUSSION

### Mortality and vigor

This study demonstrated that post-fire mortality in southern Cascade ponderosa pine forests could continue for several years. By the end of the monitoring period (four years after burning), mortality had declined in spring burn units to match the level associated with control units (two trees died in 2006 in each treatment type, 0.3% of pre-treatment populations). Mortality in fall units was declining steadily as well, although was still elevated compared to controls (13 trees died in 2006, 2.4% of pre-treatment population). Continuing the pattern found in previous surveys at this site (Perrakis and Agee 2006), mortality was strongly associated with Keen's (1943) crown class. Although this type of risk-rating system is coarse and somewhat subjective, it was significantly (inversely) correlated with the number of rings in the outer centimeter in these trees. Thus, trees in A and B classes had higher radial growth in recent years than those in C or D classes, and the former were more likely to have survived for four years after burning, regardless of burn season or control treatment. The other growth index assessed in the model, the PGR, was not related to Keen's crown vigor class. The trees studied in this experiment were very old (most estimated at > 200 years old) and had low growth rates. With no exogenous disturbances and little in-stand change during the decade prior to the burning treat-

Table 4. Anova table and summary from post-treatment resin flow measurements, August 2003-2006. DF represents degrees of freedom. The Value column shows estimates of the linear model coefficients (based on transformed data); Intercept represents Control treatments and A-class (high vigor) trees; SB (spring burn), FB (fall burn), and ClassC model terms and statistics are contrasted with high vigor (Keen's class A) trees in control units. Factors or terms marked with an asterisk (*) are significant at the $\alpha = 0.05$ level.

| Factor | DF | F | p | | Value | Std.Error | DF | t | p |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1,349 | 568.961 | <0.001 | Intercept | 3.576 | 0.35 | 349 | 10.2286 | <0.001 |
| Trt* | 2,21 | 5.731 | 0.010 | SB* | 0.892 | 0.410 | 21 | 2.178 | 0.041 |
| Year* | 3,349 | 4.278 | 0.005 | FB* | 1.349 | 0.409 | 21 | 3.294 | 0.003 |
| Cclass* | 1,349 | 21.877 | <0.001 | Year2004 | 0.479 | 0.278 | 349 | 1.724 | 0.086 |
| | | | | Year2005 | 0.412 | 0.278 | 349 | 1.482 | 0.139 |
| | | | | Year2006 | -0.398 | 0.278 | 349 | -1.431 | 0.153 |
| | | | | ClassC* | -0.922 | 0.197 | 349 | -4.677 | <0.001 |
| | | | | Random effect: | StdDev | Residual | | | |
| | | | | Unit | 0.663 | 1.911 | | | |

ments, radial growth of most trees was in a long-term pattern of decline, and the PGR varied only slightly, and inconsistently, between treatment groups.

An interpretation of these two findings suggests that overall recent radial growth rate may have been indicative of the trees' ability to withstand the stresses of fire injury and possibly post-fire beetle attacks, while minor variations in growth rate during the past decade did not influence this response pattern. With respect to growth and vigor, it is unsurprising that a higher vigor index should correspond with higher survivorship, as trees with well developed root and crown systems tend to have high carbohydrate reserves and are more resilient to environmental stresses and pathogen attacks (Waring 1987; Kozlowski and Pallardy 1997). The present findings are consistent with this conceptual model, with high crown vigor class being positively correlated with wider growth rings, higher resin flow (see below), and lower mortality rates. Several previous studies in ponderosa (Larsson et al. 1983) and lodgepole pine (Stuart 1984) have also found higher radial growth indices to be positively related to tree survival following bark beetle attacks.

The mortality levels observed in this study (2.3%, 6.1%, and 16.4% in control, spring burn, and fall burn treatments, respectively, after four years) are similar to or slightly lower than levels reported in other studies on ponderosa pine survival after fire. Thies et al. (2005) studied mortality in uneven-aged stands (7.5 to >75 cm dbh) in eastern Oregon. They noted between 0 – 0.6% annual mortality in control plots, and mortality in burn plots that peaked one year after burning (spring burns: 4.3%; fall burns: 11.8%) and leveled off (matching control levels) after four years of post-burn monitoring – a nearly identical pattern to that observed in the present study. Their

Table 5. Data summary from resin difference analysis, fall burns and controls. Pre-treatment (early September 2002) resin flow values were subtracted from measurements in subsequent years for each tree. Abbreviations are as in Table 4, above. Burn treatments were conducted on 8 experimental units; these are contrasted with 4 control units (4 sample trees per unit). Factors or terms marked with an asterisk (*) are significant at the $\alpha = 0.05$ level.

| Factor | DF | F | p | | Value | Std.Error | DF | t | p |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1,173 | 2.091 | 0.150 | Intercept | -1.742 | 0.854 | 173 | -2.040 | 0.043 |
| Trt* | 1,10 | 7.287 | 0.022 | Trt2* | 2.413 | 0.906 | 10 | 2.662 | 0.024 |
| Year | 3,173 | 2.063 | 0.107 | Yeary04 | 0.315 | 0.609 | 173 | 0.517 | 0.606 |
| Cclass | 1,173 | 2.591 | 0.109 | Yeary05 | 0.122 | 0.609 | 173 | 0.201 | 0.841 |
| | | | | Yeary06 | -1.051 | 0.609 | 173 | -1.725 | 0.086 |
| | | | | CclassC | -0.699 | 0.435 | 173 | -1.610 | 0.109 |
| | | | | Random effect: | StdDev | Residual | | | |
| | | | | Unit | 1.278 | 2.967 | | | |

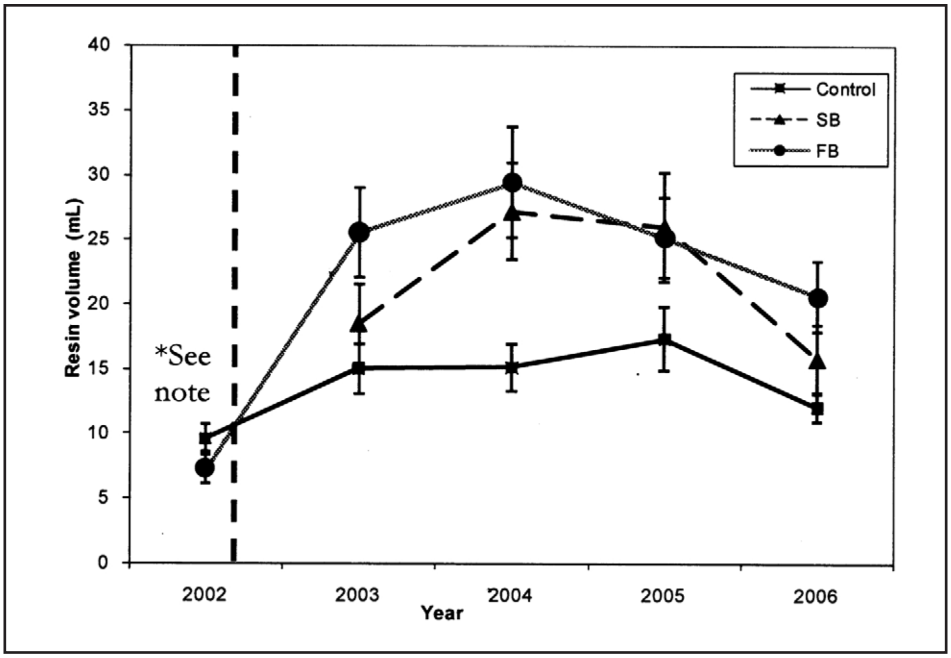


**Figure 4. Resin flow means (untransformed) and standard errors (of unit means) by year and treatment group. Dashed vertical line indicates approximate timing of burn treatments (not to scale); Control: unburned control treatments; SB: spring burn treatments; FB: fall burn treatments.**
***Note: unbiased data from spring burn treatment trees in 2002 (pre- and post-treatment) was not collected and is not presented. Control treatment mean in 2002 is a combination of early August and early September measurements; 2002 fall burn (pre-treatment) data was collected in early September. Measurements in all subsequent years were taken approximately synchronously between treatment groups.**

fall burn treatments caused higher mortality overall (29% of trees dead after four years), but the uneven-aged population structure suggests that many of the killed trees may have been much smaller than those in the present study and, therefore, susceptible to mortality from crown scorch (Harrington 1993).

As reported previously, earlier studies at Crater Lake observed higher mortality in spring burns than in fall burns (Swezy and Agee 1991; Agee 2003). However, a review of the literature on ponderosa pine mortality reveals mixed findings on seasonal fire effects. Although phenology may suggest that early season burn effects are most likely to be lethal due to reduced carbohydrate stores (Kozlowski 1992), prescribed burns later in the season tend to have higher fire intensities and proportional coverage (Ganz et al. 2003; Knapp and Keeley 2006; Perrakis and Agee 2006; Schwilk et al. 2006). A recent study comparing spring and fall burning in a Sierra Nevada mixed-conifer forest found that ponderosa and sugar pine mortality was significantly related to fire intensity, while mortality was not significantly different overall between the two burning seasons (Schwilk et al. 2006). In northern Arizona, McHugh and Kolb (2003) compared spring and early summer wildfires to a fall prescribed fire. They observed that the most significant predictors of mortality in logistic regression models were crown damage (scorch and consumption) and bole char – factors related to fire intensity rather than burn season. In the present study, with spring burns having significantly lower coverage and visibly lower intensities than fall burns, a similar pattern emerged. Although season of burn and tree phenology should not be discounted, the intensity of a particular fire is probably a more important variable overall in predicting mortality.

For management purposes, it is promising that mortality has declined steadily each year after post-burn year 1, even in the intense fall burn treatments. Thirteen years after a series of very similar burns at another Crater Lake site, Agee (2003) found no significant difference between large ponderosa pine mortality in burned units and unburned controls. Ideally, post-burn mortality should be below control unit mortality levels after a few years, in keeping with the intent of the treatments. As previously discussed, these sites are considered candidates for restoration due to the large increases in tree density and competition in the fire-exclusion era (McNeil and Zobel 1980; Agee 2003); accordingly, burning treatment objectives tend to include increased survivorship among remaining old pines (Kolb et al. 2007). Reaching a point of equal mortality levels between burn treatments and controls after a few years is a good start, but is not indicative of long-term success according to these criteria. Regardless of mortality levels, ponderosa pines in these stands are old, with very low survival and recruitment of new seedlings in unburned areas (Perrakis and Agee 2006; D. Perrakis unpubl. vegetation data). Ponderosa pine is well-known to require open stand conditions and mineral soils to regenerate naturally from seed (Habeck 1992), and these combined factors emphasize the need for restoration treatments in these stands, despite risks to the overstory trees.

## Resin flow monitoring

This study presents one of the longest annually repeated post-fire resin monitoring efforts in the literature. The pattern of increased post-fire resin flow identified in several other studies (Santoro et al. 2001; Lombardero et al. 2006; Knebel and Wentworth 2007) is hereby confirmed to continue for four years (or more) after fire in old-growth ponderosa pines. The results suggest that four years after burning, with some fire injury to tree boles and possibly root crowns (but very low crown scorch), bole resin flow remains higher in burned trees than those in unburned controls. The relative increase due to fire injury appears to be declining in the spring burns but remains elevated among trees in fall burn treatments. Although the data suggest that resin flow peaked in year two after burning (2004) for both spring and fall burn treatments, between-year differences were not statistically significant and some problems with overflowing test tubes in year 1 may have masked higher resin flow values in that year. The analysis of differences between post- and pre-treatment resin flow among fall burns and controls followed the same pattern of a greater resin increase among burned trees than controls.

Crown vigor was also a significant factor in the model, with greater absolute resin flow in trees of higher crown vigor class. In contrast, vigor was not a significant predictor of the post-treatment change in resin flow (among fall-burned trees and controls). As crown vigor class was inversely correlated with rings per cm, this suggests a positive correlation between constitutive resin flow and sapwood xylem production. This finding is in agreement with the work of McDowell et al. (2007), who noted positive correlations between basal area increment (BAI) and resin flow in a survey of several different experiments in southwestern ponderosa pine stands.

There has been considerable interest in recent decades in using plant defense theories to explain relationships between conifer trees and bark beetles. In particular, the Growth-Differentiation Balance (GDB) hypothesis (Loomis 1953; Herms and Mattson 1992) has been used in a variety of studies on Pinaceae trees to explain (or attempt to) carbohydrate allocation tradeoffs between growth processes and investment in defenses (Lorio 1986; Lorio et al. 1990; Johnson et al. 1997; Gaylord et al. 2007). According to the GDB, conifers prioritize investment in growth processes (cell division and expansion) over investments in defenses during typical favorable growing conditions. The theoretical pattern, therefore, results in an inverse relationship between growth and defense investments, and conversely suggests that plants may build stronger defenses during periods of sub-optimal growth. Although many studies appear to confirm that GDB principles are sound (see Herms and Mattson 1992; Stamp 2003), studies on conifer resin have been equivocal with respect to GDB predictions. This study supports a more complex interpretation than is suggested from the GDB, as increased resin flow did not appear to be associated with resource scarcity or sub-optimal growth. As McDowell et al. (2007) previously observed, increased resin flow in ponderosa pine appears to be associated with wider xylem rings, likely because sapwood is rich in resin canals. The interconnected architecture and long-lived nature of resin canals in pine phloem and xylem tissues (Fahn 1979; Lapasha and Wheeler 1990; Lin et al. 2002) also suggest that physiological inferences are difficult to assess from treatment effects: short-term resin measurements will not necessarily be associated with the conditions during which the resin canals (or resin itself) were produced (Gaylord et al. 2007; Wallin et al. 2008).

There remains the issue of what is causing the apparent increase in resin flow among burned trees. Little is known in this species about the sensitivity of resin canal development and oleoresin production to variable growing conditions or injury. In *Pinus taeda*, there is some evidence that pre-formed canals may not be filled to capacity during normal growing conditions. Following physical wounding to the bole, canals are rapidly filled with induced resin from surrounding epithelial cells, with production most vigorous in the fastest-growing trees with the largest crowns (Blanche et al. 1992; Lombardero et al. 2000). A similar mechanism may occur in *P. resinosa* as well, albeit on a slower time scale (Lombardero et al. 2006). In Cascade ponderosa pine stands, recent experiments compared the effects of fire and fire-surrogate treatments (bole charring, crown pruning, root trenching) on resin flow. In these trials, only the prescribed fire and bole charring treatments caused post-treatment resin increases, suggesting that bole heating or injury induce the resin response, rather than any changes in resource availability (Perrakis 2008; D. Perrakis and J. Agee, unpubl. data). However, in similar studies in Arizona, thinning treatments (with no reported injury to study trees) also appeared to cause a short term increase in resin flow (Wallin et al. 2008). The latter study used considerably smaller and younger trees (which are known to respond more rapidly to resource availability) than the present experiment, which may explain the difference (Kolb et al. 2007).

In this study, treatments associated with greatest resin flow were not those with greatest overstory ponderosa pine survival. This suggests that the resin defense hypothesis must be reexamined in this ecosystem. Primary attraction (Wood 1982) of western pine beetles to stressed ponderosa pines or resin samples has not been confirmed (Moeck et al. 1981). However, one of the constituent resin volatiles, myrcene, has long been known to be an integral part of the attractant pheromone mixture for these beetles (Bedard et al. 1969; Vité and Pitman 1969; Gaylord et al. 2006). Many other volatile compounds have been confirmed to cause antennal response in western pine beetles (Shepherd et al. 2007). Thus, we may expect that fire, through damage to live trees or volatization of resin in consumed woody debris, may increase the release of these volatiles and thereby attract beetles, particularly if beetle activity (and, therefore, other pheromone precursors) is already present in the canopy airspace. Such an effect (increased ambient resin volatiles) has been observed following thinning and chipping treatments (Schade and Goldstein 2003; Fettig et al. 2006), and is suggested as an explanation for post-treatment increases in beetle activity (Fettig et al. 2006). This suggested mechanism is also consistent with studies that observed positive relationships between scorch severity and number of beetle attacks in ponderosa pine forests (McHugh et al. 2003; Wallin et al. 2003).

The defensive role of resin flow cannot completely be rejected, however. The group producing the greatest volume of post-treatment resin (high vigor trees in intense fall burn treatments) were not those suffering greatest mortality, as the higher vigor trees overall survived the treatments much better than low vigor individuals (Table 1). We suggest that beetles were attracted to the stand via emitted resin volatiles during and after burning treatments, but that resin flow in individual trees remained important in determining the mortality and survival of individual trees.

## CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The results from this study have implications for both managers interested in fire restoration as well as researchers studying the mechanisms behind fire/bark beetle interactions. The main management-related finding from this study was that survivorship of old pines was positively related to high radial growth/BAI and high crown vigor. Treatments that improve individual tree vigor, such as removal of competing vegetation surrounding old pines, are likely beneficial to overstory survival. Additionally, resin flow monitoring in ponderosa pine is not a reliable indicator of the likelihood of survival after fire and is not suggested as a post-treatment monitoring technique.

There may also be merit to minimizing the release of resin volatiles in stand treatments or attempting other measures to mitigate bole injury, although these suggestions are somewhat speculative. Such actions may include avoiding injuring trees of concern through ignition patterns or 'cooling' segments of a fireline, raking fuel from the bases of trees prior to burning (Hood 2010), disposing of thinned biomass material off-site, restricting thinning treatments to periods of low beetle activity (fall or winter), and possibly setting conservative (low intensity) burn prescriptions.

Overall, the findings of this study support the notion of an incremental approach to fire restoration in ponderosa pine forests at Crater Lake. Restoration treatments, including burning, and possibly thinning or other mechanical fuel manipulations, should be implemented gradually. Although such treatments can probably eventually benefit these stands, it may be necessary to improve the vigor of individual trees prior to implementing all but the least intense prescribed fires, lest bark beetle populations benefit more than the trees of concern.

## ACKNOWLEDGMENTS

We would like to thank the staff at Crater Lake NP, particularly Michael Murray and Scott Girdner, for assistance and logistical support over the duration of this project. Dallas Anderson, Mike Keim, Phil Monsanto, Christine Hurst, and Rob Banes helped with fieldwork, while Phil Monsanto, Carson Sprenger, and Tania Taipale assisted with laboratory analyses. The Joint Fire Science Program, project 05-2-1-92, funded this study with additional support provided by the Western & Northern Service Centre, Parks Canada Agency; we are grateful for their contributions.

*Daniel Perrakis is a fire ecologist with the Western & Northern Service Centre, Parks Canada Agency, Calgary, AB. In addition to fire-bark beetle interactions, his research interests include burn severity monitoring using satellite imagery, fire behavior modeling and prediction, and restoration of historic fire regimes.*

*James K. Agee is Professor Emeritus of forest ecology at the School of Forest Resources, University of Washington, Seattle, WA. He has studied fire history and effects in the western United States for the past 40 years and has authored more than 200 publications on these topics.*

*Andris Eglitis is an entomologist with the USDA Forest Service, situated on the Deschutes National Forest, Bend, OR. He provides technical assistance and training on forest insects to several federal land management agencies in central Oregon.*

## LITERATURE CITED

Agee, J.K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, D.C.

Agee, J.K. 2003. Monitoring post-fire tree mortality in mixed-conifer forests of Crater Lake, Oregon. Natural Areas Journal 23:114-120.

Bedard, W.D., P.E. Tilden, D.L. Wood, R.M. Silverstein, R.G. Brownlee, and J.O. Rodin. 1969. Western pine beetle: field response to its sex pheromone and a synergistic host terpene, myrcene. Science 164:1284-1285.

Blanche, C.A., P.L.J. Lorio, R.A. Sommers, J.D. Hodges, and T.E. Nebeker. 1992. Seasonal cambial growth and development of loblolly pine: xylem formation, inner bark chemistry, resin ducts, and resin flow. Forest Ecology and Management 49:151-165.

Breece, C.R., T.E. Kolb, B.G. Dickson, J.D. McMillin, and K.M. Clancy. 2008. Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. Forest Ecology and Management 255:119-128.

Byers, J. 1995. Host-tree chemistry affecting colonization in bark beetles. Pp. 155-213 in R.T. Carde and W.J. Bell, eds., Chemical Ecology of Insects 2. Chapman and Hall, New York.

Covington, W.W., and M.M. Moore. 1994. Southwestern ponderosa pine forest structure: changes since Euro-American settlement. Journal of Forestry 92:39-47.

Dalgaard, P. 2002. Introductory Statistics With R. Springer, New York.

Fahn, A. 1979. Secretory Tissues in Plants. Academic Press, New York.

Fettig, C.J., J.D. McMillin, J.A. Anhold, S.M. Hamud, R.R. Borys, C.P. Dabney, and S.J. Seybold. 2006. The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. Forest Ecology and Management 230:55-68.

Finney, M.A., C.W. McHugh, and I.C. Grenfell. 2005. Stand- and landscape-level effects of prescribed burning on two Arizona wildfires. Canadian Journal of Forest Research 35:1714-1722.

Friederici, P. 2003. Ecological Restoration of Southwestern Ponderosa Pine Forests. Island Press, Washington, D.C.

Ganz, D.J., D.L. Dahlsten, and P.J. Shea. 2003. The post-burning response of bark beetles to prescribed burning treatments. Pp. 143-158 *in* P. Omi and L.A., Joyce, eds., Fire, Fuels and Ecological Restoration: Conference Proceedings, 16-18 April 2002. RMRS-P-29, U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station, Fort Collins, Colo.

Gaylord, M.L., T.E. Kolb, K.F. Wallin, and M.R. Wagner. 2006. Seasonality and lure preference of bark beetles (Curculionidae: Scolytinae) and associates in a northern Arizona ponderosa pine forest. Environmental Entomology 35:37-47.

Gaylord, M.L., T.E. Kolb, K.F. Wallin, and M.R. Wagner. 2007. Seasonal dynamics of tree growth, physiology, and resin defenses in a northern Arizona ponderosa pine forest. Canadian Journal of Forest Research 37:1173-1183.

Habeck, R.J. 1992. *Pinus ponderosa* var. *ponderosa*. In Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Available online: <http://www.fs.fed.us/database/feis>. Accessed 1 June 2009.

Harrington, M.G. 1993. Predicting *Pinus ponderosa* mortality from dormant season and growing season fire injury. International Journal of Wildland Fire 3:65-72.

Herms, D.A., and W.J. Mattson. 1992. The dilemma of plants: to grow or defend. Quarterly Review of Biology 67:283-335.

Hood, S. 2010. Mitigating old tree mortality in long-unburned, fire-dependent forests: a synthesis. General Technical Report RMRS-GTR-238, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, Colo.

Johnson, R.H., B.L. Young, and D.N. Alstad. 1997. Responses of ponderosa pine growth and volatile terpene concentrations to manipulation of soil water and sunlight availability. Canadian Journal of Forest Research 27:1794-1804.

Keen, F.P. 1943. Ponderosa pine tree classes redefined. Journal of Forestry 41:249-253.

Knapp, E.E., and J.E. Keeley. 2006. Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest. International Journal of Wildland Fire 15:37-45.

Knebel, L., and T.R. Wentworth. 2007. Influence of fire and southern pine beetle on pine-dominated forests in the Linville Gorge Wilderness, North Carolina. Castanea 72:214-225.

Kolb, T.E., J.K. Agee, P.Z. Fulé, N.G. McDowell, K. Pearson, A. Sala, and R.H. Waring. 2007. Perpetuating old ponderosa pine. Forest Ecology and Management 249:141-157.

Kozlowski, T.T. 1992. Carbohydrate sources and sinks in woody plants. Botanical Review 58:107-222.

Kozlowski, T.T., and S.G. Pallardy. 1997. Growth Control in Woody Plants. Academic Press, New York.

Lapasha, C.A., and E.A. Wheeler. 1990. Resin canals in *Pinus taeda*: longitudinal canal lengths and interconnections between longitudinal and radial canals. International Association of Wood Anatomists Bulletin 11:227-238.

Larsson, S., R. Oren, R.H. Waring, and J.W. Barrett. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. Forest Science 29:395-402.

Lin, J., Y. Hu, X. He, and R. Ceulemans. 2002. Systematic survey of resin canals in Pinaceae. Belgian Journal of Botany 135:3-14.

Lombardero, M.J., M.P. Ayres, and B.D. Ayres. 2006. Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens. Forest Ecology and Management 225:349-358.

Lombardero, M.J., M.P. Ayres, P.L.J. Lorio, and J.J. Ruel. 2000. Environmental effects on constitutive and inducible resin defenses of *Pinus taeda*. Ecology Letters 3:329-339.

Loomis, W.E. 1953. Growth and Differentiation in Plants. Iowa State College Press, Ames.

Lorio, P.L.J. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. Forest Ecology and Management 14:259-273.

Lorio, P.L.J., R.A. Sommers, C.A. Blanche, J.D. Hodges, and T.E. Nebeker. 1990. Modeling pine resistance to bark beetles based on growth and differentiation balance principles. Pp. 402-409 *in* R.K. Dixon, G.A. Meldahl, G.A. Ruark, and W.G. Warren, eds., Process Modeling of Forest Growth Responses to Environmental Stress. Timber Press, Portland, Ore.

McDowell, N.G., H.D. Adams, J.D. Bailey, and T.E. Kolb. 2007. The role of stand density on growth efficiency, leaf area index, and resin flow in southwestern ponderosa pine forests. Canadian Journal of Forest Research 37:343-355.

McHugh, C.W., and T.E. Kolb. 2003. Ponderosa pine mortality following fire in northern Arizona. International Journal of Wildland Fire 12:7-22.

McHugh, C.W., T.E. Kolb, and J.L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environmental Entomology 32:510-522.

McNeil, R.C., and D.B. Zobel. 1980. Vegetation and fire history of a ponderosa pine-white fir forest in Crater Lake National Park. Northwest Science 54:30-46.

Miller, J.M., and F.P. Keen. 1960. Biology and control of the western pine beetle. U.S. Department of Agriculture, Washington, D.C.

Moeck, H.A., D.L. Wood, and K.Q.J. Lindahl. 1981. Host selection behavior of bark beetles (coleoptera: scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. Journal of Chemical Ecology 7:49-83.

Oehlert, G.W. 2000. A First Course in Design and Analysis of Experiments. W.H. Freeman, New York.

Parsons, D.J., and S.H. DeBenedetti. 1979. Impact of fire-suppression on a mixed-conifer forest. Forest Ecology and Management 2:21-33.

Perrakis, D.D.B. 2004. Seasonal fire effects on mixed-conifer forest structure and pine resin properties. M.S. thesis, University of Washington, Seattle.

Perrakis, D.D.B. 2008. Fire-bark beetle interactions: exploring links between fire injury, resin defenses, and beetle-induced mortality in ponderosa pine forests. Ph.D. diss, University of Washington, Seattle.

Perrakis, D.D.B., and J.K. Agee. 2006. Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. Canadian Journal of Forest Research 36:238-254.

Phillips, M.A., and R.B. Croteau. 1999. Resin-based defenses in conifers. Trends in Plant Science 4:184-190.

Pinheiro, J.C., and D.M. Bates. 2000. Mixed-effects Models in S and S-PLUS. Springer-Verlag, New York

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

Raffa, K.F., and A.A. Berryman. 1982. Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. Environmental Entomology 11:486-492.

Raffa, K.F., T.W. Phillips, and S.M. Salom. 1993. Strategies and mechanisms of host colonization by bark beetles. Pp.103-128 in T.D. Schowalter and G.M. Filip, eds., Beetle-pathogen Interactions in Conifer Forests. Academic Press, San Diego.

Raymond, C.L., and D.L. Peterson. 2005. Fuel treatments alter the effects of wildfire in a mixed-evergreen forest, Oregon, USA. Canadian Journal of Forest Research 35:2981-2995.

Sackett, S.S., and S.M. Haase. 1998. Two case histories for using prescribed fire to restore ponderosa pine ecosystems in northern Arizona. Pp. 380-389 in Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings, No. 20, Tall Timbers Research Station, Tallahassee, Fla.

Santoro, A.E., M.J. Lombardero, M.P. Ayres, and J.J. Ruel. 2001. Interaction between fire and bark beetles in an old growth pine forest. Forest Ecology and Management 144:245-254.

Schade, G.W., and A.H. Goldstein. 2003. Increase of monoterpene emissions from a pine plantation as a result of mechanical disturbances. Geophysical Research Letters 30:1380-1383.

Schwilk, D.W., E.E. Knapp, S.M. Ferrenberg, J.E. Keeley, and A.C. Caprio. 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management 232:36-45.

Seybold, S.J., J. Bohlmann, and K.F. Raffa. 2000. Biosynthesis of coniferophagous bark beetle pheromones and conifer isoprenoids: evolutionary perspective and synthesis. Canadian Entomologist 132:697-753.

Seybold, S.J., D.P.W. Huber, J.C. Lee, A.D. Graves, and J. Bohlmann. 2006. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. Phytochemistry Reviews 5:143-178.

Shepherd, W.P., D.P.W. Huber, S.J. Seybold, and C.J. Fettig. 2007. Antennal responses of the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Curculionidae), to stem volatiles of its primary host, *Pinus ponderosa*, and nine sympatric nonhost angiosperms and conifers. Chemoecology 17:209-221.

Smith, R. H. 2000. Xylem monoterpenes of pines: distribution, variation, genetics, function. General Technical Report PSW-GTR-177, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Berkeley, Calif.

Stamp, N. 2003. Out of the quagmire of plant defense hypotheses. Quarterly Review of Biology 78:23-55.

Stephens, S.L., J.J. Moghaddas, C.B. Edminster, C.E. Fiedler, S.M. Haase, M.G. Harrington, J.E. Keeley, E.E. Knapp, J.D. McIver, K. Metlen, C.N. Skinner, and A. Youngblood. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19:305-320.

Stuart, J.D. 1984. Hazard rating of lodgepole pine stands to mountain pine beetle outbreaks in southcentral Oregon. Canadian Journal of Forest Research 14:666-671.

Sugihara, N.G., J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode (eds.). 2006. Fire in California's Ecosystems. University of California Press, Berkeley.

Swezy, D.M., and J.K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research 21:626-634.

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

Thomas, T.L., and J.K. Agee. 1986. Prescribed fire effects on mixed conifer forest structure at Crater Lake, Oregon. Canadian Journal of Forest Research 16:1082-1087.

Trapp, S., and R. Croteau. 2001. Defensive resin biosynthesis in conifers. Annual Review of Plant Physiology and Plant Molecular Biology 52:689-724.

Vité, J.P., and G.B. Pitman. 1969. Insect and host odors in the aggregation of the western pine beetle. Canadian Entomologist 101:113-117.

Wallin, K.F., T.E. Kolb, K.R. Skov, and M.R. Wagner. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. Environmental Entomology 32:652-661.

Wallin, K.F., T.E. Kolb, K.R. Skov, and M.R. Wagner. 2008. Forest management treatments, tree resistance, and bark beetle resource utilization in ponderosa pine forests of northern Arizona. Forest Ecology and Management 255:3263-3269.

Waring, R.H. 1987. Characteristics of trees predisposed to die. Bioscience 37:569-574.

Wood, D.L. 1972. Selection and colonization of ponderosa pine by bark beetles. Pp. 101-117 in H.F. van Emden, ed. Insect/Plant Relationships. Halsted Press, New York.

Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology 27:411-446.

Zar, J.H. 1999. Biostatistical Analysis, 4th ed. Prentice Hall, Upper Saddle River, N.J.