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Ponderosa Pine Mortality and Bark Beetle-Host Dynamics Following Prescribed and Wildland Fires in the Northern Rocky Mountains, USA

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PONDEROSA PINE MORTALITY AND BARK BEETLE-HOST DYNAMICS FOLLOWING PRESCRIBED AND WILDLAND FIRES IN THE NORTHERN ROCKY MOUNTAINS, USA

by

Ryan S. Davis

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Forestry

Approved:

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UTAH STATE UNIVERSITY
Logan, Utah

2008

ABSTRACT

Ponderosa Pine Mortality and Bark Beetle-Host Dynamics Following Prescribed and Wildland Fires in the Northern Rocky Mountains, USA

by

Ryan S. Davis, Master of Science

Utah State University, 2008

Major Advisor: Dr. Barbara J. Bentz
Department: Wildland Resources

Ponderosa pine delayed mortality, and bark beetle attacks and emergence were monitored on 459 trees for 3 years following one prescribed fire in Idaho and one wildland fire in Montana. Resin flow volume (ml) was measured on 145 fire-injured ponderosa pine 2 and 3 years post-fire. Logistic regression was used to construct two predictive ponderosa pine mortality models, and two predictive bark beetle-attack models. Post-fire delayed tree mortality was greater with the presence of primary bark beetles independent of diameter at breast height (DBH) (cm), and was greater in smaller diameter trees most likely due to direct effects of fire-caused injuries; mortality was lower in trees with less percent bud kill (PBK). The frequency of bark beetle attack was greater in trees with less percent bud kill and greater bole char height proportion (CHIP). Attack frequency was also greater on trees with higher percent bud kill and greater diameter at breast height. Classification tables for all predictive models were presented for application in post-fire management development.

Multivariate ANOVA analyses were used to describe the effects of morphological and fire-injury variables on ponderosa pine resin production, and bark beetle attack preference and emergence. Resin production (ml) was significantly greater on burned than unburned trees. Resin flow increased significantly between June and July 1 year following fire and from June to August 2 years following fire. Resin flow was lower on the north bole aspect than the south and west aspects of unburned trees. Resin flow of burned trees significantly increased through the summer and was greatest in trees with high pre-fire live crown length (m) (LCL). Resin flow of unburned trees differed significantly by year, month, bole aspect, and live crown length. Resin increased by month and live crown length, decreased from 2005 to 2006, and was less on the northern bole aspect than all other aspects. Bark beetles preferred to attack fire-injured trees, especially within bole-scorched areas. No significant differences in bark beetle emergence were found between fire-injured and non fire-injured trees. On burned sites, beetle emergence was greatest from larger diameter trees with less severe fire injury. Western pine beetle (*Dendroctonus brevicomis* LeConte) had the greatest emergence from fire-injured ponderosa pine, and *Ips pini* (Say) had significantly greater emergence from non fire-injured ponderosa pine.

(106 pages)

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Ryan S. Davis

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CHAPTER I

INTRODUCTION

1. Introduction

Ponderosa pine (*Pinus ponderosa* Lawson) is the host of several bark beetle species [Coleoptera: Curculionidae: Scolytinae], especially the western pine beetle (*Dendroctonus brevicomis* Hopkins), mountain pine beetle (*Dendroctonus ponderosae* Leconte) and various species of *Ips*. Since the 1900's , fire suppression policies have resulted in reduced fire frequency (Arno et al., 1995, 1997), and in some cases has led to the largest fire-return intervals in centuries (Agee, 1991). The resulting over-mature, over-stocked stands have increased susceptibility to bark beetle attacks and pathogen infection in over-mature stands (Parker et al., 2006). Today, the use of prescribed burning as a forest restoration tool (Ryan, 1989; Harrington, 1993; Feeney et al., 1998; Santoro et al., 2001; Baker et al., 2007), in addition to the cumulative effects of fire exclusion and changes in climate (Running, 2006; Westerling et al., 2006), are making post-fire ponderosa pine injury and bark beetle-mediated mortality an important issue. It is imperative that forest managers have the information necessary to devise sustainable long term post-fire management plans.

In addition to fire, epidemic populations of bark beetles within the genus *Dendroctonus* have routinely killed thousands of hectares of timber (Geiszler et al., 1980; DeMars and Roettgering, 1982), and are considered the most detrimental forest insect in the West (Furniss and Carolin, 1977; Mitchell and Martin, 1980). Some bark beetle species are attracted to fire-affected stands and often increase the frequency of tree mortality (Miller and Patterson, 1927; Miller and Keen, 1960; Furniss, 1965; Rasmussen et al., 1996; Ryan and Amman, 1996; Bradley and Tueller, 2001; Sancehz-Martinez and Wagner, 2002; McHugh et al., 2003; Wallin et al., 2003), and reduce merchantable timber by hastening tree fall rates and decomposition via blue-stain fungus inoculation (DeNitto et al., 2000). Fire injury can modify the carbon production and allocation within a tree, altering host resistance to beetles via increased resin production (Ruel et al., 1998; Wallin et al., 2003). Increased oleoresin exudation may decrease beetle attack rates, parental survival and ovipositional success, larval survival and help prevent establishment of secondary insects and fungi associates (Berryman, 1972). Resin production has been shown to vary by the season of induction, environmental conditions, host vigor, genetic factors, attack history, within and among trees and tree species (Lutier, 2002 and references therein). Because of the important role bark beetles play in the post-fire environment, managers could benefit from models predicting bark-beetle attack preference and resulting tree mortality.

Post-fire host tree-bark beetle interactions are complex and need continuing research to better understand them. In particular, managers need to know how the type and severity of fire injury impacts ponderosa pine mortality, bark beetle-host tree selection, bark beetle reproduction and survival and host-resin defenses.

2. Background

Ponderosa pine (*P. ponderosa* Douglas ex Lawson & C.Lawson) is the most important pine in western North America. It is second in timber production only to Douglas-fir (*Pseudotsuga menziesii* Douglas), making it of high economic importance (Hardin et al., 2001). Its distribution ranges from southern British Columbia, west to the Cascade and Sierra Nevada ranges, east to western South Dakota, and extends down the

Rocky Mountains into Mexico. It may be found from sea level to 3018m. The species consists of 2 published subspecies, *P. ponderosa* subsp. *ponderosa* (Lawson) and *P. ponderosa* subsp. *scopulorum* (Engelmann), and two unpublished subspecies *P. ponderosa* subsp. *benthiama* and *P. ponderosa* subsp. *brachyptera*. The focus of this research is on the subspecies *ponderosa* (Lawson), which occupies western Montana and Idaho within its northern range.

Ponderosa pine needles are 7 to 30 cm long and usually have 3, 2 and 3, or 4 and 5 per fascicle (Hardin et al., 2001). Cones are generally 5 to 15 cm long, ovoid to ellipsoidal, sessile, solitary or clustered (Hardin et al., 2001). Young ponderosa pines have brown to black bark; older trunks are generally yellowish brown to cinnamon-red, and have large flat, superficially scaly plates separated by large irregular fissures (Hardin et al., 2001). Ponderosa pine generally grows in large, park-like stands on soils of varying type. They are considered drought tolerant species, but grow best on moist, but well-drained soils (Hardin et al., 2001). Within its range in central Idaho and western Montana, it is frequently associated with Douglas-fir.

Because of its broad distribution, ponderosa pine has many insect and pathogenic associates, however the greatest cause of mortality for this species is from *Dendroctonus* and *Ips* bark beetles, in particular the western pine beetle. The western pine beetle's range is concurrent with ponderosa pine and Coulter pine (*Pinus coulteri*), its primary hosts. Western pine beetle's lifecycle is multivoltine, with one to two generations per year in the northern part of the range, and two to four generations per year in the southern part (Furniss and Carolin, 1977). Third and fourth larval instars mine into the outer bark to complete larval development, pupate and overwinter (Miller and Keen, 1960).

Overwintering stages include late-instar larvae and adults. Due to the multivoltine lifecycle, in addition to reemerging parent adults, multiple flights per season can occur from June to September depending on the location.

Western pine beetle has been shown to preferentially attack fire-injured ponderosa pines (Miller and Patterson, 1927; Miller and Keen, 1960), however there is still some dispute over the attractiveness of fire-injured trees to western pine beetle (Sanchez-Martinez and Wagner, 2002; McHugh et al., 2003).

The mountain pine beetle has a large distribution ranging from southern California to central British Columbia and east to the Black Hills of South Dakota. However, to the north, the range of mountain pine beetle is limited by climate, rather than by host tree species. As the earth's temperature increases, outbreak populations are being sustained in lodgepole pine (*Pinus contorta* Doug. ex Loud.) stands further north in British Columbia and east into Alberta than previously recorded (Carroll et al., 2004). Primary host tree species include all pine species within its range including ponderosa pine (Furniss and Carolin, 1977). At low elevations mountain pine beetle has predominantly one generation per year and overwinters in the phloem layer primarily as larvae, but can also overwinter as adults or teneral adults. Depending on weather, emergence of adult beetles can occur from mid June to late August.

Mountain pine beetle attraction to fire-injured trees is host dependant. Many studies have found that fire-injured lodgepole pine is an unsuitable host (Rasmussen et al., 1996 and references therein). The association between mountain pine beetle and fire-injured ponderosa pine is not well known, but evidence suggests that mountain pine beetle is not highly attracted to fire-injured ponderosa pine (Blackman, 1931; Kelsey and Joseph, 2003; McHugh et al., 2003).

The range of species in the genus *Ips*, particularly *I. pini* and *I. emarginatus*, follow that of their respective host trees and includes ponderosa pine. Both species generally attack unthrifty, fallen, or cut trees and are considered "secondary," or less aggressive beetles. In their northern range both species have one or two generations per year (Wood, 1982).

Ips pini has routinely been associated with fire-injured trees (Amman and Ryan, 1991; Ryan and Amman, 1996; Rasmussen et al., 1996, Santoro et al., 2001; McHugh et al., 2003) and is a major source of secondary tree mortality. Little is known about *I. emarginatus* attraction to fire-injured trees.

3. Research Objectives

This study was initiated to evaluate the effect fire-caused injury on:

1) ponderosa pine mortality three post-fire years
2) bark beetle-attack preference three post-fire years
3) bark beetle-host selection and emergence patterns
4) ponderosa pine resin defenses measured as resin volume (ml).

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CHAPTER 2

PREDICTING BARK BEETLE ATTACK AND TREE MORTALITY IN PONDEROSA PINE FOREST TYPE THREE YEARS FOLLOWING PRESCRIBED AND WILDLAND FIRES IN THE NORTHERN ROCKY MOUNTAINS

Abstract

Four hundred and fifty-nine fire-injured ponderosa pine were monitored for mortality and bark beetle attack three years following one prescribed and one wildland fire in Idaho and Montana, respectively. Logistic regression was used to construct two predictive ponderosa pine mortality models and two predictive bark beetle attack models. Diameter at breast height (DBH) (cm), percent bud kill (PBK), presence of *Ips* and/or *Dendroctonus* attacks (ATK), and an interaction between DBH and ATK were significant in predicting post-fire tree mortality. Tree mortality increased with the presence of bark beetles in larger diameter trees. Smaller diameter trees were more likely to die due to fire-caused injury alone, increasing with higher post-fire PBK. DBH, PBK, cambium kill rating (CKR), bole char proportion (CHIP), and the interaction of DBH and PBK, and DBH and CHIP were significant in predicting bark beetle attack probability. Beetle attacks occurred more often on trees with less crown damage, but high bole char. Larger diameter trees with greater crown injury (high PBK) were also attacked significantly more. Classification tables for all predictive models were presented for application in post-fire management development.

1. Introduction

Ponderosa pine (*Pinus ponderosa* Lawson) is the host of several bark beetle species [Coleoptera: Curculionidae: Scolytinae], especially the western pine beetle (*Dendroctonus brevicomis* Hopkins), mountain pine beetle (*Dendroctonus ponderosae* Leconte) and various species of *Ips*. Since the 1900's , fire suppression policies have resulted in reduced fire frequency (Arno et al., 1995, 1997), and in some cases has led to the largest fire-return intervals in centuries (Agee, 1991). The resulting over-mature, over-stocked stands have increased susceptibility to bark beetle attacks and pathogen infection in over-mature stands (Parker et al., 2006). Today, the use of prescribed burning as a forest restoration tool (Ryan, 1989; Harrington, 1993; Feeney et al., 1998; Santoro et al., 2001; Baker et al., 2007), in addition to the cumulative effects of fire exclusion and changes in climate (Running, 2006; Westerling et al., 2006), are making post-fire ponderosa pine injury and bark beetle-mediated mortality an important issue. It is imperative that forest managers have the information necessary to devise sustainable long term post-fire management plans.

Western conifers exposed to fire can die from one or a combination of the following factors: high percentage of foliage loss and bud death, high percentage of cambium death, and/or excessive tissue damage to roots (Ryan, 1989). Resistance of individual trees to fire-caused mortality depends on a number of morphological characteristics that protect vascular and meristematic tissue from heat injury, as well as the tree's ability to recover from some level of fire injury (Regelbrugge and Conrad, 1993).

Often, trees that would have survived a fire are subsequently killed by bark beetles (Miller and Patterson, 1927; Herman, 1950; Peterson and Arbaugh, 1986, 1989; Amman, 1991; Amman and Ryan, 1991; Ryan and Amman, 1994, 1996; Rasmussen et al., 1996; McHugh et al., 2003; Hood and Bentz, 2007; Schwilk et al., 2006; Sieg et al., 2006), although few post-fire tree mortality models have included bark beetle attack as a parameter (McHugh et al., 2003; Sieg et al., 2006). Of particular concern to forest managers are the primary bark beetle species which have the capacity to expand to outbreak levels in surrounding stands following buildup in fire weakened trees (Amman and Ryan, 1991; Rasmussen et al., 1996; Ryan and Amman, 1996), including *Dendroctonus* and/or *Ips* bark beetles. Because of the important role bark beetles play in the post-fire environment, managers could benefit from models predicting post-fire bark-beetle attack and subsequent tree mortality.

Predicting delayed tree mortality and bark beetle attack probability are important aspects of post-fire restoration efforts. Several post-fire ponderosa pine mortality models have been developed for the western United States, and included the use of a binary outcome variable with some measure of crown and/or bole damage (Harrington and Hawksworth, 1990; Harrington, 1993; Regelbrugge and Conrad, 1993; Stephens and Finney, 2002 Sieg et al., 2006; Theis et al., 2006). However, only a few models directly included the influence of phytophagous bark beetles on post-fire tree mortality (Miller and Patterson, 1927; Salman, 1934; McHugh et al., 2003; Sieg et al., 2006). Also, no model has been developed to predict post-fire delayed ponderosa pine mortality and associated bark beetle attack preference for the northern Rocky Mountains. In an effort to maintain consistency among the many fire-injury variables used in ponderosa pine mortality models, fire-injury definitions defined in Fowler and Sieg (2004) and used in Thies et al. (2006) and Sieg et al. (2006) were used in this study.

This study was initiated to evaluate the effect of fire-caused injury on ponderosa pine mortality, and bark beetle-attack preference 3 years following prescribed and wildland fires in the northern Rocky Mountains. Using data collected from two areas in Montana and Idaho, models were developed for predicting the probability of post-fire ponderosa pine mortality and bark beetle attack. Also, in an unreplicated paired study, bark beetle attraction to fire-injured trees within a prescribed burn area was compared to tree attack in an unburned control area.

2. Methods

2.1 Study Area Description

Black's Mountain 2 (BM2) study area, located approximately five miles Southwest of Missoula, MT, USA (UTM NAD83 Zone 11T, E` 716648 N` 5189963), is within the boundary of the fall, 2003 Black's Mountain 2 wildfire. The ~100ha study area is characterized by mixed ponderosa, Douglas-fir forest type. Site elevation is between 1,371 and 1,677m on predominately southeast facing slopes with east-facing microtopographic variation.

The Payette study area is located on the Payette National Forest, Krassel Ranger District, Valley County, Idaho, USA (UTM NAD27 Zone 11T, E`616332 N` 4979358). Within the study area are a ~300ha treatment site (Parks) that was prescribed burned in May 2004, and a ~300ha control site (Deadman) that was left unburned. The treatment and control sites were similar, characterized by mixed old growth ponderosa pine, Douglas-fir forest type with elevation ranging between 1,097 and 1,768m elevation.

Both study areas had low levels of bark beetle activity prior to burns, based on aerially-detected tree impact levels (USDA Forest Service, Forest Health Protection, http://www.fs.fed.us/r1-r4/spf/fhp/aerial/gisdata).

2.2 Plot establishment and measurement of tree variables

Fifteen plots were established in July 2004 within the BM2 study area. Within the Payette study area Twenty-one plots were established in July and August 2004 at the Parks site and 20 plots at Deadman site. Because of a concurrent, ongoing wildlife study (http://www.rmrs.nau.edu/lab/4251/birdsnburns/), sampling at the Payette sites was somewhat restricted. No trees could be removed, and the use of pheromone-baited traps to assess local beetle populations was prohibited. We established 10th acre (radius = 37.24ft) plots 61m at random azimuths from wildlife plot centers. If there was less than seven trees within a 10th acre, plots were expanded to 5th acre plots (radius= 16.06m) to increase tree sample size. All trees >9.9cm DBH within the selected radius were tagged, species recorded and numbered starting with the first tree right of the northern azimuth (declination was set to 0). Plot centers were recorded using a Garmin, Etrex Legend GPS unit, and the distance and azimuth from the closest tagged tree was recorded. Photographs were taken 10ft to the north and south of every plot center with a digital camera to monitor changes in post-fire vegetation. Similar plots were established at the Payette site that was not burned (Deadman) to enable a comparative analysis of bark beetle response to a prescribed burn.

In general, variables chosen for field measurement were selected from recent post-fire ponderosa mortality publications based on: 1) their efficacy in predicting post-fire ponderosa pine mortality, 2) the ease of measurement by managers and technicians, and 3) their range of applicability within various ponderosa pine forest types. All tree morphological variables were measured post burn, but were estimated as pre-fire measurements. Measurements of all variables followed existing methodology (Fowler and Sieg, 2004; Hood and Bentz, 2007), with variable names and definitions standardized to Fowler and Sieg (2004).

Following establishment, all plots were revisited annually for two consecutive years to monitor tree mortality and bark beetle activity. To ensure that fire-damage and bark-beetle influenced mortality were accurately estimated, fire injury measurements were collected in late August/early September, following peak bark beetle flight, on cloudless days. Eleven tree variables were directly measured in the field, and 2 variables were calculated by combining field-measured variables:

- **Tree status (STATUS):** Post-fire tree status, alive (0) or dead (1), was estimated in late August/early September. Status consisted of 5 vigor levels based on Keen's crown-vigor classes (Miller and Keen, 1960) and post-fire bole injury. Because of the subjectivity in determining vigor classes, final analysis combined all live vigor classes (high, moderate, low and very low vigor are equal to 1) and all trees labeled as dead equal 0. Trees retaining *any* green foliage were considered live for that year. Trees that appeared dead before the fire—as noted by the complete absence of needles and smaller branches—were omitted from measurement.
- **Diameter at breast height (DBH):** Tree diameter 1.4m from the ground on the uphill side of the tree, measured with a d-tape to the nearest cm.

- **Tree height (TH):** Distance from ground level on the uphill side of the tree to the top of the tree, measured to the nearest 0.25m using a laser hypsometer (Opti-Logic Corporation, Tullahoma, TN) .
- **Crown-base height (CBH):** Distance from ground level on the uphill side of the tree to the lowest branch of the main pre-fire canopy, measured to the nearest .25m using a laser hypsometer (Opti-Logic Corporation, Tullahoma, TN).
- **Crown Scorch Height (CSH):** Maximum height of foliage scorch/kill measured from ground level on the upslope side of the tree (Fowler and Sieg, 2004) using a laser hypsometer (Opti-Logic Corporation, Tullahoma, TN) to the nearest 0.25m.
- **Percent crown scorch volume (CSV):** An ocular estimate of the proportion of pre-fire foliage scorched/killed due to fire; includes needle scorch, and bud kill/crown consumption (Fowler and Sieg, 2004) in 10 percent increments from 10-90 percent and five percent increments from 0-10 and 90-100. Ten percent intervals were used to decrease subjective error among field technicians.
- **Bud kill/consumption (PBK):** Percent of crown bud volume consumed by fire in 10 percent increments from 10-90 percent and five percent increments from 0-10 and 90-100. This measurement does not include foliage with only scorched needles (Fowler and Sieg, 2004). Distinguishing between crown scorch volume and percent bud kill is only accurate after bud/needle growth initiates making the distinction between the two crown segments obvious
- **Percent crown scorch length (PSL):** PSL was calculated using tree CSH and total tree height (TH) as:

$$PSL=(CSH/ TH).$$

- **Bark char rating (CHAR):** A visual assessment of bole char severity was made in each cardinal quadrant between ground level and DBH based on qualitative bark conditions as outlined in Ryan (1982) and McHugh and Kolb (2003): 1) heavy char: bark deeply charred, but not necessarily to the wood, and surface characteristics have been lost; 2) medium char: bark uniformly black with the possible exception of the inner depths of the prominent fissures, but bark character is still discernible; 3)light char: scorch or char on edges of bark plates or where moss burned off the bole; 4) none: no evidence of flame contact with the bole and no charring of the bole.
- **Number dead cambium quadrants or Cambium Kill Rating (CKR):** Determination of cambial status was accomplished by visual inspection of cambium obtained by removing a 2.5cm phloem sample with a gas-powered drill as close to ground level as possible. Live cambium was healthy, white to pink in color and moist to touch; dead cambium was "sour," resin-impregnated, hard to the touch or burned/desiccated.
- **Percent basal girdling (PBG):** Proportion of the basal circumference in which cambial tissue is killed (Fowler and Sieg, 2004). Ocular estimates of fire-killed phloem were made during quadrant-level examination of cambial death.
- **Scorch height (SH):** Highest point of visible scorching on the tree whether it is on the tree bole or crown, measured in .25m increments.
- **Bole char height proportion (CHIP):** Mean quadrant-level bole char height (CH) divided by total tree height (where CHq1 equals char height quadrant 1,

etc.). Bole char height as a proportion of TH was a more effective variable than a bole char height index alone, and was thus chosen for use in analysis.

$$((CHq1 + CHq2 + CHq3 + CHq4)/4)/TH$$

2.3 Measurement of bark-beetle attacks

All trees were examined for insect attacks by visually assessing the entire bole circumference as high as possible from the ground. Attack presence, success and species determination were assessed by looking for frass in bark fissures and on the ground, presence of pitch tubes, fading canopies, by removing bark sections to view gallery patterns and collecting beetle samples for lab identification. All trees with successful attacks on >96% of the bole circumference—i.e. successful entrance into the tree leading to gallery construction and oviposition—were recorded as mass attacked. Trees with ~ 1 to 95% of bole circumference showing signs of attack were recorded as strip attacked, and trees with no sign of attack or only a few pitch tubes were recorded as unattacked.

2.4 Ponderosa pine post-fire mortality models

Predictive tree mortality models were developed using SAS Proc Logistic (LOGISTIC) (SAS, Version 8.1), following the logistic regression procedures outlined in Patetta (2001) and Allison (1999). Models were developed using data collected from each study area independently, and both study areas combined. The dependent variable, individual tree mortality, was defined as a dichotomous dependant variable. Trees that were living three years post-fire were assigned a code of 0, and dead trees were assigned a code of 1. Logit analysis based on the Maximum Likelihood method of estimation was selected for model development (Allison, 1999).

Multicollinearity of independent variables was tested using Pearson coefficients produced by Proc Corr (CORR). Because collinearity analysis does not utilize the dependant variable, linear regression was used (REG). Predicted values were calculated by fitting the independent variables to a Logistic model and were then used to create a matrix by which linear combinations were weighted (Allison, 1999). Tolerance (TOL) ($1-R^2$) and variance inflation (VIF) options in REG were used to identify multicollinearity. Low tolerance levels and/or higher levels of variance inflation were indicative of multicollinearity.

Univariate analysis in LOGISTIC was used to select important variables from the 13 original independent variables. Multicollinear variables were selected by their comparative efficacy in individual analysis. If collinear variables were both found significant at the $\alpha=0.05$ level, one variable was selected based on biological principle and subject knowledge. Any variable not meeting significance in the univariate model was eliminated from further analysis. Variables selected for continued analysis were plotted against their Logits to assign either a class or continuous variable designation model formulation. Variables with a nonlinear pattern were included as class variables and variables with linear associations were included as a continuous variable (Patetta, 2001).

FORWARD, BACKWARD and STEPWISE model selection options utilizing SINGLE and MULTIPLE hierarchies, and the INCLUDE equals options in LOGISTIC were used to further reduce potential model variables. INCLUDE=*x* specifies that the first *x* number of variables to enter the model are kept in the final model. In this analysis, *x* equaled the number of main effects entered. Effect inclusion was strictly specified by the SLENTRY option in LOGISTIC at $\alpha<0.01$. Variables that consistently entered final models were selected for inclusion in the best subsets, or SCORE, selection method. Output from SCORE yielded Score Chi-Squared values for 2-effect to 6-effect models. Parsimony, relevance and significant ($\alpha<0.05$) increases in the Score Chi-Squared value (i.e. >3.84 per degree of freedom increase in model complexity) were used to select three candidate models for further evaluation. Models were fit to the logistic model with the form:

$$\mathrm{P}_m = 1/[1 + \exp(-(\beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n))] \tag{1}$$

where P_m is the probability of tree mortality, β_0, β_1, and β_n are regression coefficients (parameter estimates), and X_1 and X_n are independent variables.

The area under the ROC (Receiver Operating Characteristic) (c), which ranges from 0 to 1, is equal to the proportion of correctly classified pairs of observations (Hosmer and Lemeshow, 2000). A c value equal to 0.5 suggests no discrimination, values between 0.7 and 0.8 indicate acceptable discrimination, those between 0.8 and 0.9 indicate excellent discrimination, and those greater than 0.9 are considered to have outstanding discrimination (Hosmer and Lemeshow, 2000; Hood and Bentz, 2007).

The candidate models were analyzed to assess their comparative predictive power and goodness of fit. Classification tables with probability cutoff points between $\mathrm{P}_{m=}0.20$ and $\mathrm{P}_{m=}0.80$ were generated so that the user can select the most appropriate model probability level based on management objectives. Trees with predicted values above the selected cutoff probability are classified as dead (tree mortality model) or attacked (beetle-attack model) (Hood and Bentz, 2007). Trees that are below the probability cutoff value are classified as either live or unattacked. The classification tables also include the proportion of event observations that were correctly predicted to die or be attacked (sensitivity), and the proportion of event observations that were correctly predicted to live and be unattacked (specificity).

Models with good predictive power do not necessarily fit the data well (Allison, 1999; Hosmer and Lemeshow, 2000; Patetta, 2002). Because candidate models selected for final analysis had similar levels of prediction, goodness of fit comparisons were made using the Pearson Chi-Square, deviance and the Hosmer and Lemeshow test, the –2Log Likelihood and the Akaike Information Criterion (AIC) to help choose between competing models. Final models with high predictive power and acceptable goodness of fit statistics were chosen.

2.5 Post-fire bark beetle attack model

Predictive bark beetle attack models were developed using the same methodology as tree mortality model development described above. Models had the form

$$P_a = 1/[1 + \exp(-(\beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n))] \qquad (2)$$

where P_a is the probability of bark beetle attack, β_0, β_1, and β_n are regression coefficients (parameter estimates), and X_1 and X_n are independent variables. Similar tree and fire-injury variables used in the development of the tree mortality models above were tested for significance in predicting the probability of post-fire bark beetle attack on ponderosa pine. Models were developed using data collected form each study area independently and both study areas combined.

Logistic regression using a Wald Chi-Squared contrast test was used to examine differences in the total number of bark-beetle attacked trees among all the sites individually, and between all burned (BM2 and Parks sites) and unburned (Deadman site) trees.

3. Results

3.1 Tree variables

A total of 573 ponderosa pine were assessed at three (1 control and 2 burned) sites. No significant differences in mean DBH and total height (TH) were observed between the burned (Parks) and unburned (Deadman) sites in the Payette study area. However, all pre-fire tree and post-fire tree injury variables were significantly different ($p< 0.0001$) between burned sites at the 2 study areas. In general, trees at the wildfire site, BM2 had greater levels of fire injury than trees at Parks (Table 2.1).

Of 459 trees measured on the two burned sites 201 trees (44%) were dead after 3 post-fire growing seasons; 63 (14%) trees died in post-fire year 1, 90 (20%) in year 2, and 48 (10%) in year 3 (Figure 2.1). At both study areas, live trees post-fire were significantly larger in diameter and taller than trees that died, and dead trees had significantly higher fire injury (Table 2.2).

3.2 Bark beetle attacks

Attack presence was initially measured by attack type: unattacked, mass attacked, and strip attacked, but were consolidated because determination of attack type even by trained entomologists is difficult, time consuming, and no significant differences were found between the two attack types. Figure 2.2 shows bark beetle mass and strip attack frequency by variables significant in predicting post-fire bark beetle attack.

Within the two burned site boundaries, bark beetles within the genera *Dendroctonus* and *Ips* mass-attacked 84 (0.18%) trees and strip attacked 76 (0.17%) trees (Table 2.3), and only 1 tree with no sign of fire injury was attacked by bark beetles. Of 76 recorded strip-attacked ponderosa pine 49 (71%) remained alive three years post fire. Three attacked ponderosa pine were observed on trees within the boundary of the unburned site, Deadman. The average DBH of attacked fire-injured ponderosa pine by beetle species for combined sites was 16.08cm for *Ips*, 23.56cm for mountain pine beetle, 37.41cm for western pine beetle, 27.69cm for western pine beetle and Ips combined, 24.46cm for western pine beetle and mountain pine beetle combined, and 26.92cm for all beetle species combined.

Bark beetles attacked significantly more burned than unburned ponderosa pine ($\aleph^2 = 25.1029$, $P < .0001$). With the exception of CBH and TH, bark beetles on the two fires combined generally attacked smaller trees with greater fire injury (Table 2.4). When the burned sites were analyzed separately, bark beetles attacked trees with fire injury different than for combined sites (Table 2.5). Because of the difference between BM2 and Parks beetle-attacked trees, separate beetle-attack models were made.

Overall, more trees were attacked at the wildfire site (BM2), than at the prescribed burn site (Parks) ($\aleph^2 = 36.9608$, $P < .0001$). At the Payette study area significantly more trees were attacked ($\aleph^2 = 23.0405$, $P < .0001$) in the prescribed burn site (Parks) than the unburned control (Deadman) where no attacked trees were found on plots. Red turpentine beetle (*D. valens*) was present on 97 (21%) trees. The presence of wood-boring beetles (e.g. Cerambycidae and Buprestidae) was high on fire-injured trees, although not quantified.

3.3 Ponderosa pine post-fire mortality models

Three post-fire ponderosa pine mortality models are presented below, one for each burned site, and one with burned sites combined. There were pre-fire differences in tree morphology, site topography and geographic location for burned sites used in model formulation. Because of those inherent attributes, each site yielded a slightly different model, with different goodness of fit (Table 2.6). Despite these disparities, the combined model is more robust and includes an accurate range of potential stand conditions that may exist in a northern Rocky Mountain ponderosa pine forest type. The combined model should be used in conjunction with the probability cutoff values presented in the classification table when creating post-fire salvage thinning guidelines (Table 2.7).

Variables found most significant in predicting post-fire ponderosa pine mortality at BM2 were DBH, PBK, CKR and ATK (bark beetle attacked = 1, unattacked = 0) (Table 2.8). On BM2, ponderosa pine trees with smaller DBH, greater PBK and CKR, and the presence of beetle had a higher probability of mortality.

For Parks, variables found most significant in predicting post-fire ponderosa pine mortality were DBH, PBK ATK and the interaction DBH*ATK (Table 2.8). On Parks, DBH itself did not affect the predicted probability of ponderosa pine mortality. But, when combined with ATK, predicted mortality increased with the presence of bark beetle attack as DBH increased. Predicted ponderosa pine mortality was also greater for trees with higher PBK.

Variables found most significant in predicting post-fire ponderosa pine mortality at both study areas combined were DBH, PBK, ATK, CKR and an interaction between DBH and ATK (Table 2.8). For combined sites, large trees (DBH > 46cm) unattacked by bark beetles had the greatest predicted probability of survival 3 years post-fire (Figure 2.3). Conversely, small trees (DBH < 46 cm) unattacked by bark beetles had a relatively high P_m following fire ($P_m > 0.6$), and this value changed little for small trees attacked by bark beetles. Large beetle-attacked trees had the highest predicted probability of mortality (Figure 2.3).

A classification table for the combined site model gives the spectrum of probability levels from which managers may choose a cutoff probability (Table 2.7).

3.4 Post-fire bark beetle attack models

Three post-fire ponderosa pine bark-beetle attack models are also presented below, one for each burned site, and one with burned sites combined. Because of the difference in site attributes, each site yielded a different model, with varying goodness of fit (Table 2.9). As for the tree mortality model, the combined beetle-attack model should be used in conjunction with the probability cutoff values presented in the classification table when creating post-fire salvage thinning guidelines (Table 2.10).

The best model for predicting bark beetle attack probability using data from BM2 included CHIP, DBH, SH and an interaction between CHIP and DBH (Table 2.11). On BM2, bark beetle attack probability decreased as DBH and CHIP decreased, and increased as SH increased. For larger diameter trees, greater CHIP increased bark beetle attack probability.

For Parks, variables found most significant in predicting post-fire ponderosa pine bark beetle attack probability were DBH, CKR, PBK and the interaction of DBH*PBK. (Table 2.11). On parks, trees with moderate cambial death had the highest probability of bark beetle attack. Attack probability also increased as both DBH and PBK increased.

The best model for predicting bark beetle attack probability using data from both study areas combined included PBK, CHIP and interaction terms CHIP*PBK and DBH*PBK (Table 2.11). Predicted probability of bark beetle attack was greatest on trees with greater than 50% bole char (CHIP) and less than 40% bud kill (PBK) (Figure 2.4). Although DBH alone had little effect on P_a, large trees with high levels of bud kill had the highest predicted probability of bark beetle attack (Figure 2.4).

4. Discussion

Trees at the BM2 wildfire burn site had significantly higher levels of fire-caused injury than trees at the Parks prescribed burn site, in part due to the smaller overall size of trees at BM2. Also, more bark beetle-attacked trees were found within plots at the BM2 site, although the majority of the trees at BM2 were strip attacked compared to a majority of mass-attacked trees at the Parks site. At both sites, mountain pine beetle, western pine beetle, *Ips emarginatus* and *Ips pini* preferentially attacked fire-injured compared to uninjured ponderosa pine. Moreover, bark beetles attacked significantly more trees in an area that had been prescribed burned, when compared to a nearby unburned control area. The DBH of the trees attacked by bark beetles was significantly less than unattacked trees, regardless of the fire injury. Previous studies on a variety of Dendroctonus bark beetles have found bark beetles attracted to larger trees (Rasmussen et al., 1996; Weatherby et al., 2001; Hood and Bentz, 2007). For combined beetle species majority of the smaller trees attacked were attacked by *Ips emarginatus* and *Ips pini*, which is consistent with observations of post-fire *Ips* attack preference (Kegley et al., 1997; Weatherby et al., 2001; McHugh et al., 2003). For the Dendroctonus beetles the average DBH for attacked trees was at least 23.58cm, which is within the normal DBH range for post-fire attack (Amman et al., 1990; Weatherby et al., 1994, 2001; McHugh et al., 2003).

Although previous studies observed that mountain pine beetle is either not attracted, or attracted at low levels to fire-affected trees (Hopkins, 1905; Blackman, 1931; Rasmussen et al., 1996; Ryan and Amman, 1996) mountain pine beetle played a major role in tree mortality at the BM2 site one year post-fire, mountain pine beetle rarely killed a tree by itself. Rather they were often seen in the same tree with western pine beetle, *Ips pini* and/or *Ips emarginatus*. Additionally, mountain pine beetle had poor reproductive success in these trees partly due to the apparent interspecific competition within the phloem (Chapter 1). While uncommon, mountain pine beetle have previously been observed infesting fire-injured ponderosa pine (Rust, 1933).

Variables found to be significant in predicting post-fire ponderosa pine mortality were DBH, PBK, CKR, ATK and the interaction of DBH and ATK. Predictions from the tree mortality model developed using combined data from the two study areas suggest that in the absence of bark beetle attacks, the probability of post-fire mortality is greatest for small trees, which is similar to other ponderosa pine post-fire mortality studies (Saveland and Nueunschwander, 1990; Harrington, 1993; Regelbrugge and Conrad, 1993; Sieg et al., 2006; Thies et al., 2006). Because of the positive relationship with bark thickness, DBH may serve as a surrogate for resistance to fire injury (Hare, 1965; Martin, 1963), but may vary by site, ecotype, and height above ground (Ryan, 1989).

Large, bark beetle-attacked trees were found to have the greatest probability of mortality, although predicted probability of mortality remained high in smaller trees with or without the presence of bark beetles. The majority of partial or strip attacks occurred on smaller diameter trees, and the majority of these trees remained alive three years post fire. DBH, in addition to site and tree vigor attributes, has been positively correlated with phloem thickness (Cole, 1973), which is important in beetle reproduction and nutrition (Amman and Pasek, 1986). For *D. brevicomis* bark thickness is paramount as late larval instars, pupae, and adults occur in the outer bark (Miller and Keen, 1960).

Although some measure of crown injury has been found to be important in predicting post-fire delayed tree mortality most studies have not separated crown damage into distinct measures of bud kill and/or needle scorch (Fowler and Sieg, 2004). Our results show that PBK and CSV are highly correlated, and that PBK was a better predictor of ponderosa pine mortality.

A direct measure of cambium death (e.g. CKR) has previously been found to be significant in predicting post-fire Douglas fir mortality (Ryan and Reinhardt, 1988; Hood and Bentz, 2007), and ponderosa pine mortality (Ryan and Fransden, 1991). Our ponderosa pine mortality model also includes CKR as a significant predictor, with mortality probability increasing with greater cambial death. Because direct measurement of cambium death can be difficult, time consuming and deleterious to tree health (Thies et al., 2006), attempts have been made to correlate some visible measure of bole damage, such as bole char, with cambium death (Ryan, 1989). Hood and Bentz (2007) found that a direct measurement of cambium death, rather than visible bole char measurements, was better for predicting post-fire Douglas-fir mortality. The increase in predictability was most likely because moderate levels of bole char were associated with both live and dead cambium, and therefore not a reliable measure of cambium death.

When data from both study areas were combined, tree and fire-injury variables found significant for predicting post-fire bark beetle attack were CHIP and the interaction of CHIP and PBK, and DBH and PBK. Similar to other observations in ponderosa and Jeffery pine, decreasing levels of PBK and increasing levels of CHIP appeared more attractive to bark beetles (Miller and Keen, 1960; Bradley and Tueller, 2001). Within the model, the interaction of DBH and PBK was more important than DBH itself, with increasing beetle attack probability as DBH and PBK increased together.

Several previous studies showed a relationship between post-fire ponderosa pine mortality and bark beetle activity (Miller and Patterson, 1927; Herman, 1950, 1954; Weatherby et al., 1994; McHugh and Kolb, 2003; McHugh et al., 2003; Sieg et al., 2006). However, this is the first predictive post-fire bark beetle-attack model for ponderosa pine. Hood and Bentz (2007) developed a model for predicting the probability of Douglas-fir beetle attack on fire-injured trees. Similar to the model described here for ponderosa pine, their model included a measure of bole and crown damage, and results suggest a similar relationship between Douglas-fir and ponderosa pine in fire-injury and bark beetle attack probability. In both Hood and Bentz (2007) and the model developed here, the probability of attack increased with crown injury while cambium injury was low, and attack probability decreased with crown injury while cambium injury was high. This may imply that beetles across taxa are selecting hosts based on certain levels of fire injury.

Miller and Keen (1960) summarized data from 11 burns of varying severity that occurred from 1919 to 1938. Their general conclusions indicate that western pine beetles are not attracted to fire-injured trees, that have severe crown and bole damage. Hood and Bentz (2007) found similar result for Douglas-fir. However, a marked increase in western pine beetle-attacked ponderosa pine was found when trees had 50% to 100% fire-caused crown injury (Miller and Patterson, 1927; Miller, 1943; Miller and Keen, 1960; McHugh et al., 2003; Wallin et al., 2003). Results from this study suggest that the effect of crown damage on bark beetle attack frequency varies with the amount of bole injury and tree size. As PBK and DBH increase, beetle attack frequency increases; as PBK increases and CHIP increases beetle attack frequency decreases. When moderate to low levels of PBK are combined with moderate to severe levels of CHIP attack frequency increases.

5. Conclusions

Post-fire ponderosa pine mortality has generally been attributed to tree resistance mechanisms including morphological characteristics, tree vigor, and unique stress-coping strategies (i.e. Wagener, 1961; Hare, 1965; Brown and Davis, 1973; Kozlowski et al., 1997). By quantifying the relationship between bark beetles and fire-caused tree injuries, this study adds to the vast array of previous studies relating bark beetles and secondary tree mortality in the post-fire environment (Miller and Patterson, 1927; Herman, 1950; Peterson and Arbaugh, 1986, 1989; Amman, 1991; Amman and Ryan, 1991; Ryan and Amman, 1994, 1996; Rasmussen et al., 1996; McHugh et al., 2003; Hood and Bentz, 2007; Schwilk et al., 2006; Sieg et al., 2006).

A better understanding of tree resistance to secondary causes of post-fire delayed mortality would greatly enhance our capability to predict bark beetle attacks on fire-injured trees. While we are beginning to understand the general morphological and fire injury parameters that explain post-fire tree mortality and bark beetle attack, we do not understand the underlying casual mechanisms. Researchers are beginning to examine the effects of these parameters on tree physiology and how the alterations in physiology affect the post-fire beetle-tree complex. Many studies have examined post-fire ponderosa pine mortality, and, in general, have reached similar conclusions. Producing post-fire tree mortality and bark beetle prediction models is important for management concerns, but a new focus of research into the underlying effects of fire-injury, morphology, and secondary invaders, perhaps managers can make more informed management decisions in the future.

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Table 2.1. Metrics for tree and fire-injury variables measured on plots located within the boundary of a wildfire that burned in the fall, (BM2=Blacks Mountain 2, Lolo National Forest, MT), and a prescribed burn in the spring (Parks, Payette National Forest, ID).

	BM2 (N=283)			Parks (N=176)		
Variable	Mean	SE	Range	Mean	SE	Range
DBH(cm)	21.49	0.63	7.6-69.3	44.37	1.52	7.9-120.1
TH(m)	13.48	0.28	3.1-27.7	24.29	0.58	5.9-43.3
CBH(m)	5.58	0.16	0.0-15.2	8.97	0.34	0.9-21.3
PSL(%)	0.75	0.02	0.0-1.0	0.38	0.02	0.0-1.0
SH (m)	9.52	0.23	0.0-23.2	8.76	0.58	0.0-27.7
CSV(%)	0.65	0.02	0.0-1.0	0.29	0.02	0.0-1.0
PBK(%)	0.52	0.02	0.0-1.0	0.17	0.02	0.0-1.0
GIRD(%)	0.59	0.02	0.0-1.0	0.21	0.02	0.0-1.0
CHIP(%)	0.21	0.01	0.0-1.0	0.07	0.01	0.0-0.8
CKR	2.42	0.09	0.0-4.0	0.99	0.09	0.0-4.0

*N = the number of trees measured at each site. DBH = diameter at breast height, TH = tree height, CBH = crown base height, PSL = percent scorch length, SH = scorch height, CSV = percent crown scorch volume, PBK = percent bud kill, GIRD = percent basal girdling, CHIP = bole scorch percent, and CKR = number of killed cambium quadrants.

Table 2.2. Mean, standard error, and range for tree and fire-injury variables of live and dead ponderosa pine 3 yrs post-fire in plots located within the boundary of a wildfire (BM2) and a prescribed burn (Parks). Differences in tree and fire-injury variables among live and dead trees were tested using an F-test.

	Live Trees (N=182)			Dead Trees (N=253)		
Variable *	Mean	SE	IQR	Mean	SE	IQR
DBH(cm)	37.12	1.13	24.1-45.7	21.47	1.09	11.7-25.2
TH(m)	20.77	0.46	15.2-26.5	13.48	0.47	8.5-16.8
CBH(m)	7.61	0.25	4.9-9.5	5.91	0.24	3.7-7.9
PSL(%)	0.45	0.02	0.2-0.7	0.81	0.02	0.7-1.0
SH(m)	8.54	0.39	3.9-12.2	10.09	0.33	7.6-12.2
CSV(%)	0.31	0.02	0.05-0.5	0.77	0.02	0.5-1.0
PBK(%)	0.17	0.01	0.0-0.3	0.67	0.02	0.4-1.0
GIRD(%)	0.23	0.02	0.0-0.4	0.76	0.03	0.5-1.0
CHIP(%)	0.09	0.01	0.03-0.1	0.24	0.02	0.1-0.3
CKR	1.01	0.07	0.0-2.0	2.98	0.1	2.0-4.0

*DBH = diameter at breast height, TH = tree height, CBH = crown base height, PSL = percent scorch length, SH = scorch height, CSV = percent crown scorch volume, PBK = percent bud kill, GIRD = percent basal girdling, CHIP = bole scorch percent, and CKR = number of killed cambium quadrants. IQR is the inter-quartile range, or the range of values for a specific variable between the 25th and 75th percentiles.

Table 2.3. Number of ponderosa pine attacked by bark beetles at 2 burned areas, BM2 and Parks 3 years post-fire. IPS = *Ips Pini* and *I. emarginatus*; MPB = *Dendroctonus ponderosae*, WPB = *D. brevicomis* and Mix = some combination of the three beetle groups.

	2004*			2005			2006			
	Mass	Strip	Total	Mass	Strip	Total	Mass	Strip	Total	Total
BM2										
IPS	17	0	17	0	0	0	0	0	0	17
MPB	12	55	67	0	0	0	0	2	2	69
WPB	11	8	19	2	0	2	0	0	0	21
MIX	6	5	11	0	0	0	0	0	0	11
Total	46	68	114	2	0	2	0	2	2	116
Park's										
IPS	1	0	1	0	0	0	1	0	1	2
MPB	0	0	0	0	0	0	0	0	0	0
WPB	5	4	9	26	2	28	3	1	4	41
MIX	0	0	0	0	0	0	0	0	0	0
Total	6	4	10	26	2	28	4	1	5	43

*2004 totals represent the number of trees attacked by bark beetles 1 year post-fire. At BM2, the 2004 bark beetle survey was 8 months after an August fire; at Parks, the 2004 survey was 3 months following a May fire.

Table 2.4. Metrics of fire-injured ponderosa pine attacked and unattacked by bark beetles 3 years post-fire at two sites, BM2 and Parks.

	Unattacked Trees (N=285)			Attacked Trees (N=152)		
Variable	Mean	SE	IQR	Mean	SE	IQR
DBH(cm)	32.15	1.17	17.8-48.8	28.49	1.31	16.5-35.1
TH(m)	18.23	0.5	10.9-25.9	17.17	0.55	12.6-19.8
CBH(m)	22.43	0.77	3.9-8.8	23.77	0.93	4.9-8.8
PSL(%)	0.54	0.02	0.3-0.9	0.7	0.02	0.6-0.9
SH(m)	8.27	0.33	4.6-11.6	11.13	0.4	8.5-12.8
CSV(%)	0.45	0.02	0.05-0.9	0.58	0.03	0.3-0.9
PBK(%)	0.32	0.02	0.0-0.7	0.46	0.03	0.1-0.7
GIRD(%)	0.38	0.02	0.0-0.8	0.56	0.03	0.3-1.0
CHIP(%)	0.14	0.01	0.04-0.2	0.18	0.01	0.1-0.2
CKR	1.58	0.09	0.0-3.0	2.26	0.12	1.0-4.0

*DBH = diameter at breast height, TH = tree height, CBH = crown base height, PSL = percent scorch length, SH = scorch height, CSV = percent crown scorch volume, PBK = percent bud kill, GIRD = percent basal girdling, CHIP = bole scorch percent, and CKR = number of killed cambium quadrants. IQR is the inter-quartile range, or the range of values for a specific variable between the 25th and 75th percentiles.

Table 2.5. Univariate Chi-Squared tests for all morphological and fire-injury variables for attacked and unattacked fire-injured ponderosa pine on BM2 and Parks 3 years post-fire.

	Attacked vs.		Attacked vs.	
Variable	Pr > ?	Value ?	Pr > ?	Value ?
DBH(cm)	0.6329	0.2282	0.7118	0.1365
TH(m)	0.002	9.5775	0.8085	0.0587
CBH(m)	0.0001	15.08901	0.4884	0.48
PSL(%)	0.0608	3.52	0.017	5.6914
SH(m)	<.0001	26.0943	0.0143	5.9955
CSV(%)	0.59	0.2903	0.0365	4.3737
PBK(%)	0.882	0.022	0.0003	12.9382
GIRD(%)	0.3288	0.9535	0.0131	6.1528
CHIP(%)	0.339	0.9143	0.0272	4.8782
CKR	0.3084	4.8004	0.0016	17.4881

*DBH = diameter at breast height, TH = tree height, CBH = crown base height, PSL = percent scorch length, SH = scorch height, CSV = percent crown scorch volume, PBK = percent bud kill, GIRD = percent basal girdling, CHIP = bole scorch percent, and CKR = number of killed cambium quadrants.

Table 2.6. Goodness of fit statistics for ponderosa pine mortality for combined sites (Model 1), BM2 (Model 2) and Parks (Model 3) 3 years post-fire. Model 1 data from two burned areas, Parks and BM2, were used for combined model development.

	Deviance Pr>ChiSq	Pearson Pr>ChiSq	Hosmer and Lemmeshow	-2LL	c	Max Rescaled R^2
Model 1	1	1	0.3383	253.27	0.961	0.7187
Model 2	1	0.9975	0.6669	168.991	0.944	0.7221
Model 3	1	0.9981	0.8607	66.084	0.972	0.786

Table 2.7. Classification table for BM2 and Parks combined post-fire ponderosa pine mortality model 1.

P(m)*	Total Correct (%)	Correctly Predicted Mortality (%) (Sensitivity)	Correctly Predicted Survival (%) (Specificity)	False Positive (%)	False Negative (%)
0.2	85.9	94.2	81.2	25.9	3.9
0.3	86.6	91.8	83.7	23.7	5.3
0.4	87.9	90.3	86.5	20.8	6
0.5	88.4	86	89.8	17.2	8.2
0.6	88	79.7	92.8	13.6	11.1
0.7	87	73.4	94.8	11.1	13.8
0.8	86.1	64.7	98.3	4.3	17

*P(m) is the probability of tree mortality 3 years post-fire. Sensitivity is the proportion of event observations that were predicted to die and did die. Specificity is the proportion of event observations that were predicted to live and did live. False positive equals the percent of trees that were erroneously predicted to die when they remained alive; false negative equals the percent of trees that were erroneously predicted to live, but did actually die.

Table 2.8. Logistic regression model statistics for ponderosa pine mortality for combined sites (Model 1), BM2 (Model 2) and Parks (Model 3) 3 years post-fire. Model 1 data from two burned areas, Parks and BM2 were used for combined model development.

Model 1: Combined				
*Variable:	â Estimate	SE	Chi-Square	Pr > ChiSq
Intercept	-0.3043	0.8309	0.1341	<.7142
DBH(cm)	-0.1444	0.0346	17.4519	<.0001
PBK(%)	3.2406	0.5516	34.5136	<.0001
CKR	0.6138	0.1239	24.5323	<.0001
ATK	-2.57	0.8375	9.4153	0.0022
DBH*ATK	0.1884	0.0371	25.8204	<.0001
Model 2: BM2				
*Variable:	â Estimate	SE	Chi-Square	Pr > ChiSq
Intercept	1.3403	0.7258	3.4106	0.0648
DBH(cm)	-0.1273	0.029	19.34	<.0001
PBK(%)	3.2549	0.6789	22.9882	<.0001
CKR	0.7439	0.1481	25.2353	<.0001
ATK	-0.7795	0.2151	13.1325	0.0003
Model 3: Parks				
*Variable:	â Estimate	SE	Chi-Square	Pr > ChiSq
Intercept	-0.3289	0.9555	0.1185	0.7307
DBH(cm)	-0.0365	0.0254	2.0631	0.1509
PBK(%)	3.9441	1.1789	11.1926	0.0008
ATK	0.3678	0.8668	0.1801	0.6713
DBH*ATK	-0.0701	0.0252	7.7264	0.0008

*ATK is a class variable with 2 levels: 0=unattacked by bark beetles and, 1= attacked by bark beetles, DBH = diameter at breast height, PBK = percent bud kill, CKR = number of killed cambium quadrants. Model 1 = LOGIT $P(\text{m}) = \beta_0 + \beta_1\text{DBH} + \beta_2\text{PBK} + \beta_3\text{CKR} + \beta_4\text{ATK} + \beta_5(\text{DBH*ATK})$, Model 2 = LOGIT $P(\text{a}) = \beta_0 + \beta_1\text{DBH} + \beta_2\text{PBK} + \beta_3\text{CKR} + \beta_4$ Attack, and Model 3 = LOGIT $P(\text{a}) = \beta_0 + \beta_1\text{DBH} + \beta_2\text{PBK} + \beta_3\text{Attack} + \beta_4(\text{DBH*Attack})$.

Table 2.9. Goodness of fit statistics for ponderosa pine bark beetle attack for combined sites (Model 4), BM2 (Model 5) and Parks (Model 6) 3 years post-fire. Model 4 data from two burned areas, Parks and BM2, were used for combined model development.

	Deviance Pr>ChiSq	Pearson Pr>ChiSq	Hosmer and Lemmeshow	-2LL	c	Max Rescaled R^2
Model 4	0.0201	0.315	0.1478	508.3	0.739	0.2041
Model 5	0.0349	0.4594	0.2745	322.337	0.76	0.2581
Model 6	0.6165	0.2712	0.9223	152.946	0.776	0.2945

Table 2.10. Classification table for post-fire ponderosa pine bark beetle-attack probability Model 4.

P(a)*	Total Correct (%)	Correctly Predicted Attacked (%) (Sensitivity)	Correctly Predicted Unattacked (%) (Specificity)	False Positive (%)	False Negative (%)
0.2	51	91	30.1	59.5	13.6
0.3	61	82.6	49.7	53.8	15.5
0.4	69.8	53.5	78.4	43.5	23.7
0.5	70.7	31.6	91.2	34.7	28.2
0.6	68.1	15.5	95.6	35.1	31.6
0.7	67.8	10.3	98	27.3	32.4
0.8	67	5.2	99.3	20	33.3

* P(a) is the probability of bark beetle attack 3 years post-fire. Sensitivity is the proportion of event observations that were predicted to be attacked and were attacked. Specificity is the proportion of event observations that were predicted to be unattacked and were unattacked. False positive equals the percent of trees that were erroneously predicted to die when they remained alive; false negative equals the percent of trees that were erroneously predicted to live, but did actually die.

Table 2.11. Logistic regression model statistics for bark beetle-attack probability for combined sites (Model 4), BM2 (Model 5) and Parks (Model 6) 3 years post-fire. Model 1 data from two burned areas, Parks and BM2 were used for combined model development.

Model 4: Combined				
*Variables:	â Estimate	SE	Chi-Square	Pr > ChiSq
Intercept	0.143	0.4109	0.1211	0.7278
DBH(cm)	-0.0548	0.0124	19.61	<.0001
PBK(%)	-0.6885	0.7001	0.9672	0.3254
CHIP(%)	-6.8089	1.8511	13.5293	0.0002
DBH*CHIP	0.4053	0.0899	20.336	<.0001
DBH*PBK	0.0834	0.0287	8.4699	0.0036
Model 5: BM2				
*Variable:	â Estimate	SE	Chi-Square	Pr > ChiSq
Intercept	0.1662	0.6851	0.0589	0.8083
CHIP(%)	-11.618	2.7611	17.7052	<.0001
DBH(cm)	-0.1121	0.0275	16.6611	<.0001
SH(m)	0.1819	0.0438	17.2536	<.0001
CHIP*DBH	0.6237	0.1516	16.9355	<.0001
Model 6: Parks				
*Variable:	â Estimate	SE	Chi-Square	Pr > ChiSq
Intercept	-0.8526	0.7222	1.3938	0.2378
DBH(cm)	-0.0089	0.014	0.4023	0.5259
CKR	0.6367	0.1931	15.425	0.0039
PBK(%)	-2.1779	1.886	1.3336	0.2482
DBH*PBK	0.13	0.0476	7.4435	0.0064

*DBH = diameter at breast height, PBK = percent bud kill, CHIP = bole scorch percent, SH = scorch height and CKR = number of killed cambium quadrants. Model 4 = LOGIT $P(\text{a}) = \beta_0 + \beta_1\text{DBH} + \beta_2\text{PBK} + \beta_3\text{CHIP} + \beta_4(\text{DBH*CHIP}) + \beta_5(\text{DBH*PBK})$, Model 5 = LOGIT $P(\text{a}) = \beta_0 + \beta_1\text{CHIP} + \beta_2\text{DBH} + \beta_3\text{SH} + \beta_4(\text{CHIP*DBH})$, and Model 6 = LOGIT $P(\text{a}) = \beta_0 + \beta_1\text{DBH} + \beta_2\text{CKR} + \beta_3\text{PBK} + \beta_4(\text{DBH*PBK})$.

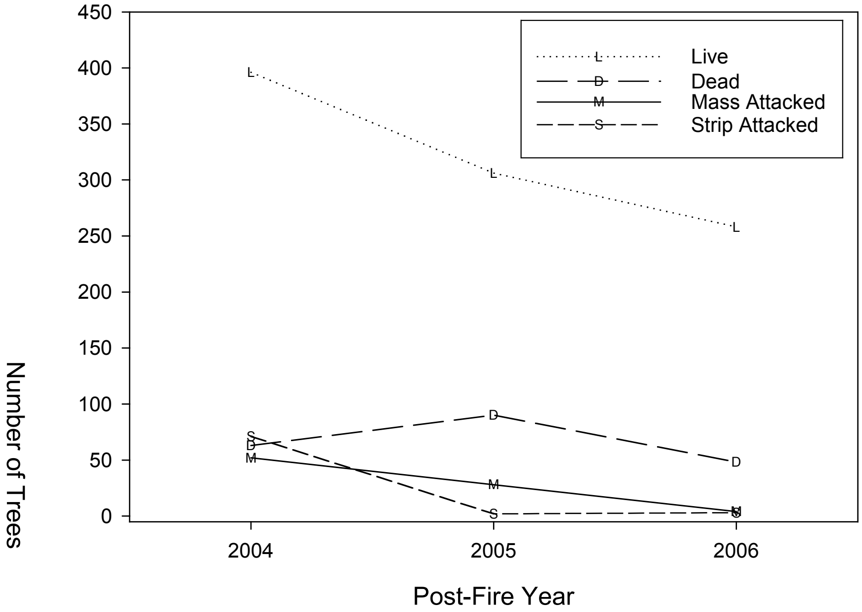

Figure 2.1. Number of trees alive, dead, strip and mass attacked one, two and three years following mixed-severity prescribed and wildland fire at two sites, BM2 and Parks, on the Lolo and Payette National Forests.

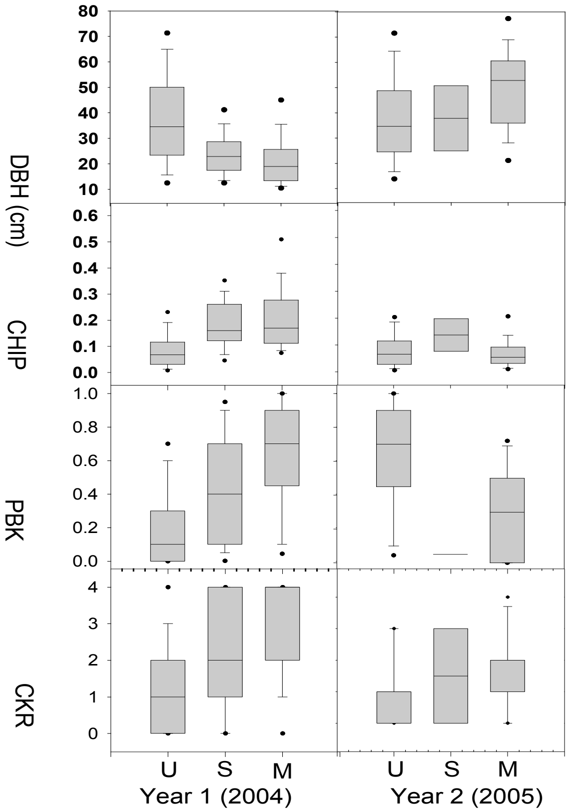

Figure 2.2. Diameter breast height (cm) (DBH), bole scorch proportion (CHIP), percent bud kill (PBK) and cambium kill rating (CKR) of fire-injured trees unattacked (U), mass (M) and strip (S) attacked by bark beetles at two sites, BM2 and Parks on the Lolo and Payette National Forests, 1 and 2 years post-fire. Bark beetle species included in attack categories are *Dendroctonus ponderosae*, *D. brevicomis, Ips pini* and *I. emarginatus*. Shown are the median and 5th and 95th percentile.

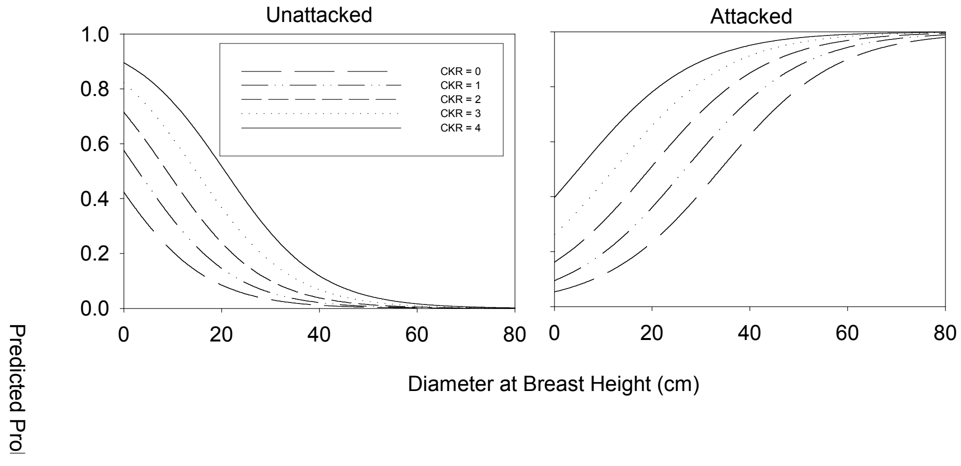

Figure 2.3. Predicted post-fire ponderosa pine mortality from combined model showing the relationship with DBH and bark beetle attack presence (ATK) by 5 levels of cambium kill rating (CKR).

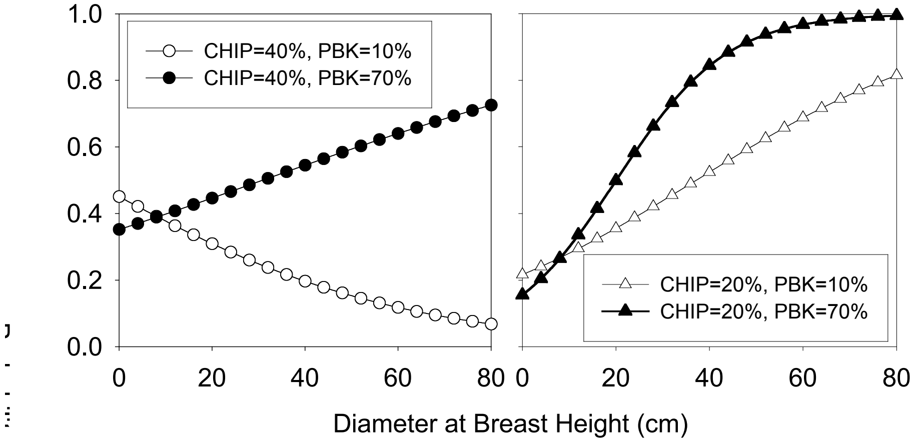

Figure 2.4. Predicted probability of bark beetle attack as a function of diameter at breast height (DBH), bole char height proportion (CHIP), and percent bud kill (PBK). For simplicity, results for two levels of CHIP and PBK are shown.

CHAPTER 3

EFFECTS OF FIRE INJURY ON PONDEROSA PINE RESON FLOW, BARK BEELTE ATTACK PROBABILITY AND EMERGENCE FOLLOWING PRESCRIBED AND WILDLAND FIRES

Abstract

One hundred and eighty-five fire-injured ponderosa pine (*Pinus ponderosa* subsp. *ponderosa* Doug. Ex Laws.) were monitored for bark beetle attack and emergence for three years following one prescribed and one wildland fire in Idaho and Montana, respectively. Multivariate ANOVA analyses were used to describe the effects of morphological and fire-injury variables on host resin production of 145 trees. Resin production (ml) was significantly greater on burned than unburned trees two and three years after fire. Two years post-fire (2005), resin flow of burned trees significantly increased between June and July. Resin flow of unburned trees increased significantly over the summer growing season three years post-fire (2006). Resin flow of unburned trees was significantly lower on north than the south and west tree bole aspects, although no differences were found in burned trees. Burned trees that were larger with greater pre-fire crown length had significantly greater resin flow. Significantly more attacks by mountain pine beetle, western pine beetle, *Ips pini* and *Ips emarginatus* were found on fire-injured, compared to un-injured, ponderosa pine, especially within scorched areas of tree boles. When all beetle species were combined, no significant differences in numbers of adult beetles emerging were found between fire-injured and non fire-injured trees. However, western pine beetle emergence was greatest in fire-injured trees and more *Ips*

pini emerged from un-injured trees. Beetle brood production was greatest in trees with less fire injury at the site with larger trees.

Introduction

Historical fire regimes in ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., forests have varied greatly in frequency (Brown et al. 1999; Sherriff and Veblen 2006) and severity (Sherriff and Veblen 2006; Baker et al. 2007). Since 1900, fire suppression policies have resulted in reduced fire frequency (Arno et al. 1995, 1997), and in some cases has led to the largest fire-return interval in centuries (Agee 1991). In many forest ecosystems, reduced fore frequency has created dense and over-mature stands that have increased susceptibility to bark beetle outbreaks (Parker et al. 2006). In addition to expected increases in forest fires due to climactic changes (Running 2006; Westerling et al. 2006), recent research suggests that forest restoration efforts should focus on restoring and maintaining stand structure with the use of prescribed burning (Feeney et al. 1998; Baker et al. 2007). As natural wildfires and the use of prescribed burning become more frequent, understanding the effects of fire injury on host tree-bark beetle dynamics will be paramount.

Epidemic populations of bark beetles within the genus *Dendroctonus* [Coleoptera: Curculionidae: Scolytinae] have historically killed thousands of hectares of timber per year (Geiszler et al. 1980; DeMars and Roettgering 1982), and are considered the most detrimental forest insects in the western United States (Furniss and Carolin 1977; Mitchell and Martin 1980). Some bark beetles species are attracted to fire-affected stands and can increase the frequency of post-fire delayed tree mortality (Miller and Patterson 1927; Miller and Keen 1960; Furniss 1965; Rasmussen et al. 1996; Ryan and

Amman 1996; Bradley and Tueller 2001; Sancehz-Martinez and Wagner 2002; McHugh et al. 2003; Wallin et al. 2003), and also reduce merchantable timber by hastening tree fall rates and decomposition via blue-stain fungus inoculation (DeNitto et al., 2000). Little is known about bark beetle brood production in fire-injured trees, and what levels of fire-injury will result in good, adequate, or poor resources for population expansion. It is conceivable that heavily damaged trees could be attractive to beetles, but poor for brood production. Although brood production was not investigated, Cunningham (2005) found that moderately fire-damaged Douglas-fir were colonized by Douglas-fir beetle at higher densities than other host trees. Knowing which fire-injured trees may provide quality host material to attacking bark beetles could be used in post-fire areas to remove trees with high brood potential. Of particular interest to forest managers in the northern Rocky Mountains of the U.S. is ponderosa pine and associated bark beetles including: mountain pine beetle (*Dendroctonus ponderosae* (Hopkins)), western pine beetle (*Dendroctonus brevicomis* (LeConte)), *Ips pini* (Say), and *Ips emarginatus* (LeConte).

For successful oviposition and brood development, *Dendroctonus* beetles must attack trees with living or recently killed phloem. Certain levels of fire injury could decrease phloem quality (Miller and Keen 1960; Ryan and Amman, 1996), and modify carbon production and allocation within a tree, thereby increasing host resistance to beetles via increased resin production (Ruel et al. 1998; Wallin et al. 2003). Resin flow is widely considered an important defense against bark beetles (Berryman 1972; Christiansen et al. 1987; Raffa 1991; Nebeker et al. 1993; Lorio et al. 1995). Resin flow has been shown to increase in mechanically wounded (Harper 1944; Ruel et al. 1998; Lombardero et al. 2000) and fire-injured trees (Feeney et al. 1998; Santoro et al. 2001;

Wallin et al. 2003; Lombardero et al. 2006; Perrakis and Agee 2006). Resin production was also found to be greater on burned sides of red pine than on unburned sides (Lombardero et al. 2006) and can vary by season of induction, temperature, precipitation, host vigor, and within and among trees and tree species (Hodges et al. 1979; Lutier 2002; Roberds and Strom 2006). While trees affected by fire appear to have increased resin defenses, bark beetles are still attracted to fire-injured trees. Understanding which type and severity of fire injury increases or decreases resin flow may increase understanding of post-fire bark beetle host-tree selection.

Post-fire management efforts would be enhanced with a better understanding of the effect of fire injury on ponderosa pine resin defenses and bark beetle brood production. The objectives of this study were to: 1) correlate post-fire resin production with ponderosa pine morphological and fire-injury variables through time, and 2) evaluate bark beetle attack preference, and brood production as a function of ponderosa pine fire-injury level.

Methods

Study Area and Plot Establishment

The Lolo study area is located approximately five miles Southwest of Missoula, MT, USA (UTM NAD83 Zone 11T, E` 716648 N` 5189963). This study area included one site, Black’s Mountain 2 (BM2), that is ~100ha within the boundary of the fall, 2003 Black’s Mountain 2 wildfire, and is characterized by a mixed ponderosa pine, Douglas-fir forest type. Site elevation is between 1,371 and 1,677m on predominately southeast facing slopes with east-facing microtopographic variation.

The Payette study area is located on the Payette National Forest, Krassel Ranger District, Valley County, Idaho, USA (UTM NAD27 Zone 11T, E`616332 N` 4979358). Within the study area are a ~300ha treatment site (Parks) that was prescribed burned in May 2004, and a ~300ha control site (Deadman) that was left unburned. The treatment and control sites were similar, characterized by mixed old growth ponderosa pine, Douglas-fir forest type with elevation ranging between 1,097 and 1,768m elevation. The presence of active bark beetle populations prior to the burns was determined using aerial detection survey ADS) data (USDA Forest Service, Forest Health Protection, http://www.fs.fed.us/r1-r4/spf/fhp/aerial/gisdata).

Plot Establishment and Measurement of Tree Variables

Fifteen plots were established in July 2004 within the BM2 burn boundary. At the Payette study area twenty-one plots were established throughout July and August 2004 on the burned site (Parks) and 20 on Deadman, the control plot. Plot establishment and data collection followed similar protocol at all sites. Burned and control sites at the Payette study area were selected to evaluate differences in post-fire bark beetle-attack pressure. Because of a concurrent, ongoing wildlife study (USDA, Forest Service, http://www.rmrs.nau.edu/lab/4251/birdsnburns/), sampling on the Payette was somewhat restricted, and all plots were established approximately 61m at random azimuths from existing wildlife plots. Trees could not be removed, and the use of pheromone-baited traps to assess local beetle populations was prohibited. Tenth acre (radius = 11.34m) plots were established on each site. If there was less than seven trees within a 10th acre plot, the plot was expanded to a 5th acre (radius = 16.06m) to increase tree sample size. All trees >9.9cm DBH within the selected radius were tagged, species recorded and numbered starting with the first tree right of the northern azimuth (declination was set to 0). Plot centers were recorded utilizing a Garmin, Etrex Legend GPS unit, as the distance and azimuth from the closest tagged tree. Photographs were taken 10ft to the north and south of every plot center with a digital camera to monitor post-fire vegetation.

Tree morphological traits and variables chosen for field measurement were representative of post-fire tree injury, and were selected from recent post-fire ponderosa mortality publications. All morphological variables were measured post burn, but were estimated as pre-fire measurements. All variables measured followed existing methodology (Fowler and Sieg 2004; Hood and Bentz 2007), with variable names and definitions standardized to Fowler and Sieg (2004) and described in Chapter 2.

MONTH, YEAR, diameter at breast height (1.4m on uphill side of tree) (DBH), tree height (TH), bole aspect (ASPECT), side of charring (CHAR SIDE), crown-base height (CBH), crown scorch height (CSH), percent crown scorch volume (CSV), percent bud kill (PBK), bark char severity (BCS), number of dead cambium quadrants (CKR), presence of bark beetles (ATK) were measured for every on-plot tree. Measurements were taken in late August every year starting in 2004 to ensure accurate fire-damage estimation and that beetle flight had occurred. All fire-injury measurements follow predetermined methodologies (Fowler and Sieg 2004; Hood and Bentz 2007; Chapter 2).

MONTH and YEAR were recorded every time resin flow was measured. Bark beetle attacks were recorded as present, or absent on every tree in each plot. DBH was measured to the nearest cm on the uphill side of the tree at 1.4m with a standard logger's tape. ASPECT was recorded when measuring cambium status, resin flow, bark char severity and bark beetle emergence. CHAR SIDE was noted when taking resin flow measurements, and was recorded as charred or uncharred on the side of induction. All height measurements were attained using a laser hypsometer (Opti-Logic Corporation, Tullahoma, TN), and was the distance from the ground on the uphill side of the root collar to the height of the desired measurement (crown base height, crown scorch height, and total tree height) Measurements were taken in feet and converted into SI to the nearest meter.

CSV, the percentage of needles scorched, and PBK, the percentage of buds killed, were estimated via ocular inspection of heat-damaged trees on a percentage scale of ten percent increments from 10-90 percent, and five percent increments from 0-10 and 90-100. Ten percent intervals were used to decrease subjective error among field technicians.

Bark char rating (CHAR) was rated in each quadrant between ground level and DBH based on qualitative bark condition as follows: 1) deep: the xylem is visible and charred; 2) moderate: bark is completely scorched, but retains a "characteristic" look; 3) light: minor charring on bark-- fissures not burned; 4) none: no visible char.

Cambium death was assessed by drilling 0.25 inch plugs from each of the four quadrants as close to the ground as possible with a gas-powered drill. The cambium is removed and noted as "dead" or "alive" based on phloem moisture and color (brown, dry, or resinous phloem is considered dead).

Additional variables created from field-measured variables were pre-fire live crown length, pre-fire live crown proportion and percent bole scorch. Equations used to calculate these variables are as follows:

LCL = crown base height – total tree height

LCP = LCL / total tree height

CHIP = ((char height quadrant 1) + (char height quadrant 2) + (char height quadrant 3) + (char height quadrant 4)) / total tree height.

All plots were revisited annually for two consecutive years to monitor tree mortality and bark beetle activity. To ensure that fire-damage and bark-beetle attacks were accurately estimated, fire injury measurements were collected in late August/early September, following peak bark beetle flight, on cloudless days.

Resin Flow Measurement

For this study, constitutive resin flow was defined as the resin exuded (ml) from an unwounded tree (Ruel et al. 1998) that occurred after fire, but before beetle attack (Wallin and Raffa 2001; Wallin et al. 2003). To account for natural within-tree variation of resin production (Roberds and Strom 2006), 2 volumetric measurements were made on every tree in late June, July, and August, 2 years (2005) and 3 years (2006) post fire using methods outlined in Zausen et al. (2005). Sample trees at each site were randomly selected from established plots based on biologically critical values of CSV (McHugh et al. 2003; Wallin et al. 2003) and CKR (Ryan and Amman 1994) to select trees within a continuous range of fire injury. To reduce among-tree variability, only ponderosa pine 20 to 46cm DBH were selected (Zausen et al. 2005). Control, unburned trees in the same DBH range were selected on the unburned Deadman (Payette study area) site and outside the BM2 burn area (Lolo study area).

In 2005 12 fire-injured trees on Parks and BM2 were selected along a continuum of fire-injured trees from established plots—3 each in 4 fire-injury categories—and were sampled 3 times throughout the summer. At each measurement period 5 new uninjured control trees were selected at the Deadman site and outside the BM2 burn boundary. New control trees were selected each measurement period because 4, 2.54cm measurements on the same tree over three induction periods would effectively girdle the trees, and could have artificially increased our constitutive resin measurements (Lombardero et al. 2006). Four samples were taken on each control tree to elucidate the variation among tree aspect without the confounding effect of fire.

In 2006, the design was slightly modified. Twenty fire-injured trees on Parks and BM2 were randomly selected as described above, and at each measurement period 2 samples on the north and south aspects were taken. Ten control trees at each study area were repeatedly remeasured with two new samples taken per measurement period on the north and south aspects. Additionally, 5 new control trees at each study area were selected each measurement period and 4 samples were taken on cardinal bole directions to determine among-aspect variation.

Resin flow was sampled on the burned and unburned sides of each tree bole (where possible) at 1.5m. Subsequent measurements were made a minimum of 3 cm to the right or left of the previous wound to minimize confounding of mechanically induced resin production (Lombardero et al. 2006). Bark beneath measurement areas was smoothed with a drawknife to create a flat surface against which collection tubes were secured. Care was taken not to puncture the phloem with the drawknife. A 2.54cm diameter arch punch was used to excavate a circular section of phloem and bark down to the xylem layer, but not into the xylem. Funnels were constructed out of clear silicon caulking 3 to 5ml directly below the bottom of the excised phloem directing resin into the vial. Two 5cm steel nails and an 8cm strip of plumbers tape adhered 50ml plastic graduated test tubes (Nalgene Corp. Rochester, NY) to sample trees, and remained on the trees for 24 hours (+/- 2 hours). *Pinus* resin flow quantity has been found to not significantly change between six and twenty-four hours (Santoro et al. 2001). Resin volume was measured ocularly to the nearest 0.5ml.

Field Measurement of Bark-Beetle Attack Preference and Brood Production

At each plot all trees were examined for bark beetle attacks by visually assessing the entire bole circumference as high as possible from the ground. Attack presence and success were assessed by looking for reddish boring dust in bark fissures and on the ground, presence of pitch tubes, and fading canopies. Beetle species were confirmed by removing bark sections to view gallery patterns and by collecting adult beetles for identification. Attacked trees were visually divided into quadrants on the cardinal directions and the percent circumference of bole attacked was estimated via ocular inspection of entrance/ventilation/exit holes, frass, and pitch tubes. Bole circumference attacked was measured on a percentage scale in five percent increments from 0-10% and 90 - 100%, and in 10% increments from 10 to 90%. Larger percentage increments helped mitigate subjective error between technicians. Height of beetle attack on each tree bole was also recorded.

All trees with successful attacks on > 96% of the bole circumference—i.e. successful entrance into the tree leading to gallery construction and oviposition—were recorded as mass attacked. Trees with ~ 1 to 95% of bole circumference showing signs of attack were recorded as strip attacked, and trees with no sign of attack or only a few pitch tubes were recorded as unattacked. Also, because beetle brood production, survival, and developmental rates are closely related to ambient air temperature (Bentz et al. 1991), temperature was recorded at each site (Onsite, Inc. Jacksonville, FL) throughout the season.

Preference of bark beetles attacking charred verses uncharred bole areas was measured by noting attack allocation in each bole quadrant. Each bole quadrant was recorded to have: 1) no attacks, 2) attacks in charred areas, or 3) attacks in uncharred areas. Aspect preference is inherent in the quadrant measurements.

Bark beetle brood production was measured as adult emergence into cages placed on fire-injured and unburned control trees infested with live beetle brood. All tree and fire-injury variables measured during plot establishment were available for caged trees located on established plots. Cambium condition (e.g. live or dead) on the same aspect as the cage (CKCS) and attack year (ATKYR) were also recorded for each caged tree. Cages were constructed of green screen material cut in dimensions of 42 x 74cm, which when mounted occupied a 30 x 60cm area. Screens were shaped at one end into a funnel and stapled together. Using scissors, a 2.5cm diameter hole was incised at the bottom of the funnel where a 50ml centrifugal tube was mounted with plastic twisty-ties. Three holes were poked into the bottom of each centrifuge tubes to allow water drainage. Selected trees were first inspected for an appropriate area to mount the cage. Cages were mounted over areas of obvious beetle attack and suspected developing brood. A 30cm (width) x 60cm (height) area of bark was pre-marked with a marker and smoothed with a draw knife. Care was taken not to remove too much of the bark, as western pine beetle-late larval instars, pupae, and developing adults occur in the outer bark. Cages were stapled to the tree so that there was a ~ 5cm gap between the bark surface and the cage. Aspect and height to mid cage was recorded; cages were assigned individual identification numbers. Two cages were placed on most trees, however some trees had up to 4 depending on tree size and accessibility.

Adult beetle emergence was monitored on a weekly basis. All beetles were collected and saved in self-sealing bags, returned to the laboratory in Logan, UT, and frozen. Date of collection, tree number, cage number, and site was recorded on each bag. Beetle species was identified using Wood (1982) and a microscope, and total number were recorded by date. Six infested trees not located on established plots were also caged to increase inference and sample size. All measurements taken for caged trees on plots were also recorded for off-plot cage trees.

Laboratory Measurement of Brood Production

Laboratory rearing of infested tree bolts was conducted as an additional measure of brood production. Burned and unburned beetle-infested trees were removed from the BM2 site and surrounding unburned stands (within .25 miles of the burn) in May 2005 and 2006. Selected burned trees for removal were representative of low to moderate fire injury classes. Infested unburned trees were also harvested. Felled trees were divided into 30.5-45.7cm bolts taken every 154.2cm along the stem starting with a bolt at ground level. Bolts were returned to the lab, and cut ends of bolts were sealed with paraffin wax to minimize desiccation. Each bolt was put in a rearing can, and placed in the lab at ~21°C.

To obtain the surface area of each bolt, diameter of the top and bottom, as well as height of each bolt was measured. Cylindrical surface area was calculated using:

$$2(\pi r^2) + r(2\pi r).$$

Beetle emergence from respective heights along tree boles was recorded daily. Archetypical specimens were collected, identified, and placed in the USDA Forest Service Project 4501 insect collection.

Data Analysis

Resin Flow Analysis

Significance of tree and fire-injury variables in explaining resin flow was analyzed using SAS (SAS Institute Inc. Cary, NC) version 8.6. To meet the assumption of normality and homoskedasticity, data were transformed using a cube root function. Univariate, mixed model analyses (MIXED) was used to narrow the number of variables considered. Significant (α=0.05), and biologically important variables were then analyzed for correlation. Variables with Pearson correlation coefficients greater than or equal to 0.75 were considered highly correlated, and were eliminated based on statistical and biological importance.

Variables found to be significant in the univariate analyses were then analyzed collectively, testing for significance in explaining resin flow (MIXED). All main effects and interactions were analyzed using a general Satterthwaite approximation for denominator degrees of freedom (DDFM=SATTERTH), while levels of discrete, nominal (CLASS) variables were tested using Tukey's Honestly Significant Differences, adjusted least squared means (LSMEANS, ADJUST=TUKEY) and contrast analyses

(CONTRAST). To acquire model convergence, a simple covariance structure was selected—TYPE=CS (compound symmetry). Repeated tree-level (SUBJECT=tree(study area)) resin measurements for each month by year were accounted for using the REPEATED command. Study area (e.g. Payette or Lolo) and tree were declared as random effects (RANDOM). Control (unburned) and fire-injured trees were analyzed together to test for significant difference in resin flow, and separately to test for the effects of morphological and fire injuries on measured resin flow (MIXED). Differences in resin flow between charred and uncharred sides of trees was tested using a multivariable ANOVA analysis (MIXED).

Beetle-Attack Preference and Emergence

Contingency table analysis using a Chi-Square test for significance (LOGISTIC) was used to test for differences in the binary response variable, beetle attack absence/presence, between charred and uncharred areas of fire-injured tree boles. Differences in number of beetles emerging among all morphological and fire-injury characteristics was tested using the GLIMMIX macro with a Poisson distribution corrected for overdispersion, and study area as a random variable. Tukey's Honestly Significant Difference multiple comparison procedure was used to test for significant differences among nominal variables, and F-tests were used among continuous variables.

Results

General Site Statistics

Five hundred seventy-three ponderosa pine were assessed at 3 (1 control and 2 burned) sites. Twenty-one plots were established on Parks, 20 on Deadman, and 15 on

BM2. No statistical differences were observed in mean DBH and total height (TH) of trees at the 2 sites in the Payette study area (e.g. Parks and Deadman). All variables except pre-fire live crown proportion were significantly different ($\alpha=0.05$) between all trees, live trees, and dead trees on BM2 and Parks.

Of 459 trees measured on the two burned sites (e.g. Parks and BM2), 201 trees (44%) were dead after 3 post-fire growing seasons. Mean morphological and fire injury measurements between live and dead trees on burned sites varied (Table 3.1). Measures of crown damage and bole damage—GIRD, CKR and CHIP—also varied among live and dead trees on burned sites (Table 3.1).

Resin Flow

In post-fire years two (2005) and three (2006) a total of 141 trees were sampled for resin flow volume (ml). Because of a wildfire in the study area, the 2006 August resin flow samples at Parks and Deadman were not completed. Differences in resin flow were not significant between the two study areas (e.g. Lolo and Payette), therefore analyses were conducted on data pooled for both sites.

When both sample years were pooled, resin flow volume of burned trees was significantly greater and more variable (mean=12.89, SD=11.85) than unburned trees (mean=8.31, SD=5.90) ($t_{1,\,151}=2.42$, P=0.0166) (Figure 3.1). Resin flow of both burned and unburned trees was greater in post-fire year 2 (2005) than year 3 (2006), although not significantly for burned trees ($t_{1,\,146}=1.89$, P=0.0606) (Figure 3.2). In 2005, resin flow of burned trees significantly increased between June and July ($t_{1,\,52}=2.50$, P=0.0403), but not in 2006. In 2006, resin flow of unburned trees increased significantly between June and

July ($t_{1,\,27.2}$=4.12, P=0.0009), and June and August ($t_{1,\,30.1}$=4.57, P=0.0002), although no significant differences were observed in 2005 (Fig. 3.2).

Univariate analyses found no significant differences in resin flow between charred and uncharred sides of burned trees, ($t_{1,\,324}$=-0.26, P=0.7957). Of all variables tested, only LCL, TH and DBH were significant in explaining differences in resin flow of burned trees (α=0.05). Resin flow of burned trees was greatest on large trees and trees with more pre-fire live crown length. Resin flow of unburned trees was significantly less on the north bole aspect than the south, and no other significant differences were observed for variables measured.

Pearson correlation analysis of all significant continuous covariates selected for multivariate analysis showed that pre-fire live crown length (LCL) was highly correlated with tree height (TH) (Pearson Corr. Coeff = 0.7956). Pre-fire live crown length was considered more biologically important as a measure of overall tree vigor than tree height because of its influence on total photosynthetic volume, and was hence selected. Results from mixed-effect analysis suggest that resin flow of unburned trees is significantly different among months, years, bole aspect and LCL. These analyses also suggest that resin production of unburned trees was greater in 2005 than 2006, and greater in July than June, and August than June. Resin flow of unburned trees was also significantly greater on the south and west bole aspects than the north and was positively correlated with LCL.

Mixed model results of burned tree resin flow volume showed that only MONTH and LCL were significantly different (α=0.05). Resin flow of burned trees increased between June and August when aggregated over both years. Similar to resin flow of unburned trees, resin flow of burned trees was greatest in trees with greater LCL.

Bark Beetle-Attack Preference

On trees within plots established at burned sites BM2, Parks and the unburned control Deadman, there were significantly more bark beetle attacks on burned trees than on control trees ($\aleph^2 = 57.9360$, $P < .0001$). There were a greater number of mass and strip bark beetle-attacked trees at the BM2 site than the Parks site ($\aleph^2 = 22.1148$, $P < .0001$) (Table 3.6). No bark beetle attacked trees were found on established plots at the unburned site (Deadman). Of 430 fire-injured ponderosa pine trees, 134 (31 %) were either mass (61, 14%) or strip (73, 17%) attacked by bark beetles. Of all attacked fire-injured trees, 64 (48%) were attacked by *D. ponderosae* (all *D. ponderosae* attacks occurred on BM2), 41 (31%) were attacked by *D. brevicomis*, 17 (13%) were attacked by *Ips pini* or *emarginatus* and 11 (8%) had some mix of the four species (Table 3.2). *Ips emarginatus* and mountain pine beetle have similar gallery patterns, some of the attacks recorded as mountain pine beetle may actually have been *Ips emarginatus* attacks, and visa versa. Red turpentine beetle (*D. valens*) was present on 97 (23%) trees. The majority of attacks at the BM2 site occurred one year (2004) after the 2003 August burn, although the greatest number of attacked trees at the Parks site were observed 2 years (2005) after the May 2004 prescribed burn. Wood-boring beetles (Cerambycidae and Buprestidae) were observed on fire-injured trees, however were not quantified.

Of the 459 fire-injured trees that showed signs of bark beetle attack, significantly more attacks were located within scorched areas of tree boles than unscorched ($\aleph^2_1=20.8$, $p<0.0001$) (Table 3.3).

Bark Beetle Brood Production

Of 114 ponderosa pine on BM2 that were strip or mass attacked in 2004 by a primary bark beetle, only 16 were sampled. The remaining 97 trees attacked by bark beetles had either high or complete brood mortality, or were too small to sample. At the Parks site, some off-plot, large diameter, fire-injured, mass-attacked trees had sour sap (*sensu* Miller and Patterson 1927), killing all western pine beetle brood. Woodpecker foraging was very high in attacked trees throughout all burned plots at both study areas. High levels of Clerid species (Coleoptera: Cleridae) were observed on newly attacked trees in 2005 at the Parks site (R.S., Davis, unpublished data).

Sixty-nine, $1858 cm^2$ emergence cages were hung on ponderosa pine at the study areas combined. At the Lolo study area, 18 cages were placed on 12 burned trees and 13 cages were placed on 4 unburned control trees. At the Payette study area 34 cages were placed on 17 burned trees and 4 cages on 2 unburned control trees. Surface area of infested trees removed from the Lolo study area to monitor adult emergence in the laboratory, were calculated and then standardized to $1858 cm^2$ for analysis.

When all bark beetle species were combined, no significant difference in the number of beetles emerging was observed between burned and unburned trees. For all bark beetle species combined for BM2, there was significantly more bark beetle emergence from unburned trees than burned trees ($t_{1, 33}$=-3.53, P=0.0012) (Table 3.4). When all bark beetle species were combined for Parks, significantly more bark beetles emerged from unburned than burned trees ($t_{1, 36}$=2.13, P=0.0403) (Table 3.4).

When combined sites were examined by beetle species, significantly more Ips (a majority *Ips pini*) emerged from unburned than burned trees ($t_{1, 24}$=-3.32, P=0.0029) and more western pine beetles emerged from burned trees than unburned trees ($t_{1,\ 69}$=2.16, Adjp=0.0339) (Table 3.4). Although a relatively large number of trees were attacked by mountain pine beetle at the BM2 site (Table 3.2), adult emergence from these trees was minimal. Significantly more beetles of all species emerged from trees at the Parks site than from trees at the BM2 site ($F_{1,\ 59.0}$=12.80, p=0.0007) (Figure 3.3). None of the tree and fire-injury variables tested were significant in explaining emergence of bark beetles from burned and unburned trees at the two study areas.

There were no significant differences in number of beetles emerged from burned and unburned trees at the Parks site when western pine beetle and mountain pine beetle were combined, and both *Ips. Spp* were combined. However, at the BM2 site, significantly more *Ips* (majority *Ips pini)* emerged from unburned than unburned trees ($t_{1,\ 24}$=-3.32, Adjp=0.0029) and more western pine beetles emerged from burned trees than unburned trees ($t_{1,\ 33}$=-1.95, Adjp=0.0597).

Discussion

Post-fire constitutive resin flow was significantly higher in fire-injured ponderosa pine than in unburned control trees two and three years after fire. These results are consistent with other post-fire resin flow studies (Harper 1944; Feeney et al. 1998; Santoro et al. 2001; Wallin et al. 2003; Lombardero et al. 2006; Perrakis and Agee 2006). Although Lombardero et al. (2006) observed differences in charred and uncharred sides of fire-injured red pine 55 days following fire, resin flow of fire-injured ponderosa pine in this study did not vary by burned versus unburned sides of trees. Differences in this study may be due to the methodology employed to simulate ground fires on sampled red pine, which may not replicate the pattern of mixed severity fire- injury observed on ponderosa pine at the Parks and BM2 study sites.

Different from Cunningham's 1955 study of ponderosa pine-resin production, resin flow on the north bole aspect was significantly less than the south bole aspect of unburned trees. This phenomenon could have been a product of temperature and resin viscosity (Hodges et al. 1979), as the north sides of trees generally receive less direct radiation. This effect, however, was not observed on burned trees, as north bole aspects yielded similar resin volumes as the south bole aspects. This increased resin flow may be attributed to increased fire injury, as the north bole aspect was generally the uphill side of trees on both study areas. An increase in resin flow throughout the summer growing season on unburned trees agrees with previous research (Callaham 1955; Tisdale and Nebeker 1992; Perrakis and Agee 2006) and may be associated with moisture regimes (Blanche et al. 1992; Dunn and Lorio 1993). In general, it appears that genetic and environmental effects on resin flow are superseded or exaggerated by host response to fire injury, as seen by the loss of the aspect effect on burned trees.

For unburned and burned trees, pre-fire live crown length was positively correlated with resin flow. This variable is a measure of overall tree vigor. LCL's close relationship with tree height and DBH suggests that it is a relative measure indicating dominance, co-dominance, intermediate or suppressed/understory status. Trees with larger pre-fire live crown length likely have greater access to water, nutrients and light, giving them more resources for post-fire secondary metabolism (Wilkens et al. 1997).

Many studies agree that bark beetle attack increases post fire tree mortality (Miller and Patterson 1927; Herman 1950; Peterson and Arbaugh 1986, 1989; Amman

1991; Amman and Ryan 1991; Ryan and Amman 1994, 1996; Rasmussen et al. 1996; Bradley and Tueller 2001; McHugh et al. 2003; Schwilk et al. 2006; Sieg et al. 2006; Hood and Bentz 2007). A paradox applicable to our findings, set forth by Santoro (2001), follows observations and data from prior studies examining post-fire bark beetle activity and resin production (Feeney et al. 1998; Wallin et al. 2003; Lombardero et al. 2006; Perrakis and Agee 2006): why would bark beetles preferentially attack burned trees within fire boundaries, when fire-injured trees appear to have greater resin defenses than concomitant control trees?

Bark beetle-attack frequency generally increased within burned areas, however, beetles may have been selecting fire-injured trees with less resin storage and reduced resin production capacity. Beetles may also be able to select trees with less toxic monoterpene ratios (Smith 1965, 1966) leaving resistant trees unattacked. Bark beetles have selective abilities allowing them to identify, attack, aggregate and colonize susceptible trees (Smith 1966; Wood 1982; Hynum and Berryman 1980; Raffa and Berryman 1982). Slight (albeit statistically different) differences in mean resin flow might be unimportant to beetles because of several adaptive strategies including 1) attack density modification given a tree's resistance (Berryman 1972), 2) utilization of host resin in pheromone production (Silverstein 1969; Hughes 1974; Borden 1974; Hughes and Renwick 1977), 3) tolerance to specific host-resin compounds (Smith 1966), 4) the ability to "swim" through host resin (Lutier 2002), 5) removal of large resin quantities by bark beetles for extended periods (Callaham 1955), 6) delayed oviposition until host resin canals have been drained (Raffa and Berryman 1987), and 7) avoidance of preformed defenses (Ferrell 1983; Lutier et al. 1995).

Another hypothesis is that fire-injured trees/areas concentrate surrounding beetle populations creating an ephemeral, but epidemic-level population within fire boundaries (Miller and Keen 1960). The flood of beetles may enable them to overcome better-defended trees, increasing the frequency of beetle-caused tree mortality within the burned area. Classic host-insect population dynamic models infer that resin defenses are a type of intolerant population mediator (Berryman 1982). If bark beetles aggregate to fire-affected areas then host-tree resin defenses that maintained beetle populations at endemic levels (tolerant) become less effective (intolerant) in the presence of elevated beetle numbers. However, increased numbers of beetles that would be needed to overcome well-defended trees (including fire-injured trees with increased resin flow) might reduce brood production as part of density dependent, intraspecific competition for host resources (Raffa and Berryman 1983). The reduced number of mountain pine beetle emerging form attacked trees observed in this study partially agrees with this reasoning. However, the increased number of western pine beetle emerging from trees compared to unburned trees potentially suggests that western pine beetle has coevolved reciprocal adaptations to the effects of fire on tree resin defense systems.

Majority of bark beetle attacks on fire-injured trees occurred within charred areas, which has been previously observed in red pine (Santoro et al. 2001; Lombardero et al. 2006). Charred bole areas mostly occur near the base of tree boles. Bark beetles attacks in bole-charred areas might be confounded with a lower resin flow production compared to the rest of the tree bole length, however consistent results on resin flow by tree height have not been produced (Callaham 1955; Tisdale and Nebeker 1992; Schmitt et al. 1988;

Roberds and Strom 2006). It is more likely that beetles are cuing in on host volatiles produced in bole-charred areas and the dark color of bole char.

Although mountain pine beetle attacks on fire-injured trees are considered uncommon (Hopkins 1905; Blackman 1931; Geiszler et al. 1980; Amman 1991), mountain pine beetle was found attacking both burned and unburned trees at the BM2 site. However, as seen in other studies (Amman and Ryan 1991; Ryan and Amman 1994) mountain pine beetle was almost always associated with Ips species and western pine beetle. This may have been a result of flight timing. Ips species and western pine beetle emerged from brood trees and colonized new susceptible trees before mountain pine beetle flight, dominating the resources within a tree. Also, at the BM2 site, mountain pine beetle requires an entire year to complete a generation while Ips species and western pine beetle have at least 2 generations per year. High interspecific competition with *Ips* and western pine beetle, and slower mountain pine beetle development time most likely negatively affected mountain pine beetle brood production.

When all species were combined, numbers of adult brood emerging from burned and unburned trees was not significantly different. These results suggest that fire-injured trees do not act as population sinks. However, the larger trees at the Parks site, where western pine beetle attacked more burned trees, and emergence was greater from burned trees, the fire-injured trees may indeed be considered a population source. Additional years of data would need to be collected to evaluate if the western pine beetle populations in this area continued to grow or decline.

Brood survival may be caused by one, or a combination of phloem desiccation/quality, “sour sap,” inter- and intraspecific competition, predation and/or low winter temperatures. Miller and Patterson (1927) found that brood survival in burned ponderosa pine decreased 7.7%, whereas populations developing in unburned trees increased 318%. Those results are commensurate with bark beetle emergence from fire-injured trees at the BM2, likely because those trees were much smaller and had greater fire injury than trees at the Parks site. Maybe beetles did better at the Parks site because the trees were larger and fire injuries were not as severe.

Increased resin production as a host defense is widely accepted (Stark 1965; Hodges et al. 1977, 1979; Cook and Hain 1987; Nebeker et al. 1988; Lorio et al. 1995; Strom et al. 2002), but it may be less important than believed. The very complex bark beetle-host relationship is still not well understood (Strom et al. 2002). For logistical reasons, most resin flow studies have limited their resin sampling to the lower bole. Resin flow results from non fire-injured, ponderosa pine and loblolly pine indicate that resin flow tends to be highest at the lower part of the bole, least in the middle of the bole, and moderately more toward the top (Callaham 1955; Tisdale and Nebeker 1992), however resin flow is likely more variable between trees than within trees (Schmitt et al. 1988; Roberds and Strom 2006). Because bark beetles attack trees at heights along the entire bole surface, future studies should incorporate resin flow measurements along the whole tree bole, as perceived increases in resin flow might be localized to the lower bole, especially in fire-injured trees.

While not evaluated in this study, tree resistance to bark beetle attack is also affected by monoterpene ratios and concentrations (Smith 1961, 1965, 1966; Reid and Gates 1970; Raffa et al. 1985; Raffa and Smalley 1995; Lutier 2002). In 1966 Smith (Forest Science) found that the difference in monoterpene concentrations between pitch tubes on living and beetle-killed trees was significantly different, with living trees having a greater amount of limonene plus myrcene. Evidence also suggests that historic attack pressure exerted on ponderosa pine trees throughout their range by bark beetles correlates to an increase in the ratio of monoterpenes considered detrimental to scolytine beetles (Smith 1977; Sturgeon 1979).

Ideally, pre- and post-fire monoterpene analysis would be conducted to evaluate how resin toxicity is affected by fire and bark beetle-attack history. Ideally, future resin flow studies should also include resin measurements in milliliters and grams as there is likely a non-linear relationship between resin flow volume and weight. No correlation has been drawn between resin volume, weight and monoterpene concentration, yet both weight and volume as measures of resin defenses are still used. Host resistance is extremely complex and highly variable; by standardizing our resin measurement protocol and dealing with each tree species and associated bark beetle species separately, perhaps we can gain a greater understanding of this complex system.

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Table 3.1. Mean, standard error, and range for tree and fire-injury variables of live and dead ponderosa pine 3 yrs post-fire in plots located within the boundary of a wildfire (BM2) and a prescribed burn (Parks).

	Live Trees (N=182)			Dead Trees (N=253)		
Variable *	Mean	SE	IQR	Mean	SE	IQR
DBH(cm)	37.12	1.13	24.1-45.7	21.47	1.09	11.7-25.2
TH(m)	20.77	0.46	15.2-26.5	13.48	0.47	8.5-16.8
CBH(m)	7.61	0.25	4.9-9.5	5.91	0.24	3.7-7.9
PSL(%)	0.45	0.02	0.2-0.7	0.81	0.02	0.7-1.0
SH(m)	8.54	0.39	3.9-12.2	10.09	0.33	7.6-12.2
CSV(%)	0.31	0.02	0.05-0.5	0.77	0.02	0.5-1.0
PBK(%)	0.17	0.01	0.0-0.3	0.67	0.02	0.4-1.0
GIRD(%)	0.23	0.02	0.0-0.4	0.76	0.03	0.5-1.0
CHIP(%)	0.09	0.01	0.03-0.1	0.24	0.02	0.1-0.3
CKR	1.01	0.07	0.0-2.0	2.98	0.1	2.0-4.0

*DBH = diameter at breast height, TH = tree height, CBH = crown base height, PSL = percent scorch length, SH = scorch height, CSV = percent crown scorch volume, PBK = percent bud kill, GIRD = percent basal girdling, CHIP = bole scorch percent, and CKR = number of killed cambium quadrants. IQR is the inter-quartile range, or the range of values for a specific variable between the 25th and 75th percentiles.

Table 3.2. Number of ponderosa pine attacked by bark beetles at 2 burned areas, BM2 and Parks 3 years post-fire. IPS = *Ips Pini* and *I. emarginatus*; MPB = *Dendroctonus ponderosae*, WPB = *D. brevicomis* and Mix = some combination of the three beetle groups.

	2004*			2005			2006			
	Mass	Strip	Total	Mass	Strip	Total	Mass	Strip	Total	Total
BM2										
IPS	17	0	17	0	0	0	0	0	0	17
MPB	12	55	67	0	0	0	0	2	2	69
WPB	11	8	19	2	0	2	0	0	0	21
MIX	6	5	11	0	0	0	0	0	0	11
Total	46	68	114	2	0	2	0	2	2	116
Park's										
IPS	1	0	1	0	0	0	1	0	1	2
MPB	0	0	0	0	0	0	0	0	0	0
WPB	5	4	9	26	2	28	3	1	4	41
MIX	0	0	0	0	0	0	0	0	0	0
Total	6	4	10	26	2	28	4	1	5	43

*2004 totals represent the number of trees attacked by bark beetles 1 year post-fire. At BM2, the 2004 bark beetle survey was 8 months after an August fire; at Parks, the 2004 survey was 3 months following a May fire.

Table 3.3. Contingency table of bark beetle attack frequency within burned and unburned ponderosa pine bole aspects. Bole quadrant burned = 1 and unburned = 0; bark beetle attack presence within bole quadrant = 1, and unattacked = 0. Chi-Square test for differences in attack presence among burned and unburned quadrants was significant (df = 1; Chi-Square value = 20.7944 and P < 0.0001).

		Burned		
	Attack	No	Yes	Total
Frequency	No	4	128	132
Percent		0.59	18.93	19.53
Row Percent		3.03	96.97	
Column Percent		3.67	22.57	
Frequency	Yes	105	439	544
Percent		15.53	64.94	80.47
Row Percent		19.3	80.7	
Column Percent		96.33	77.43	
	Total*	109	567	676
		16.12	83.88	100

Table 3.4. Mean bark beetle emergence from burned and unburned ponderosa pine from the Lolo and Payette study areas by bark beetle species. Mean emergence counts are for standardized 1858cm^2 sample areas.

	Burned			
	I. pini	I. emarg.	D. pond.	D. brev.
BM2	1.8	1.6	5.7	10.1
Parks	4.3	1.6	0	110.2
	Unburned			
BM2	37.9	3.1	6.9	26.3
Parks	0	8.5	0	16

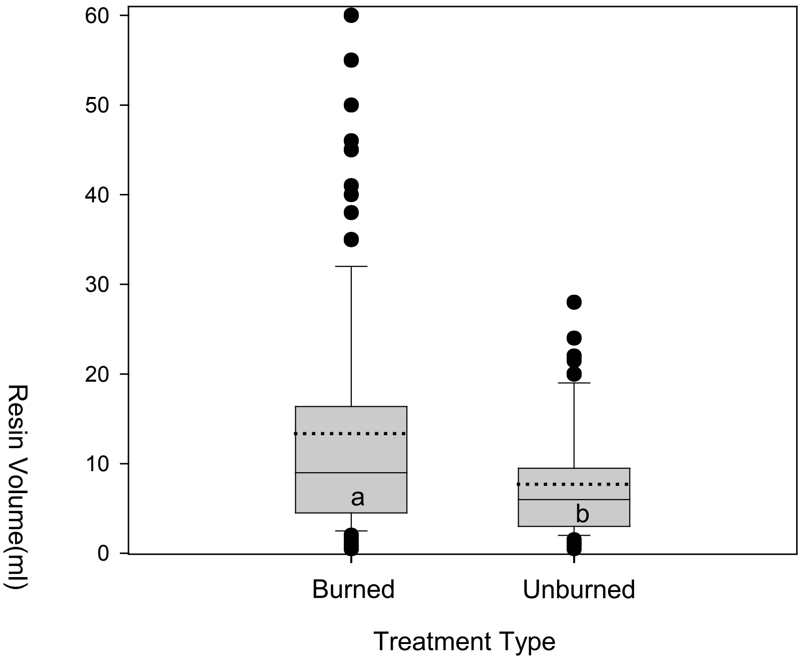

Figure 3.1. Resin flow volume (ml) of burned and unburned ponderosa pine at the Lolo and Payette study areas. Different letters indicate significant differences (α=0.05) in resin flow volume. Shown are outliers beyond the 75th percentile, whiskers indicate the 90th and 10th percentiles, and the mean (dotted line) and median (solid line).

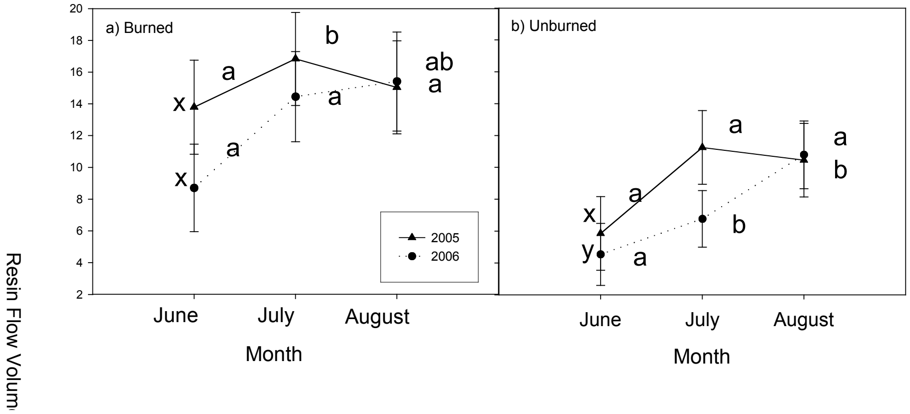

Figure 3.2. Resin flow volume (ml) of a) burned and b) unburned ponderosa pine at the Lolo and Payette study areas 2 years (2005) and 3 years (2006) post-fire. Within year, month of induction with different letters are significantly different (α = 0.05). Aggregated resin flow by year is significantly different between x and y (α = 0.05).

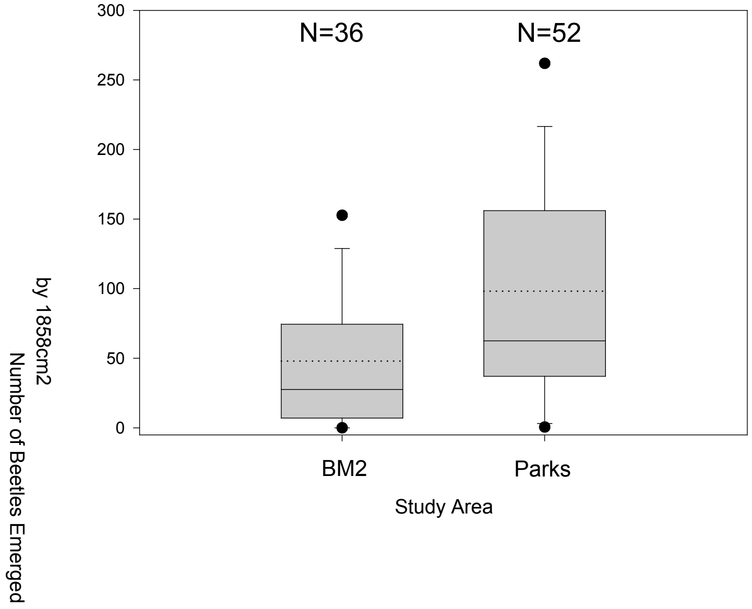

Figure 3.3. Beetle emergence by study area. Upper and lower dots represent the 95th percentiles, and the upper and lower whiskers represent the 90th and 10th percentiles. The upper, middle and lower sections of the main box represent the 75th, 50th and 25th percentiles, respectively. The dotted line is the mean and the solid line is the median. N is the number of samples including cages and ponderosa pine bolts sampled in the lab, standardized to 1858cm^2.

CHAPTER 4

SUMMARY AND CONCLUSIONS

Two predictive post-fire ponderosa pine mortality models were presented. At a probability cutoff of P(m) = 0.60, these models are capable of correctly predicting between 81% and 84% ponderosa pine mortality. These models add to a large base of post-fire tree mortality models, but are specific to *Pinus ponderosa* subsp. *ponderosa* Doug. ex. Laws, especially in mixed Douglas-fir stands of western Montana and central Idaho, USA.

Two post-fire bark beetle-attack probability models were also presented. Post-fire bark beetle-attack modeling for ponderosa pine in the western United States using a variety of fire-injury, morphological and time variables had not been previously accomplished. Classification tables show that models predicting post-fire bark beetle attack are not as accurate as those for tree mortality. At a probability level of P(a) = 0.60, the models only correctly predict between 14% and 17% of bark beetle attacks. More accurately, trees correctly predicted as unattacked at P(a) = 0.60 might give managers an indication of which trees are likely to remain unattacked.

Using the specific fire-injury and tree morphological variables of diameter at breast height, percent bud kill and bole scorch proportion (and/or cambium kill rating) will allow managers to assess which trees will likely be bark beetle-attacked (or unattacked) post fire. Initial harvesting guidelines could be made based on the bark beetle-attack probability models and then augmented by using the tree mortality models. Trees with high bark beetle-attack probabilities could be entered into the tree mortality model as attacked trees, thus giving a more accurate estimate of potential tree mortality from fire injury and bark beetles.

Many observations of post-fire bark beetle activity indicate that certain species are attracted to fire-injured trees. Data from this study corroborates those observations. It appeared that fire-injured ponderosa pine on BM2 acted as a population sink for bark beetles, while results from Parks show an opposite trend in terms of bark beetle emergence. Whether or not this was truly the case, the frequency of attacks by the 3rd post-fire year on both sites dramatically declined, indicating there was an initial surge in beetle population that was greatly reduced within 3 years. Larger sample sizes of bark beetle productivity data are needed to truly realize the effect of fire-injury on brood production, including: accurately counting bark-beetle attacks per given area, separating re-emerged adult beetles from newly emerged brood adults, and estimating ovipositional success by counting the number of eggs deposited by each female.

Ponderosa pine resin defenses may be the key to understanding bark beetle-host selection and success, especially in the post-fire environment. It has been shown that resin production increases in many tree species when they are mechanically wounded, inoculated with blue-staining fungus, or are treated with fire. The effect of resin volume on attacking bark beetles may be evidenced by the general observation that larger beetle populations usually present within 1 post-fire year usually curtail within 3 to 4 post-fire years. Resin flow as a measure of host defenses must become standardized. Future resin flow research should regress resin flow volume against weight to test if they are interchangeable measurements. In addition, chemical analysis of resin should become standard protocol when feasible. Specifically, future post-fire resin research needs to address resin chemical composition immediately before and after fire to identify, if any, changes in the concentrations or principal components of resin.