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Title: Prescribed Fire in a Ponderosa Pine Stand in the Blue Mountains, Oregon: Relationships among Post-Fire Scolytidae Incidence, Delayed Tree Mortality, Snag Decay Dynamics, and Woodpecker Snag Use.

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Delayed tree mortality is an unpredictable occurrence when prescribed burning is implemented. Fire scorched trees may die as the result of crown scorching, stem charring, root injury, bark beetle attack, or through a combination of these factors.

This study examined ponderosa pine mortality and the incidence of two bark beetle species (*Dendroctonus brevicomis* LeConte and *Ips pini* Say Coleoptera: Scolytidae) following spring and fall prescribed burning on four replicated ponderosa pine stands. There was a positive linear relationship for total tree mortality and Scolytidae incidence with stem char height. No relationship in total tree mortality or Scolytidae incidence was observed between seasons of burn when accounting for stem char height. The presence of established bark beetle galleries was negatively correlated with external stem charring within destructively sampled ponderosa pines that died following burn application.

In a related study, woodpecker use and decay dynamics of ponderosa pines dying post-fire were assessed. Woodpecker bark foraging was closely associated with the presence of bark beetles and woodborers (Coleoptera: Buprestidae and Cerambycidae). There was a positive linear relationship between woodpecker cavity excavation and snag DBH. The probability of a snag possessing a woodpecker cavity was significantly greater if the snag had sustained a broken top. Wood deterioration within destructively sampled ponderosa pine snags was negatively influenced by charring sustained to the bark in comparison to uncharred portions of the tree.

Prescribed Fire in a Ponderosa Pine Stand in the Blue Mountains, Oregon: Relationships among Post-Fire Scolytidae Incidence, Delayed Tree Mortality, Snag Decay Dynamics, and Woodpecker Snag Use.

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Michael Kangas, Author

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CHAPTER 1. BACKGROUND AND OBJECTIVES

BACKGROUND

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is a conifer with a wide geographical range in western North America, covering nearly 40 million acres (Arno 1995). Typically it is found on warm dry sites characterized by a short growing season and minimal precipitation. The successional status of ponderosa pine is greatly influenced by the moisture conditions of the site. It is often a climax dominant species on dry sites and an early seral species eventually being replaced by more shade-tolerant species on mesic sites (Agee 1993).

Fire favors fire-tolerant trees such as ponderosa pine in western North America forests. The autecological adaptations of ponderosa pine such as thick bark, branch-free boles, and deep roots make the species more able to withstand frequent low-intensity surface fires than other conifers (Burns and Honkala 1990, Agee 1993, Weaver 1959).

The ponderosa pine communities of the western United States have experienced great ecological changes as the result of fire suppression in the past century. Conventional forestry of the early 1900s viewed fire as an undesirable occurrence in the management of fiber (Mutch 1993). The 1930s saw the first organized efforts to control fire in these western forest communities. In the absence of frequent fires, species that are less tolerant to fire and more tolerant of shaded light conditions than ponderosa pine survive in the understory (Agee 1993, Fiedler 1996). These shade-tolerant species provide a vertical avenue for the spread of fire and compete for resources with the dominant ponderosa pines in the stand. On resource-limited sites this contributes to the physiological stress of dominant ponderosa pines and may increase their susceptibility to insects and pathogens (Fiedler 1996, Arno 1995).

The structural changes to these forests including increased canopy closure, stand density, surface fuel loads, and vertical fuel continuity, have created conditions conducive to stand replacement wildfires. In a sense, the fire regime in ponderosa pine forests has shifted from frequent, low-intensity surface fires to infrequent, stand-replacing fires (Mutch 1993) resulting in the loss of timber resources, rural homes, and human lives.

Prescribed fire and thinning have been employed to reduce fuel loads and mimic processes associated with the historical fire regime (Mutch 1993, Fiedler 1996). Prescribed burning (or prescribed fire) is the controlled application of fire to wildland fuels in either their natural or modified state under specific environmental conditions to produce desired fire behavior. The use of prescribed burning has important implications for natural regeneration (Hasse 1986), nutrient cycling (Covington 1990), and forest protection (Fiedler 1996). Although thinning may eliminate the vertical avenues for fire spread, high fuel loads may still exist in the form of litter and down woody fuels. Potential tree mortality from increased fire intensity due to high fuel loads has prompted managers to burn in early spring or late fall when weather conditions reduce fire intensity (Harrington 1987, Swezy and Agee 1991).

Even when such precautionary measures are taken, some tree mortality can be expected when prescribed fire is used. Crown injury (Harrington 1987, Wyant et al. 1986, Peterson 1985), cambial and stem injury (Wyant et al. 1986, Dixon et al. 1984), root injury (Swezy and Agee 1991) and combinations of these can result in the eventual death of a tree (Wyant et al. 1986, Dixon et al. 1984). Often these physical injuries may predispose a tree to bark beetle (Coleoptera: Scolytidae) attack and eventual tree death (Dixon et al. 1984, Geiszler et al.1984). Two common bark beetles identified in fire-injured ponderosa pine are the western pine beetle (*Dendroctonus brevicomis* LeConte) and pine engraver beetle (*Ips pini* Say) (Furniss and Carolin 1977). Despite the widespread use of prescribed burning, little information exists on the incidence of these bark beetles following implementation of this management practice.

In contrast to concerns of delayed tree mortality, the importance of snags (standing dead trees) for wildlife are continually being recognized (Bull et al. 1997). Of the 80 species of wildlife associated with snags in the western United States, the family Picidae (woodpeckers) stands out. Woodpecker foraging may help to reduce timber losses through predation on bark beetles (Koplin 1970, Otvos 1970, Kroll et al. 1980). In addition, secondary cavity nesting birds and several small mammals use old, abandoned woodpecker cavities for nesting purposes (Bull et al. 1997, Saab and Dudley 1997, Li and Martin 1991).

The common use of prescribed fire and annual acreage of forestland burned by wildfire in western North America suggest that fire and associated beetle caused mortality will continue to be common components of these ecosystems. Information regarding delayed tree mortality, bark beetle incidence, and corresponding cavity-nester use of these snags may help in determining appropriate post-burning treatments for pest management and snag dependent wildlife.

OBJECTIVES

There were two areas of concentration for this research. The first centered on delayed tree mortality and bark beetle incidence following prescribed fire. The objectives of this study were three-fold: 1) Quantify ponderosa pine mortality following prescribed fire based on stem charring, 2) Determine how stem charring and the season of burn application influenced the predicted Scolytidae incidence (for the western pine beetle and the pine engraver beetle) throughout a stand of ponderosa pine, and 3) Determine how stem charring potentially influences host resistance and subsequent establishment patterns of Scolytidae within ponderosa pine dying post fire.

There are 2 objectives for second area of concentration of this study: 1) Quantify the extent to which fire charring to the tree stem influences snag decay rate, specifically top breakage and wood deterioration, and 2) Quantify woodpecker snag use of ponderosa pine trees that died post-fire, specifically the type of woodpecker bark foraging relative to subcortical insect type and woodpecker cavity excavation relative to snag characteristics (DBH, top condition, and decay rate).

CHAPTER 2. POST-FIRE DELAYED TREE MORTALITY AND SCOLYTIDAE INCIDENCE STUDY

INTRODUCTION

Prescribed fire and thinning have been employed to reduce fuel loads and mimic processes associated with the historical fire regime in ponderosa pine ecosystems (Mutch 1993, Fiedler 1996). Prescribed burning is the controlled application of fire to forest fuels in either their natural or modified state under specific environmental conditions to produce desired fire behavior and meet management objectives. The use of prescribed burning has important implications for natural regeneration (Hasse 1986), nutrient cycling (Covington 1990), and forest protection (Fiedler 1996).

Even when precautionary measures are taken such as burning in early spring or late fall when weather conditions reduce tree mortality (Harrington 1987, Swezy and Agee 1991), some tree mortality can be expected. Extensive fire injury may cause immediate tree mortality, however, some fire-injured trees may persist for several years before succumbing to death. Factors such as crown injury (Harrington 1987, Wyant et al. 1986, Peterson 1985), cambial and stem injury (Wyant et al. 1986, Dixon et al.1984), root injury (Swezy and Agee 1991) and combinations of these can result in eventual tree death (Wyant et al. 1986, Dixon et al. 1984). Often such fire injuries may predispose a tree to bark beetle (Coleoptera: Scolytidae) attack and eventual tree death (Geiszler et al.1984).

Several studies have attempted to identify post-fire tree characteristics to predict conifer mortality. Dixon et al. (1984) assessed the utility of using stem char height as a predictive measure of post-fire tree mortality for slash pine (*P. elliottii* Engelm.) in the southern United States. They concluded that the magnitude and rapidity of tree mortality was directly related to the height of stem charring. Harrington (1987) assessed the use of crown scorching as a predictive tool of ponderosa pine mortality in southwestern Colorado and found mortality increased linearly with the extent of crown scorch. However, mortality rates decreased for a given percentage of crown scorching as tree size increased. Further, the season of burn application influenced the observed mortality rates. Specifically, mortality in the first post-treatment year was far less in fall burned units than units burned in the spring and summer. Harrington (1987) stated that determination of exact cause of death was difficult and suggested that stem damage also contributed to mortality. Wyant et al. (1986) modeled several variables to predict ponderosa pine mortality following fire. They concluded that crown scorch, stem char, and tree diameter were the most important factors influencing post-fire survival. Swezy and Agee (1991) found similar results but also concluded that fine root mortality contributed to death of ponderosa pine. These studies suggest that a myriad of factors influence tree mortality. However the influence of bark beetles was not accounted for with the exception of Dixon et al. (1984) who identified *Ips pini* Say infesting slash pine dying post-fire and Geiszler et al. (1984) who determined that percent root kill and tree diameter were significant predictors of *Dendroctonus ponderosae* Hopk. colonization of lodgepole pine (*P. contorta* Dougl. ex Loud.). Despite the widespread use of prescribed fire, little information exists on the influence of prescribed burning on bark beetle incidence.

LITERATURE REVIEW

Bark beetles

The family Scolytidae (Class Insecta, Order Coleoptera) constitutes a diverse and widely distributed taxonomic group of subcortical beetles. The family encompasses about 73 genera and over 600 species worldwide. Members of the genera *Dendroctonus, Ips,* and *Scolytus* are considered the most economically important genera of the family (Paine et al. 1997, Rudinsky 1962).

Bark beetles cause tree mortality through the construction of larval galleries and inoculation of symbiotic fungi in the phloem, cambium, and outer sapwood region of the tree. These galleries restrict the transport of nutrients, producing a girdling effect on the host tree (Coulson 1979, Paine et al. 1997).

Host colonization by bark beetles may be viewed in four phases: dispersal, selection, concentration, and establishment (Wood 1982, Waters 1985). The dispersal phase begins with adult emergence from host trees and ends with responses to pheromones or host stimuli. Selection includes the landing of beetles on the host tree and sustained feeding in the phloem. Concentration begins with responses to beetle-produced aggregation pheromones and ends with responses to anti-aggregation pheromones. Lastly, establishment includes mating, egg gallery construction, and oviposition once host defenses have been exhausted (Wood 1982, Paine et al. 1997).

Two economically important bark beetle species that attack ponderosa pine are the western pine beetle (*Dendroctonus brevicomis* LeConte) and the pine engraver beetle (*Ips pini* Say). The western pine beetle (WPB) is generally considered a monophagous scolytid, although it does attack Coulter pine (*Pinus coulteri* Torrey) in southern California (Waters 1985). Under endemic conditions, WPB attack is usually restricted to diseased, low vigor, or senescent trees of adequate size and bark thickness to protect the insects development (Furniss and Carolin 1977, Waters 1985). When WPB populations reach epidemic levels, trees of all vigor conditions and sizes (over approximately 20 cm DBH) can be attacked and killed (Waters 1985).

The WPB's selection of the host is likely a random process. Moeck et al. (1981) found no significant difference in landing rates of WPB on healthy, diseased, or stressed ponderosa pine. Any discrimination to host condition is likely to be made after landing on the stem (Waters 1985, Moeck et al. 1981).

WPB can have one to four generations per year. Generally, the number of generations per year decreases with increasing latitude. The first beetles to attack the host are females that bore directly through the bark into the phloem region of the stem. Upon colonization, aggregation pheromones are produced to attract conspecifics. Depending on attack density and host condition, this mass attack coupled with blue stain fungi (*Ceratocystis minor* Hedgc.) vectored by the beetles may eventually overwhelm the host's defenses (Waters 1985, Paine et al. 1997). The establishment phase (including mating, egg gallery construction, and oviposition) may begin when enough beetles have attacked the tree and oleoresin flow ceases (Waters 1985, Wood 1982). Eggs are laid in niches (typically 60 per egg gallery) along the sides of these sinuous galleries (Waters 1985). After hatching, larvae feed through the phloem in a direction perpendicular to the egg gallery. After several instar stages, the larvae move to the outer bark region, create small cavities, pupate and mature. Eventually, the new adults emerge and seek new host material for reproduction (Waters 1985).

Another scolytid that frequently attacks ponderosa pine is the pine engraver beetle. This polyphagous beetle is one of the most widely distributed species in North America due to the distribution and variety of its *Pinus* sp. hosts (Furniss and Carolin 1977). The pine engraver beetle is often associated with logging slash, recently killed, severely weakened, or windthrown pines (Schenk and Benjamin 1969, Gara et al. 1999). Often, these beetles damage trees by killing the upper third of the stem (known as top killing) (Furniss and Carolin 1977). When host material is abundant and pine engraver beetle populations reach high levels, apparently healthy trees may be attacked and killed (Gara et al. 1999, Raffa and Smalley 1995).

Typically, pine engraver beetles have one to five generations per year. Males initiate host colonization and pheromone production (Robins and Reid 1997). Pine engraver beetles have associations with fungi that are thought to be symbiotic. Spores of the blue stain fungus, *Ophiostoma ips* Rumbold, carried on the strial pits on the elytra may help overcome host responses to pine engraver beetle attack (Furniss et al. 1995, Raffa and Smalley 1995). Colonizing males create a nuptial chamber beneath the bark for mating. Typically 3 to 4 females enter the nuptial chamber, mate, and excavate an egg gallery. Larvae feed outward from the egg gallery in the phloem after hatching, eventually pupating and emerging as adults. Time from attack to emergence is usually 1.5 to 2 months (Furniss and Carolin 1977).

Bark beetles and host resistance

Host resistance to bark beetle attack is dependent on the ability of the host to produce defensive compounds and the density of attacking beetles (Paine et al. 1997, Raffa and Berryman 1983). Generally, when bark beetle populations are low, host mortality is usually restricted to trees of poor physiological condition. When populations are high, healthy trees may be attacked and killed (Paine et al. 1997). Conifers defend against bark beetle attack through the production of oleoresin, a compound consisting of monoterpene olefins and diterpene resin acids (Berryman 1972, Gershenzon 1994). Bark beetles counter this response through mass attack and the utilization of symbiotic fungi to exhaust host defenses (Raffa and Berryman 1982a, Paine et al. 1997). Construction of egg galleries, mating, and initiation of oviposition occurs only upon cessation of host resistance (Paine et al. 1997, Berryman 1982, Waters 1985).

Two defensive strategies possessed by *Pinus* species are the preformed (also known as constitutive defense) and induced resin systems. The defensive mechanism first encountered by attacking organisms is the preformed resin system consisting of radial resin ducts and associated secretory cells (epithelial and sheathing cells) (Paine et al 1997, Nebeker et al. 1993). These resin ducts serve two functions: synthesizing new resin and delivering resin to attacked sites (Nebeker et al. 1993). If resin ducts are severed by colonizing beetles, the beetles may be pitched out or their brood intoxicated (Raffa and Berryman 1982a).

Bark beetle attack, fungal inoculation, and mechanical wounding can also initiate a secondary defensive system, the induced resin system (also known as a dynamic, hypersensitive, or wound response) (Miller and Berryman 1985, Raffa and Berryman 1982b, Lombardero et al. 2000, Paine et al. 1997, Ruel et al. 1998). This defensive mechanism compartmentalizes the invading organism in a nutritionally deprived toxic environment (Nebeker et al. 1993, Miller and Berryman 1985). Specifically, the induced response consists of localized autolysis of parenchyma cells, tissue necrosis (lesion formation coupled with compounds toxic to the invading organism), secondary resinosis by adjacent secretory cells, and the formation of an impenetrable periderm that isolates and intoxicates the beetles and (or) fungus (Miller and Berryman 1985, Nebeker et al. 1993).

Defense is very demanding of plant resources and may be viewed as a carbohydrate sink. Synthesis of oleoresin in the preformed system is a metabolically expensive process (Miller and Berryman 1985, Paine et al. 1997, Gershenzon 1994). Terpene production requires more energy than other secondary metabolites because terpenes are very chemically reduced (Gershenzon 1994). Secondly, production and maintenance of secretory structures, such as epithelial and sheathing cells, require substantial amount of energy to produce and maintain (Gershenzon 1994).

Induced wound responses are also carbohydrate sinks for plants. Induced responses are rapid, localized, and related to the general vigor of the tree (Raffa and Berryman 1982a, Croise and Lieutier 1993, Klepzig et al. 1996). Secondary resisnosis following depletion of the preformed resin system requires an energetically demanding translocation of photosynthate to the reaction zone (Miller and Berryman 1985, Nebeker et al. 1993). Additionally, energy is required for localized production of monoterpenes at the point of infection (Gershenzon 1994, Miller and Berryman 1985). The size of a wound also influences the carbohydrate budget of the tree. Nebeker et al. (1995) observed that oleoresin flow is directly related to the size of the wound. Therefore, the amount of monoterpene synthesis and subsequent resistance to a given level of bark beetle attack density is dependent on the current physiological condition of the tree, the energy available to produce defensive compounds, and the extent of injury caused by beetles or other organisms (Miller and Berryman 1985, Paine et al. 1997, Nebeker et al.

1995). A tree lacking sufficient energy reserves, or lacking the energy to translocate photosynthate to wounded regions of the tree, will more readily succumb to mortality at a given level of bark beetle and fungal colonization than a tree in better physiological condition (Dunn and Lorio 1992, Paine et al. 1997).

Host resistance to subcortical herbivory has received much attention over recent years and several theories have been proposed to explain the mechanisms of host defense. These include growth-differentiation balance (Lorio 1986), plant vigor (Honkanen et al. 1994), and plant stress models (Mattson and Haack 1987).

The foundation of the growth-differentiation theory centers on the manner by which carbohydrates are allocated during different phases of development. Plant development occurs in two phases: growth (cell division and enlargement) and differentiation (chemical changes to the cell). Differentiation includes lignification of cell walls, thickening of leaf cuticles, and production of defensive resins. According to Lorio (1986), growth is preferred over differentiation when resources are abundant. When water or essential nutrients for growth become limited, growth is stopped and remaining carbohydrate reserves are allocated to production of defensive compounds. Moderate levels of stress, such as short-term drought or light defoliation, may encourage differentiation and actually increase host resistance (Lorio 1986, Honkanen et al. 1994). However, chronic drought stress and defoliation may result in source limitations and eventual exhaustion of host resources for differentiation and growth, thus decreasing host resistance (Ruel et al. 1998, Lorio 1986).

Somewhat divergent to the growth-differentiation model are the plant stress and plant vigor hypotheses. The plant stress hypothesis emphasizes that the overall size of the carbohydrate pool available for allocation of resources is of greater importance in determining resistance (Mattson and Haack 1987). Depending on the size of the pool, resistance may actually be enhanced for a period of time until reserves become depleted. The plant vigor hypothesis suggests allocation is contingent upon sink and source conversions (Honkanen et al. 1994). Basically, removal of a carbohydrate sink may enhance growth, whereas removal of a carbohydrate source may enhance differentiation.

Although these models provide a foundation for understanding physiological processes of tree resistance, they emphasize constitutive defenses (Lombardero et al. 2000). Far less information exists on induced responses to acute injury (Lombardero et al. 2000). Unlike constitutive defenses, induced responses are not active in uninjured trees (Gijzen et al. 1992) and resin production becomes a priority only after wounding (Lombardero et al. 2000).

Although little information exists on the effect of fire injury on constitutive and induced defense mechanisms, it is likely that fire influences both systems. Moderate crown scorching may result in source limitations that favor differentiation, similar to defoliation described by Honkanen et al. (1994). Feeney et al. (1998) observed that resin flow was greater in burned ponderosa pine plots versus unburned plots in Arizona. Fire may also trigger an induced response from wounding on the stem. Mechanical injury from fire and exposure of xylem to airborne fungal spores or heat trauma may induce localized, rapid monoterpene production (Geiszler et al. 1984, Gara et al. 1986). Santoro et al. (2001) observed a positive linear increase in resin flow with the height of stem charring from prescribed burning on a red pine (*Pinus resinosa* Aiton) forest in Minnesota. They propose two potential explanations for this relationship between resin flow and the height of char. First, increased resin flow is an adaptation of pine to fire that occurs throughout the entire tree. However, this conclusion is counter to many observations of bark beetle infestation following fire (Salman 1933, Rasmussen et al 1996, Amman and Ryan 1991, Dixon et al. 1984). Alternatively, they propose that resin flow may be a function of a localized induced response to heat trauma.

The presence of bark beetles in fire-injured trees has often been observed (Salman 1933, Furniss and Carolin 1977, Amman and Ryan 1991, Rasmussen et al. 1996). However, few attempts have been made to identify the underlying mechanisms of delayed tree mortality following prescribed fire that incorporate both fire injury and beetle colonization.

The western pine beetle and pine engraver beetle are frequently found in fire-injured ponderosa pine (Furniss and Carolin 1977). Yet, the responses of these beetles to prescribed burning remains relatively unstudied. Decades of fire suppression have increased fuel loads, resulting in higher fire intensity and greater injury to pines when prescribed fire is used (Mutch 1993, Fiedler 1996). Consequently, induced wounding from fire may deplete the tree of carbohydrate reserves or inhibit its ability to allocate resources for defense, reducing the tree's resistance to scolytid attack. An integrated examination of the effects of fire injury to ponderosa pine coupled with the patterns of bark beetle establishment may enhance our understanding of the underlying mechanisms of delayed tree mortality following fire.

The objective of this study are three-fold: 1) Quantify ponderosa pine mortality following prescribed fire based on stem charring, 2) Determine how stem charring and the season of burn application influence the predicted Scolytidae incidence (for the western pine beetle and the pine engraver beetle) throughout a stand of ponderosa pine, and 3) Determine how stem charring potentially influences host resistance and subsequent establishment patterns of Scolytidae within ponderosa pine dying post fire.

MATERIALS AND METHODS

The study area is located on the Burns Ranger District in the Malheur National Forest in eastern Oregon. The study area (Lat 43° 54' N; Long 118° 45' W) consisted of 4 mixed-aged ponderosa pine timber sale units (DW14, DW17, DW26, and DW28) designated for prescribed burning. All stands were similar in age (80 to 100 years), aspect (SW), elevation (~1700 m), and mean annual precipitation (38 cm/year). Soils were primarily gravelly loam and clay loam. In 1995, all units were commercially thinned to basal areas of 18 m^2/ha and approximately 250 trees/ha. Site indices were similar for all stands, averaging 15.2 m (50 ft) at age 100. The sites were identified as being within the ponderosa pine/Idaho fescue (*Festuca idahoensis* Pavlick) plant association (PIPO/FEID) (Johnson 1998).

This research utilized a replicated, randomized complete block design that was established for previous research by Thies et al. (1999). Investigators divided each of four timber sale units (hereafter each will be referred to as a block) into three 12-ha sections (hereafter, treatment plot) for randomized treatment application. The three treatments applied to each block were spring-burn, fall-burn and no burn (control). Treatment plots selected for fall burning were burned in October 1997. Treatment plots selected for spring burning were burned the following spring (mid June) of 1998. Table 2.1 provides the conditions at the time of burn ignitions.

Table 2.1: Conditions at the time of burning.

Block	**Season of Burn**	**Temp (C°)**	**Relative Humidity (%)**	**Wind Speed (kmph)**
DW14	fall	20	28	4.83
DW17	fall	19.5	25	4.83
DW26	fall	18.9	25	4.83
DW28	fall	20.5	26	6.44
DW14	spring	15.5	40	3.22
DW17	spring	19.5	30	4.83
DW26	spring	20	34	6.44
DW28	spring	20	34	6.44

Following application of burn treatments, six randomly selected circular sampling plots, 0.2 hectare in area (hereafter, sampling plots), were established in each treatment plot to monitor mortality and post-fire effects.

Circular sampling plot surveys

Immediately after the prescribed burns in the spring of 1998 (mid June), all ponderosa pine within sampling plots were evaluated for the presence of green needles. Any tree without live foliage was marked and recorded as a fire-killed tree. This was done to eliminate any ponderosa pine killed directly by the fire.

After the first post-fire growing season, surveys were conducted on the circular sampling plots in September 1998. For all ponderosa pine (>15 cm dbh) within these plots, stem char height (calculated as the average height of charring on the uphill and downhill sides of the tree to the nearest 0.1m), tree height (nearest 0.1m), diameter (nearest 0.1cm), and mortality (live or dead) were recorded. Post-fire mortality was monitored in these plots after each growing season for three post-fire years (Sept. 1998, Sept. 1999, Sept. 2000). These data were recorded as part of the previous study by Thies et al. (1999), and the principal researcher permitted its use in this thesis.

For this study, stem char height was selected to assess correlations with tree mortality and bark beetle incidence for several reasons. Several studies have assessed the usefulness of this parameter as a predictor of pine mortality (Dixon et al. 1984, Wyant et al. 1986, Swezy and Agee 1991). Stem char height also serves as a reliable indicator of relative fire intensity that can be measured many years after a fire, making it useful for post-fire studies (Cain 1984). Average stem char height of the sampling plot was then calculated by averaging the stem char heights of all trees within the sampling plot. Hereafter, this will be referred to as Average Stem Char Height.

Bark beetle sampling in dead ponderosa pine

Randomly selected ponderosa pine snags were felled in June of 2001 to determine the presence of established bark beetle galleries within trees dying post-fire. For purposes of this study, a snag was defined as any dead ponderosa pine greater than 15 cm DBH that was recorded as dead following the first post-fire growing season. Trees that were recorded as fire-killed were not included.

Two years of delayed tree mortality were examined (trees that died after the 1st and 2nd post-fire growing seasons) within each season of burn (spring burn or fall burn). Snags could not be sampled from control treatment plots or for trees that died in the 3rd post-fire year because mortality was insufficient for random sampling. Therefore, a ponderosa pine snag could fall into four possible snag categories based on the burn treatment applied and year of tree death. These four categories are: fall burn treatment and 1st year death, fall burn treatment and 2nd year death, spring burn treatment and 1st year death, and spring burn treatment and 2nd year death. Two snags were randomly selected from each of these categories for all 4-blocks resulting in a total of 32 ponderosa pine snags (2 snags per category * 4 categories * 4 blocks = 32 snags).

Once the snags were felled, bark was removed at random points from the base of the tree up to a 12-cm diameter top using a circular hole-saw (92-mm diameter) and a cordless 12-volt power drill. The snag was divided into 3-m length sections from the base to the 12-cm top diameter. Within each of these sections, 4 bark samples were removed from the top side of the felled snag. This was done to ensure a relatively even distribution of sample taken along the bole of the snag. For each bark sample, the presence of bark charring, bark beetle establishment (defined here as the presence of bark beetle egg galleries with extensions of larval mines), the species of bark beetle egg gallery, and the diameter (cm) and height (m) of the sampling point on the snag were recorded.

Statistical methods

Post-fire ponderosa Pine mortality

Analysis of covariance (SAS Institute Inc. 1999) with a randomized complete block design was used to determine if total tree mortality (sum of 1st and 2nd years mortality per sampling plot) was best explained categorically among treatments (spring or fall burn) or as a function of average stem char height of the sampling plot. The variables, Block and Total Trees per Hectare (pre-fire) were treated as random effects. A square root transformation was used on the variable, Total Tree Mortality, to meet normality requirements of ANCOVA.

Analysis of variance with a randomized complete block design was used to assess observed differences in the sizes (mean DBH) of trees dying between treatments (spring or fall burn) and year of death (1st or 2nd year).

Binary logistic regression models for bark beetle incidence

Since all of the destructively sampled snags were not infested with bark beetles and it was not logistically feasible to sample all snags in the study area, models were developed to predict the presence or absence of established bark beetle egg galleries within a tree that died post-fire (1st or 2nd year) for both pine engraver beetle and western pine beetle. Using data from the randomly selected snags, binary logistic regression (S-Plus 2000) was used to predict bark beetle presence. The model resulting from this test only refers to the probability of an established bark beetle gallery being present within the tree. It does not refer to the extent or distribution of established galleries within the tree. For example, two trees with 50% and 10% of their bole covered with established bark beetle galleries would both receive the same binary response of 1. Only a tree with no established galleries would receive a binary response of zero.

The binary response of bark beetle presence (0 for a tree with no galleries, 1 for a tree with galleries) was tested independently against 6 variables including: percent stem charring, season of burn application, year of tree death, DBH, percent crown scorch, and depth of basal charring. Since these variables were known for all trees within the sampling plots (Thies, unpublished data), this mathematical model could be used to assign the probability of Scolytidae establishment to all ponderosa pine that died in 1st and 2nd years after burn application. These assigned probabilities were then summed to estimate the number of dead ponderosa pine trees that were infested with bark beetles per sampling plot. For example, a particular sampling plot had 4 dead ponderosa pines and based on a hypothetical binary logistic model, these 4 ponderosa pines received the following probabilities of pine engraver beetle presence: 0.25, 0.5, 0.75, and 0.5. Therefore, the predicted pine engraver beetle incidence for the sampling plot would be 2 trees (0.25 + 0.50 + 0.75 + 0.50 = 2). This estimate (converted and expressed as the number of bark beetle infested ponderosa pine trees per hectare), hereafter, is referred to as bark beetle incidence. This procedure was implemented for both bark beetle species (western pine beetle and pine engraver beetle) on all dead ponderosa pine (> 15 cm DBH that died in the 1st and 2nd post-fire years) within burned sampling plots.

Post-fire incidence of Scolytidae across treatment plots

Analysis of covariance (Steel and Torrie 1997) with a randomized complete block design was then used to determine if observed differences of western pine beetle and pine engraver beetle incidence (i.e. the number of bark beetle infested ponderosa pine per hectare) were best explained by season of burn application or as a function of average stem char height across the sampling plot. Again, the variables Block and Total Trees per Hectare were treated as random effects. A square root data transformation was used for bark beetle incidence to satisfy the normality requirements of this statistical tool.

Scolytidae establishment within ponderosa pine that died post-fire

Finally, binary logistic regression (S-Plus 2000) was used to determine how stem charring affected distribution of egg gallery establishment of these bark beetle species along the stems of the randomly selected, destructively sampled ponderosa pines. The binary response (0 for a bark sample with no bark beetle galleries, 1 for a bark sample with bark beetle galleries present) was regressed against the height on the tree and the bark condition (charred or uncharred) (Ramsey and Schafer 1997).

RESULTS

Post-fire delayed ponderosa pine mortality

Total tree mortality (sum of 1st and 2nd year-killed trees per hectare) was positively related to average stem char height (Figure 2.1). Burn treatment (season of burn application) and the interaction of burn treatment and average stem char height did not significantly influence the total tree mortality when accounting for average stem char height (F=1.04 P=0.31, F = 1.78, P = 0.19, respectively) (Table 2.2). The linear equation for Total Ponderosa Pine Mortality is:

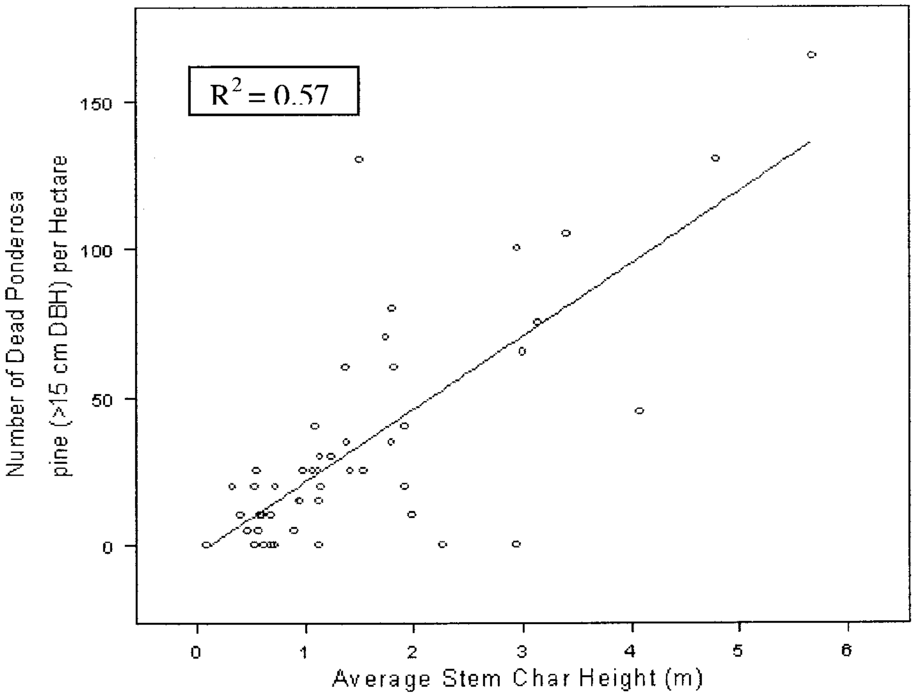
*Square Root Mortality = -2.09 + 2.31*ASCH*

Where, Mortality = sum of 1998 and 1999 killed trees per hectare
ASCH = Average Stem Char Height(m)

Table 2.2: ANCOVA results for total ponderosa pine mortality

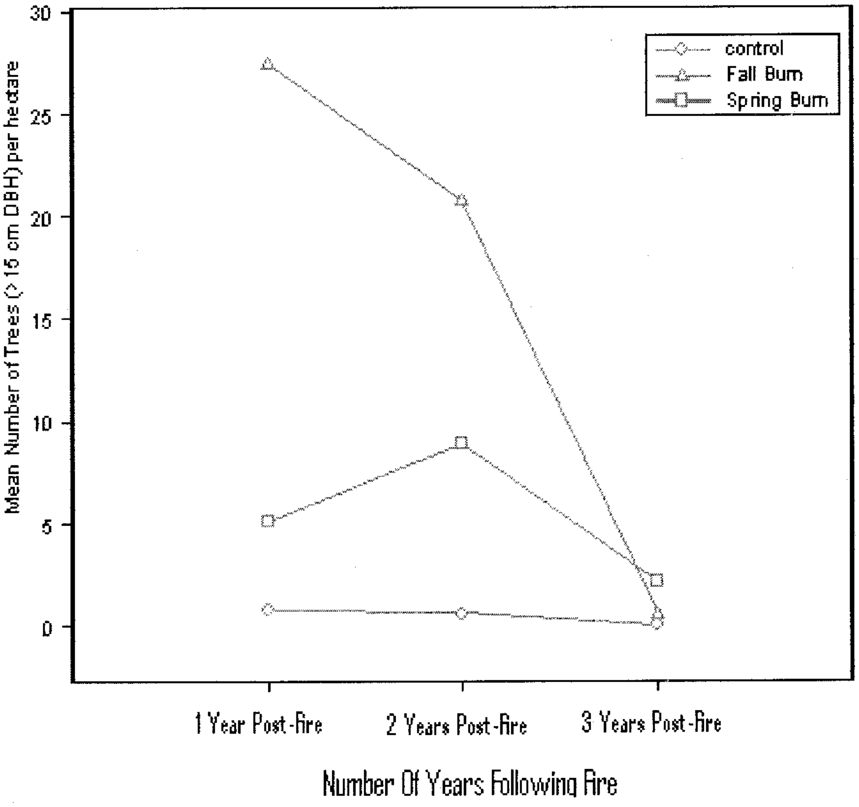
effect	num DF	den DF	F-value	P-value
Stem Char ht	1	41	38.24	<0.0001
Burn Treatment	1	41	1.04	0.31
Stem Char Ht*Burn Trt.	1	41	1.78	0.19
TPHa	1	41	x	x
Block	3	41	x	x

Figure 2.1: Ponderosa pine mortality as a function of stem char height for ponderosa pine dead 1 and 2 years post-fire.



Over a three-year period, most tree mortality occurred in the first two years following burn applications (Figure 2.2). Although total tree mortality (sum of 1st and 2nd year-killed trees) was not influenced by burn season when accounting for average stem char height, different patterns were observed for mortality between

Figure 2.2: Average ponderosa pine mortality for 3 post-fire years.



season of burn and year post-burn. Tree mortality was greatest in the first year post-fire for fall burned units and decreased the following two years. Conversely, mortality was greatest in the second post-fire year of spring burned plots (figure

2.2). By the third post-fire year, mortality for both burn treatments had returned to levels similar to the unburned treatment plots (controls).

Significant differences were observed in mean DBH of trees that died for a given cohort (treatment/year of death group) (Table 2.3 and Table 2.4). The mean DBH of dead ponderosa pine increased 4.5-cm in the second year following the fall burned units. This was consistent for spring-burned treatment plots that experienced an increase in mean DBH of 4.0-cm in the second post-fire year (Figure 2.3). These observed differences were significant for both burn treatments (Table 2.5).

Table 2.3: ANOVA results for mean dbh (cm) among year of death and treatment

effect	**num DF**	**den DF**	**F-value**	**P-value**
Cohort	3	292	11.21	<0.001
Block	3	292	x	x

Table 2.4: Estimated dbh (cm) for burn treatment and year of death

Burn Treatment/Year	**Estimate**	**SE**
fall, 1st Year	25.87	2.74
spring 1st Year	19.67	3.19
fall, 2nd Year	29.83	2.76
spring, 2nd Year	24.17	2.93

Figure 2.3: Diameter distributions for year of tree death and season of burn application (cohort).

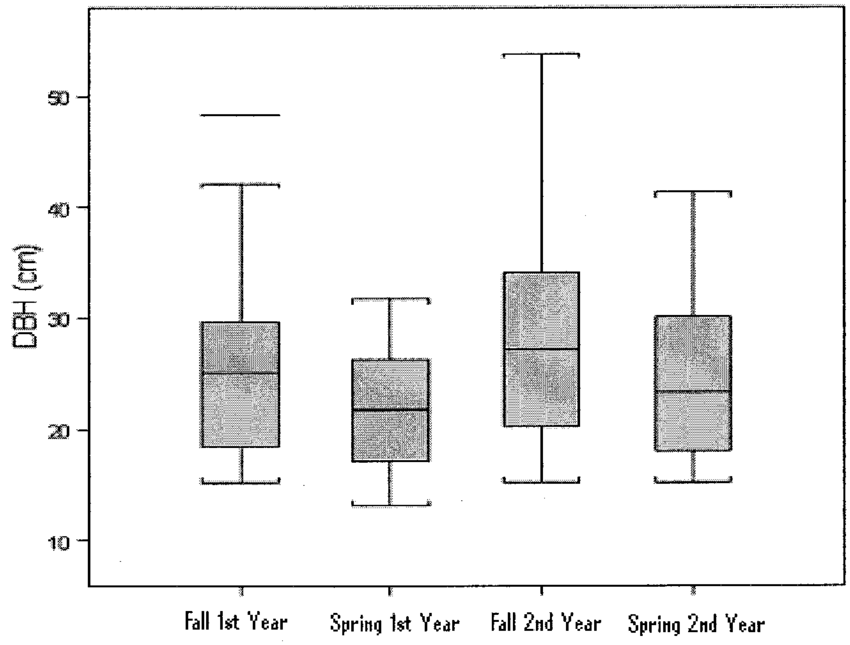


Table 2.5: Comparisons of mean dbh (cm) among year of death and treatment

Comparison	Estimate	SE	T-value	P-value
spring 2^{nd} – spring 1^{st}	4.49	2.14	2.1	0.036
Fall 2nd – fall 1st	3.96	1.05	3.78	0.0002

Binary logistic regression models for bark beetle incidence

For both bark beetle species, DBH was the only significant variable for predicting probability of bark beetle incidence (P = 0.002 for western pine beetle, P = 0.0001 for pine engraver beetle). Figures 2.4 and 2.5 show the final models for probability of western pine beetle and pine engraver beetle presence as a function of tree diameter. These mathematical probability models were used to assign probabilities of scolytidae establishment to all ponderosa pine dying (< 15 cm DBH) in the two years following burn application. These assigned probabilities were then summed to estimate the number of dead ponderosa pine infested with bark beetles per sampling plot and converted to a per hectare quotient.

Figure 2.4: Probability of western pine beetle presence by dbh (cm) in ponderosa pine trees killed 1 and 2 years following fire.

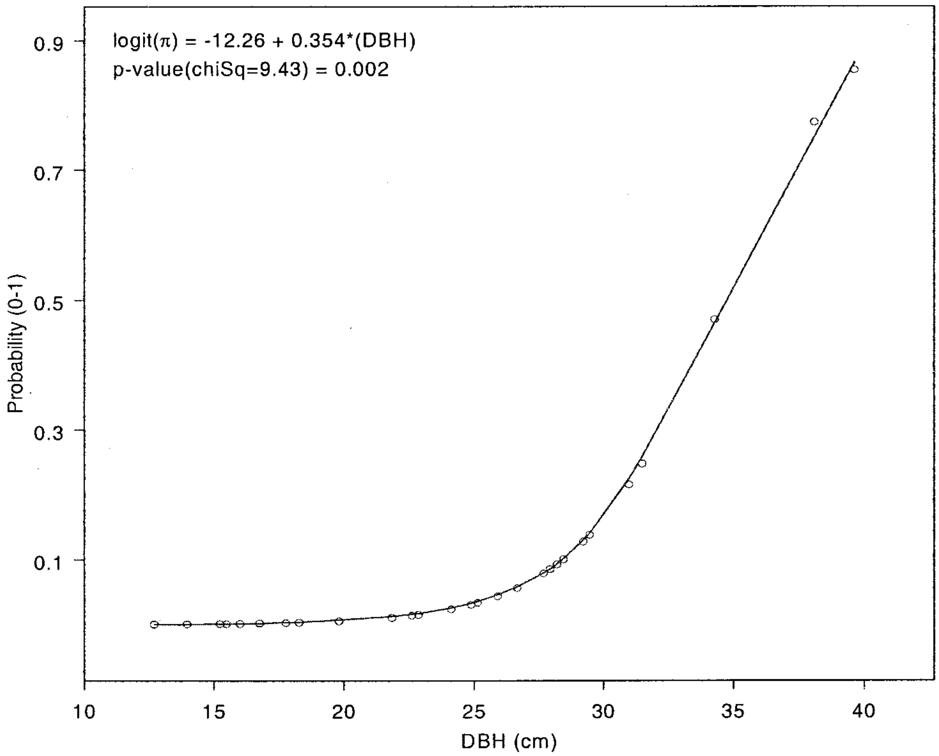
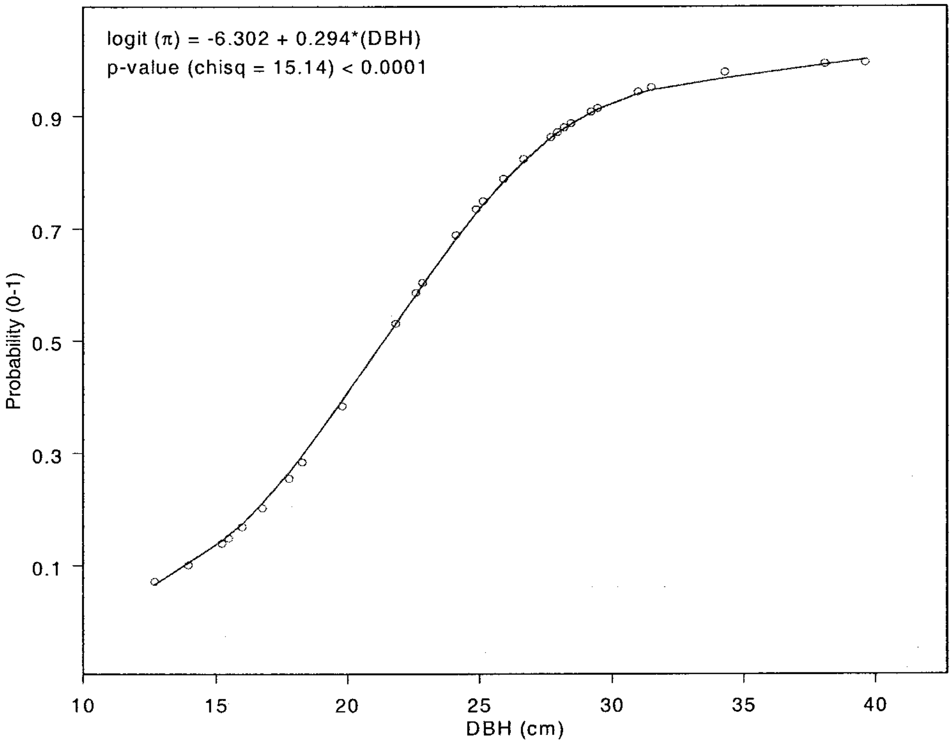


Figure 2.5: Probability of pine engraver beetle presence by dbh (cm) in ponderosa pine trees killed 1 and 2 years following fire.



Post-fire incidence of scolytidae across treatment plots

The predicted number of bark beetle infested ponderosa pine per hectare increased in a positive linear fashion with the average stem char height across sampling plots (Figures 2.6 and 2.7). In burned treatment plots, the incidence the number of ponderosa pine > 15 cm DBH per hectare infested with bark beetle was not significantly influenced by season of burn or the interaction effect of average stem char height X season of burn when accounting for average stem char height

(Tables 2.6 and 2.7) of the sampling plot. For a given average stem char height, the incidence of both beetle species was not affected by the season in which burning was conducted. Rather, bark beetle incidence increased as a linear function of the average stem char height. The linear regression models for number post-fire scolytidae-infested ponderosa pine per hectare are:

*Square Root of WPB = 0.07 + 1.06*ASCH*
Where WPB = number of infested ponderosa pine per hectare
ASCH = Average Stem Char Height(m)

*Square Root of PEB = -0.95 + 2.04*ASCH*
Where PEB = number of infested ponderosa pine per hectare
ASCH = Average Stem Char Height(m)

Table 2.6: ANOVA table for western pine beetle incidence.

effect	num DF	den DF	F-value	P-value
Stem Char ht	1	40	11.37	0.0017
Burn Treatment	1	40	0.02	0.89
Stem Char Ht*Burn Trt.	1	40	0.09	0.77
TPHa	1	40	--	--
Block	3	40	--	--

Table 2.7: ANOVA table for pine engraver beetle incidence.

effect	num DF	den DF	F-value	P-value
Stem Char ht	1	40	22.8	<0.0001
Burn Treatment	1	40	0.93	0.34
Stem Char Ht*Burn Trt.	1	40	1.23	0.27
TPHa	1	40	--	--
Block	3	40	--	--

Figure 2.6: Western pine beetle incidence in dead ponderosa pine trees as a function of stem char height.

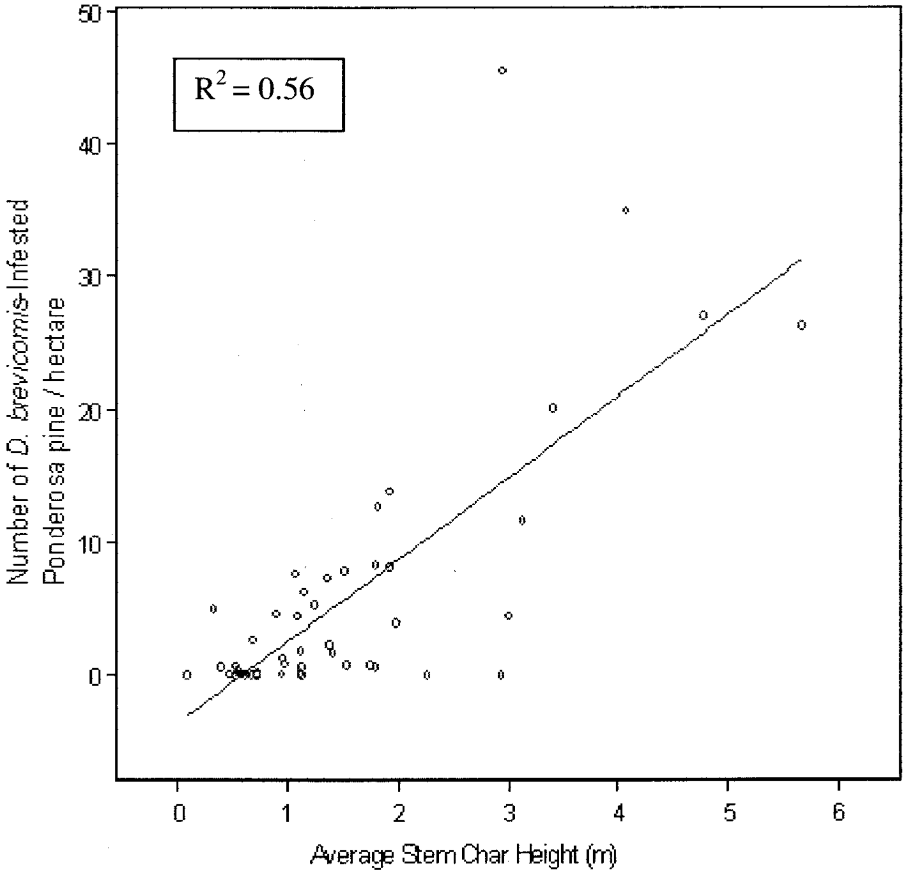
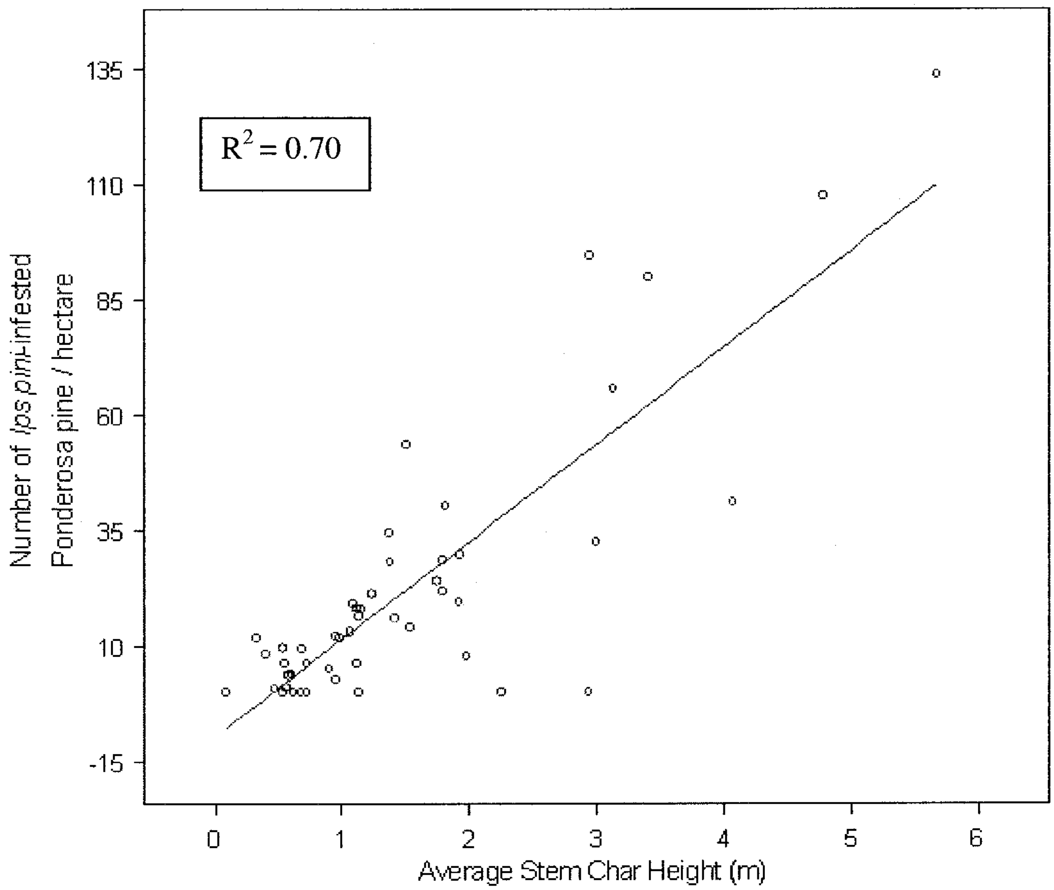


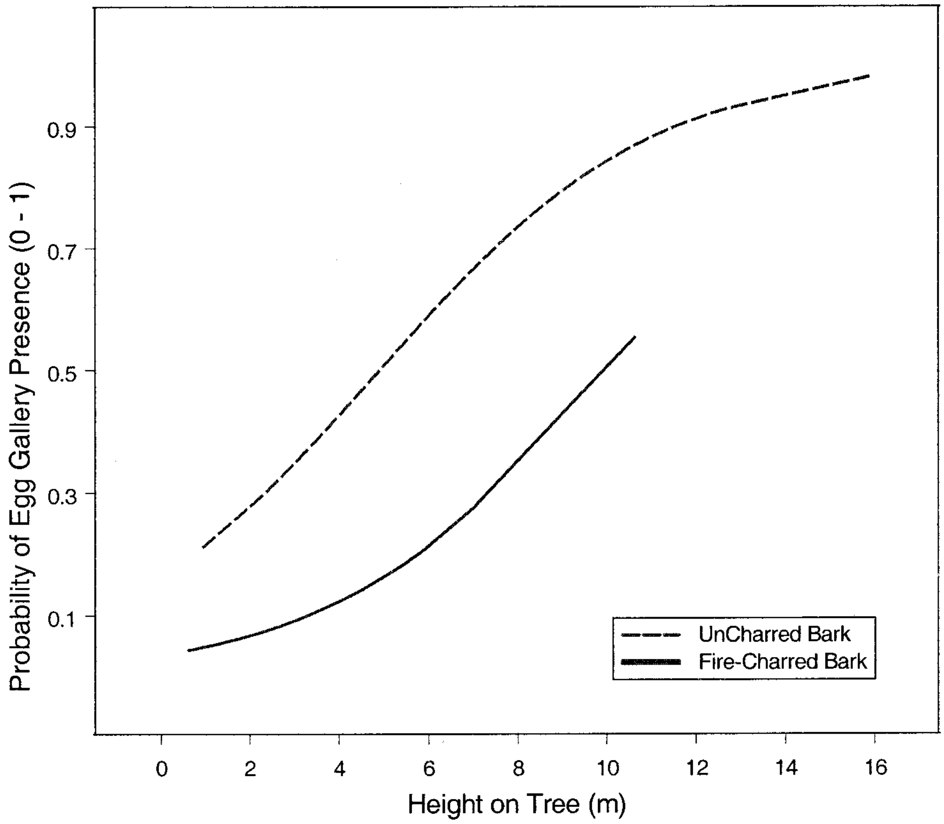
Figure 2.7: Pine engraver beetle incidence in dead ponderosa pine trees as a function of stem char height.



Scolytidae establishment within ponderosa pine dying post-fire

For the destructively sampled snags infested with bark beetles, the presence of established egg galleries of either species was influenced by the height on the tree and bark sample char. The probability of egg gallery establishment increased with the height on the stem (figure 2.8). However, this probability of egg gallery establishment was significantly reduced if the bark sustained charring, regardless of height (Table 2.8).

Figure 2.8: Probability of bark beetle egg gallery presence as a function of bark charring and the height on the tree.



The linear additive model is:

$$\text{Logit}(\pi) = -1.62 + 0.33{*}\text{HT} - 1.68{*}\text{BARK}$$

Deviance = 25.3, 303 d.f.

Where, HT = height on snag (m),
BARK = bark condition (1 for charred, 0 for uncharred)

Table 2.8: Binary regression output for egg gallery establishment

effect	Value	SE	T-value	P-value
Y - Intercept	-1.62	0.36	-4.45	<0.0001
Bark Condition	-1.68	0.43	-3.86	<0.0001
Height	0.33	0.05	6.41	<0.0001

DISCUSSION

Delayed ponderosa pine mortality

The positive linear relationship between total tree mortality and average stem char height was similar to that reported by Dixon et al. (1984). Differences were observed for the number and sizes of trees that died among subsequent post-fire years for both burn treatments. In fall-burned plots, mortality was greatest in the first year (1998) following fire application, decreased slightly by the second year (1999), and returned to levels similar to unburned plots by the third year (2000). In contrast, mortality was greatest in the second post-fire year for spring burned plots. Consistent for both burn treatments, mean DBH of dead ponderosa pine increased in the second post-fire year. The underlying mechanisms of these relationships may be understood through an examination of bark beetle incidence throughout the stands and establishment patterns of egg galleries within the destructively sampled ponderosa pines.

Binary logistic models of bark beetle incidence

Calculations of incidence for both bark beetle species were determined through the use of binary logistic models. Prior to discussion regarding beetle incidence, it is important to assess the biological validity of these models.

DBH was identified as the only significant variable for predicting the probability of established bark beetle egg galleries within ponderosa pine that died within two years. It is likely that this variable serves as a good predictor of bark beetle establishment because it is related to the height of the tree, the height of the lower crown, and may represent a range of bark and phloem thicknesses along the stem of the tree. Nested variables such as bark thickness and phloem thickness may account for bark beetle preference (Waters 1985) and the tolerance of the tree to heat trauma along the bole (Vines 1968). Since DBH is also related to tree height and lower crown height, this variable may also account for other fire effects on the tree not examined in this study, such as the extent of crown scorching (Wyant et al. 1986). Taller trees will have less crown scorching than shorter trees for a given height of flame length. Thus, these simple models potentially account for beetle preference of larger trees and the effects of fire relative to tree size. Lastly, the model was developed from randomly selected snags representing the blocks, burn treatments, and two years of post fire mortality. Therefore, these models are intended to predict the probability of Scolytidae establishment for this study and should not be extended to other data without further work.

Post-fire incidence of Scolytidae across treatment plots

Feeney et al. (1998) concluded that prescribed fire increased resin flow and thus decreased bark beetle susceptibility for a ponderosa pine stand in Arizona. Enhanced resistance to bark beetle establishment following prescribed fire was not observed here. Rather a positive linear relationship between scolytidae incidence and average stem char height was observed. Increases in the severity of the fire resulted in an increased number of dead ponderosa pines per hectare with established bark beetle galleries.

The lack of consensus between my results and those of Feeney's et al. (1998) may center on the degree of fire injury. A moderate amount of fire injury may in fact reduce bark beetle susceptibility as they suggest. However, based on their reported average flame length of 15 cm, it would seem that Feeney's study area was subjected to much lower fire intensities than my study area. Thies et al. (1999) reported a mean flame length of 60 cm for the burns conducted on these study areas (a 4-fold increase in comparison to the Feeney et al. 1998 study). This increase in fire intensity is likely to increase the extent of injuries sustained by the ponderosa pines on these study areas.

Santoro et al. (2001) observed a linear relationship in resin flow and stem charring on red pine in Minnesota. Resin exudation occurs at the expense of the carbohydrate pool of the tree (Gershenzon 1994, Miller and Berryman 1985). If the Santoro et al. (2001) observation is consistent for ponderosa pine, increases in the extent of charring should inversely affect carbohydrate reserves because energy is spent for translocation and monoterpene production (Gershenzon 1994, Miller and Berryman 1985). If the extent of injury is large, carbohydrate reserves may be depleted to a point that facilitates bark beetle attack and establishment (Nebeker et al. 1993, Paine et al. 1997). Depending on the density of attacking bark beetles, a threshold may eventually be reached that will allow successful bark beetle establishment (Berryman 1982, Paine et al. 1997). This may explain the increase in scolytidae incidence as a function of average stem char height across treatment plots (Figures 2.6 and 2.7).

Although stem charring may in fact decrease carbohydrate reserves, it is likely to be confounded by other effects of the fire such as crown scorching (Harrington 1987, Wyant et al. 1986), cambial injury (Wyant et al. 1986), and fine root mortality (Swezy and Agee 1991). Injuries such as these would likely restrict the trees ability to sequester resources (photosythate) and allocate carbohydrates (damaged conductive tissues) for defense purposes. The physiological condition of the tree prior to any fire injury may also influence tree survival. A weakened tree may die, whereas a healthier tree will survive a given level of fire injury and beetle attack. For these reasons, a certain level of caution must be exercised when assessing the effects of stem charring on host defenses.

Scolytidae establishment within ponderosa pine that died 2 years post-fire

The increase of Scolytidae incidence across treatment plots as a function of average char height highlights the contributions of bark beetles to delayed tree mortality. However, within infested trees establishment of the area of bark beetle galleries was negatively influenced by stem charring.

Although my study did not quantify post-fire resin flow, the reduced probability of established bark beetle egg galleries under fire-charred bark (Figure 2.8) suggests that the response of ponderosa pine to stem charring and heat trauma was localized. This statement supports an alternative explanation by Santoro et al. (2001) who proposed that the observed positive linear relationship between resin flow and the height of stem charring may be a function of a localized induced response to heat trauma.

Pine engraver beetles tend to attack the upper stem portions of large trees (Furniss and Carolin 1977). Initial attacks by the western pine beetle typically occur at mid-bole and additional attacks occur below and above the initial attack site (Stark 1970). This may help to explain the positive linear relationship between probability of establishment and height on the stem. However, the probability of establishment is negatively affected by bark charring regardless of height on the tree (Figure 2.8) suggesting, that charring reduced the suitability for successful establishment by bark beetles. As previously stated, beetle establishment (egg gallery construction, mating, and ovipostion) only occurs once tree defenses have been exhausted and resin flow ceases (Paine et al. 1997, Berryman 1982, Waters 1985). Had stem charring increased resin flow throughout the entire tree, the observed increased probability of Scolytidae establishment in uncharred portions of the stem should not exist.

Increased resin flow from induced responses may create a toxic environment for bark beetle colonization and establishment (Miller and Berryman 1985, Paine et al. 1997, Nebeker et al 1993). It is likely this response not only restricts beetle establishment on charred portions of the bole but also reduces tree resources available for preformed responses to beetle-fungal attack on uncharred portions of the bole (Paine et al. 1997). This may explain why the probability of egg gallery establishment in my study was greater on uncharred portions of tree stems.

The response to fire may exist as a gradient along the bole since beetle egg gallery presence was reduced, but not excluded, from charred portions of the stem. Ponderosa pine possesses thick, heat-tolerant bark (Wyant et al. 1986, Burns and Honkala 1990, Agee 1993). Superficial charring to the external bark surface may not induce any chemical or physical changes within the conductive tissues (Vines 1968). In contrast, the depth of charring and degree of heat trauma is likely to be greatest at the base of the tree where the fire is hotter and the residence time may be greater. As a result, lower portions of the stem may sustain a greater degree of heat trauma that could trigger an induced resin response similar to that reported by Santoro et al. (2001), Gara et al. (1986) and Geiszler et al. (1984). Conversely, on higher portions of the stem, the heat load per unit time and subsequent response of the defensive system are likely to decrease and may have little if any effect on the tree. Thus, the response of the tree to stem charring may exist as a gradient of greater localized induced responses near the base to progressively smaller responses on higher, less fire-damaged portions of the bole.

Integration with host resistance models

It is difficult to examine relationships among induced tree responses with models of host resistance to bark beetles because these models focus primarily on constitutive defenses. However, a couple of striking observations from this study may lend support to the growth-differentiation and plant-stress models of host defense.

Total tree mortality and bark beetle incidence increased with average stem char height regardless of the season of burn application. However, tree mortality was lower for the first post-fire year in spring-burned treatment plots than the second year. The opposite was true for fall-burned treatment plots (mortality was greatest for the 1st year and decreased in the 2nd) (Figure 2.2). Consistent for both burn treatments, mean DBH of trees that died in the 2nd post-fire year was greater than the 1st post-fire year (Figure 2.3, Table 2.4). Assuming that tree mortality results from the cumulative effects of fire injury and bark beetle establishment, the aforementioned host resistance models might explain these observations.

According to the growth-differentiation hypothesis, differentiation is favored over growth when water becomes limiting in the summer months. It is quite plausible that water limitations prior to these springtime burns (mid-June 1998) shifted resource allocation from growth to defensive compound production. This would result in increased host resistance to bark beetles, perhaps even when induced resin flow occurred from stem charring or other forms of fire injury. This may explain why mortality was lower in the 1st post-fire year compared to the 2nd year in the spring-burned treatment plots.

The plant-stress hypothesis emphasizes that the overall size of the carbohydrate pool available for allocation of resources is of greater importance in determining resistance (Mattson and Haack 1987). Depending on the size of the pool, resistance may actually be enhanced for a period of time until reserves become depleted. The 2nd post-fire year was characterized by substantial mortality and significant increases in mean DBH of those dead trees for both burn treatments (Table 2.4, Figure 2.3). This is likely a function of carbohydrate pool size associated with tree size (Mattson and Haack 1987). If it is assumed that larger trees possess a greater carbohydrate reserve, larger trees are more likely to resist bark beetle attack for the 1st post-fire year. However, if stem charring has caused extensive resin flow (sink) and if a source limitation has occurred (crown scorching and/or disruption of conductive tissues), it is quite plausible that the carbohydrate reserves are too low to adequately resist bark beetle attack in the 2nd post-fire year. Thus, mean tree DBH increased in the 2nd year because greater carbohydrate reserves enabled larger pines to resist attack in the 1st post-fire year but not the 2nd year. Smaller trees with lower carbohydrate reserves are more likely to die in the 1st year following fire, resulting in a lower mean DBH for that year in both burn treatments.

This study examined the use of stem charring for predicting tree mortality, bark beetle incidence across a stand, and patterns of established bark beetle galleries within ponderosa pines dying post-fire. Although the presence of bark beetles in fire-injured trees has been observed for many years, the underlying mechanisms are quite complex. Post-fire delayed tree mortality highlights the foundational principles of forest entomology including the conceptual insect-host-environment triangle. The interactions of fire injury, host-tree autecology, and bark beetle dynamics suggest that a universal model for predicting post-fire tree mortality will be difficult to develop. However, integration of fire effects, potential host responses, bark beetle dynamics, and host defensive strategies may reduce the high variance associated with delayed-tree mortality predictions.

In conclusion, the incidence of bark beetles increases with fire severity, yet the area within an individual ponderosa pine that is suitable for beetle establishment may decrease due to defensive responses associated with the charring sustained to the stem. This suggests that the response of ponderosa pine to stem charring is localized and may not occur throughout the entire tree.

MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH NEEDS

Management implications

These results suggest that stem char height may be used as a predictive tool for estimations of delayed ponderosa pine mortality following prescribed burning in thinned stands. It assumes that the causes of tree death result from the additive effects of fire injury and bark beetle establishment. In doing so, these results have implications for managers who must determine if salvage logging is required. Reasonable predictions of delayed tree mortality based on fire effects such as stem char are also important for determining desired fire behavior to meet management objectives prior to burning.

Fire severity, as determined from average stem char height, exerted a greater influence on ponderosa pine mortality and Scolytidae incidence than the season of burn application. The greater mortality observed in fall-burned plots in this study was likely due to drier conditions at the time of burn ignition that prompted greater fire intensity (See Table 2.1, p 19). Although the amount of tree mortality for a given year varied among burn treatments, total tree mortality was still best expressed as a function of average stem char height. Therefore, managers should consider weather and fuel conditions that reduce fire intensity and severity if tree mortality is a concern. Specifically, fire intensities that result in stem char heights below 1-m should significantly reduce the total delayed tree mortality based on this study.

The injuries induced on ponderosa pine by prescribed fire must be considered on local and regional scales when used as a fuel reduction tool. This is of special concern in areas that have experienced prolonged periods of fire suppression and subsequent increased fuels. These results show that increases in fire severity will cause greater levels of ponderosa pine mortality and bark beetle incidence. A potential, local bark beetle outbreak could ensue from severe prescribed fires that substantially increase available brood habitat. One interesting note, although not examined in this study, was the observation of a fair amount of top-kill of ponderosa pines in the 3rd and 4th post-fire years on these study sites. This top damage may have resulted from a localized increase in the pine engraver beetle population.

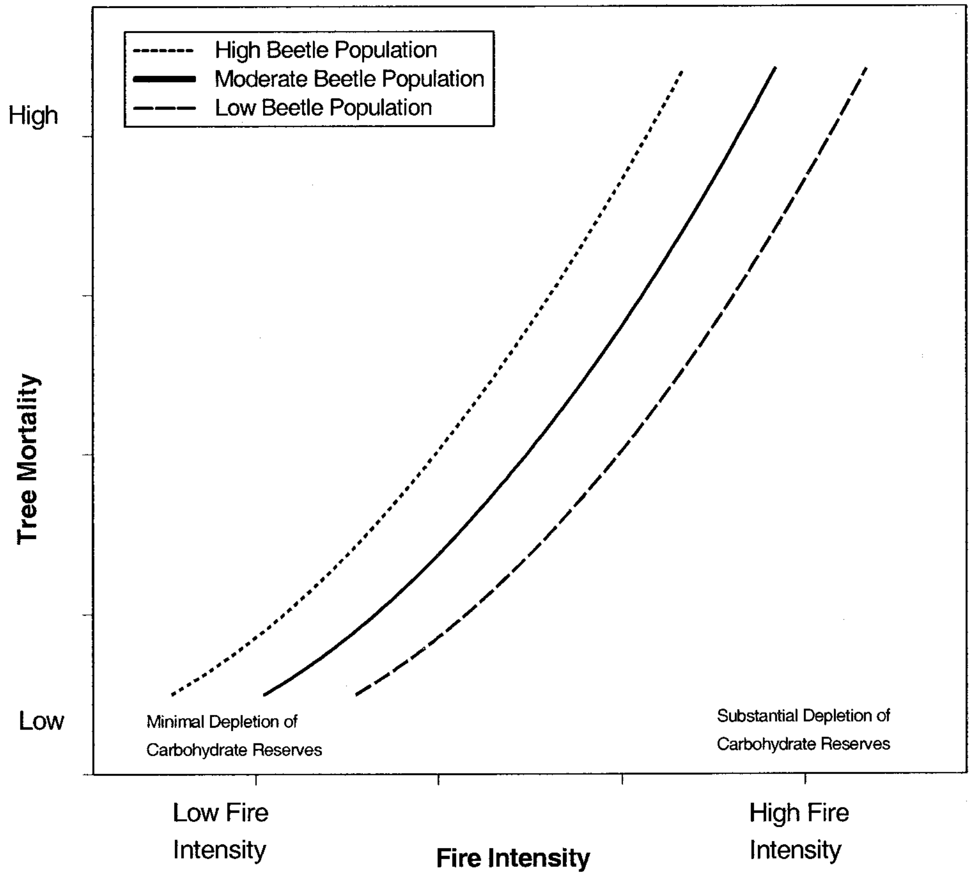
Future research needs

This thesis incorporated a commonly used fire effect with theories on host resistance. This study was conducted prospectively, and as a result, direct measurements of resin flow resulting from stem injury could not be made. Quantification of resin flow from fire injury may provide greater insight to the processes of host defense. It is apparent from qualitative field assessments that fire effects such as crown scorching, root injury, and cambial injury also influence the mechanisms of host defense. Therefore, future studies that incorporate these variables may provide a more thorough assessment of the effects of fire on host resistance and tree mortality.

Another factor contributing to tree mortality is the population dynamics of bark beetles. Fire severity exerted a great influence on tree susceptibility to beetles. However, the extent of mortality is also likely to fluctuate with varying levels of bark beetle density. For example, a higher bark beetle population in the years following burn application may result in much greater levels of ponderosa pine mortality. Figure 2.9 represent a hypothetical model of how varying beetle populations might influence mortality on these study sites in the years following burn application.

Lastly, information is also needed on the productivity of these fire-injured pines for bark beetle brood development. Although the quantity of brood rearing habitat increased relative to the severity of the fire (i.e. the number of bark beetle infested trees per hectare), these trees may be of poor productivity for beetle production. For example, higher fire severity resulted in a higher incidence of bark beetles, yet these trees may be of very poor quality for beetle development due to necrotic lesion formations or the selective nature of fire to predispose trees of poorer physiological condition (and thus poor phloem quality).

Figure 2.9: Model describing the additive effects of scolytidae population and fire-induced response on ponderosa pine mortality



CHAPTER 3. POST-FIRE SNAG DYNAMICS AND WOODPECKER SNAG USE STUDY

INTRODUCTION

Prescribed fire and thinning have been employed to reduce fuel loads and mimic processes associated with the historical fire regime of western ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws) ecosystems (Mutch 1993, Fiedler 1996). Prescribed burning (or prescribed fire) is the controlled application of fire to wildland fuels in either their natural or modified state under specific environmental conditions to produce desired fire behavior. Autecological adaptations of ponderosa pine and historical fire records suggest the species is tolerant of low severity surface fires (Burns and Honkala 1990, Agee 1993, Weaver 1959). However, as fire severity increases, some tree mortality can be expected (Wyant et al. 1986, Harrington 1987). Fire scorched trees are likely to die as the result of crown scorching (Harrington 1987, Wyant et al. 1986), stem charring (Swezy and Agee 1991, Wyant et al 1986), bark beetle attack (Geiszler et al. 1984), or through a combination of these factors.

In contrast to concerns of tree mortality, the importance of snags for wildlife is continually being recognized. Snags are an important habitat component of forested communities, providing foraging and nesting opportunities for many species of wildlife.

The snag component of a forest is dynamic, experiencing temporal and spatial changes. Snag abundance fluctuates based on recruitment (number of trees dying each year) and loss (snag collapse). Individual snags progressively decay over time, losing bark, tops and limbs (Cline et al. 1980, Raphael and Morrison 1987). Visual classification systems have been developed to qualitatively assess the structural condition and relative time since death (Cline et al. 1980). These temporal changes in snag abundance and structural characteristics are likely to influence use by snag-dependent wildlife.

Of the 80 wildlife species in the western United States associated with snags, the bird family, Picidae (woodpeckers) stands out. Woodpeckers may reduce timber mortality through predation on forest pests such as bark beetles (Koplin 1970, Otvos 1985, Kroll et al. 1980). In addition, secondary cavity-nesting birds and several small mammals use old, abandoned woodpecker cavities for nesting purposes (Bull et al. 1997, Saab and Dudley 1997, Li and Martin 1991).

The use of prescribed fire and acreage of forestland burned by wildfire each year in western North America suggest that fire-caused tree mortality will continue to be a common feature of forested ecosystems. Information regarding cavity-nester use of these snags relative to the structural deterioration may help to determine post-fire habitat suitability for snag dependent wildlife.

LITERATURE REVIEW

Woodpecker predation of bark beetles and woodborers

Woodborers (Coleoptera: Cerambycidae and Buprestidae) are often associated with dead and/or severely senescent trees. They can be found in roots, branches, stems, or cones. Eggs of the stem boring species are often laid in bark crevasses. Upon hatching, larvae feed throughout the inner bark and eventually bore into the tree, creating extensive tunnels throughout the stem. These tunnels not only reduce the structural soundness of the tree but also may provide an avenue for wood decaying fungi (Garcia and Morrell 1999). Eventually, adults emerge from the tree and seek new host material. Development typically takes one to several years (Furniss and Carolin 1977). Although capable of killing trees, these beetles are usually found in trees killed by other organisms such as bark beetles (Coleoptera: Scolytidae) (Coulson et al. 1985). Bark beetles cause tree mortality through the construction of larval galleries and inoculation of symbiotic fungi in the phloem, cambium, and outer sapwood regions of the tree (Rudinsky 1962, Paine et al. 1997). These galleries restrict the transport of nutrients, producing a girdling effect on the host tree (Raffa and Berryman 1982a, Coulson 1979, Paine et al. 1997).

Despite their status as forest pests, bark beetles and woodborers are also important sources of prey for several species of woodpeckers (Otvos 1985, Kroll et al. 1980, Koplin 1970). Woodpeckers consume large amounts of beetle larvae and pupae by scaling and drilling into the bark of infested trees (Kroll et al. 1980, Otvos 1970).

Often, woodpecker abundance is correlated with localized bark beetle outbreaks. For example, Koplin (1969) observed a significant increase in the abundance of northern three-toed (*Picoides tridactylus* Linne), hairy (*P. villosus* Linne), and downy (*P. pubescens* Linne) woodpeckers in a Colorado spruce forest infested by *Ips pilifrons* and *Pityophtorus* spp. bark beetles compared to neighboring non-infested forests. Similarly, Goggans et al. (1988) observed increased abundance of black-backed (*P. arcticus* Swainson) and three-toed woodpeckers following a mountain pine beetle (*Dendroctonus ponderosae* Hopk.) outbreak in a lodgepole pine (*P. contorta* Dougl. ex Laws.) stand of central Oregon. Goggans et al. (1988) determined that 81% of all lodgepole pines used for foraging were infested with mountain pine beetle.

In addition, woodpecker foraging and woodpecker abundance increases in early post-wildfire habitats (Kreisel 1999, Murphy 1998, Saab and Dudley 1997). Following bark beetle infestations of a burned spruce forest in Alaska, Murphy (1998) observed significant increases in black-backed and three-toed woodpecker abundance in burned areas compared to unburned sites. Black-backed woodpeckers foraged primarily for woodborers (Cerambycidae and Buprestidae) on heavily charred spruce whereas three-toed woodpeckers fed mostly upon bark beetles (Scolytidae) on lightly charred spruces.

Kreisel (1999) found similar results in regards to early post-fire responses of cavity-nesters. Species such as the three-toed, black-backed, downy, and hairy woodpeckers were 2.5 times greater in burned areas than unburned areas. Ninety-nine percent of the foraging by woodpeckers occurred on recently killed trees colonized by bark beetles and woodborers. Despite the post-fire pulse, Kreisel (1999) suggested that the abundance of woodpeckers is relatively short in duration. Gradual decreases in abundance were observed in the four subsequent years following the initial post-fire woodpecker population peak.

Woodpecker cavity excavation

In addition to insect prey, snags also provide nesting habitat for cavity-nesting birds. Woodpeckers, regarded as primary cavity nesters, often excavate a new cavity each year for purposes of brood rearing (McClelland et al. 1979). Abandoned cavities left from previous years provide important habitat for secondary cavity nesters including house wrens (*Trolodytes aedon* Viellot), bluebirds (*Sialia* sp.), tree swallows (*Iridoprocne bicolor* Viellot), kestrels (*Falco sparverius* Paulus), chickadees (*Parus* sp.) (McClelland et al. 1979, Li and Martin 1991), small mammals, reptiles, and amphibians (Bull et al. 1997, McClelland et al. 1979). Because these secondary cavity-nesting species lack the ability to excavate cavities, the presence of primary cavity nesters is critical for the creation of their nest sites.

The utility of a snag for nest excavation is a function of the excavation ability of the primary nester and the extent of snag decay (Schepps et al. 1999). Excavation abilities vary greatly among the many species of cavity nesters (Schepps et al. 1999). Additionally, decay rates within and among tree species vary based on environmental, entomological, and mycological processes occurring through time (Eslyn and Highly 1976).

Although these interactions are complex, some patterns between snag decay dynamics and primary cavity excavation have been described. Snag size (Bull 1983), degree of heartwood decay (Conner and Locke 1982, Goggans et al. 1988), structural and top condition (Cline et al. 1980), and snag height (McClelland and Frissell 1975, Mannan et al. 1980) have been identified as important characteristics for nest selection by many species of cavity nesters.

Several authors have identified snag top breakage as an important characteristic of cavity sites (McClelland and Frissell 1975, Mannan et al. 1980). Following a stand replacing wildfire in Idaho, Saab and Dudley (1997) found that broken top snags predating the fire were most frequently used for cavity excavation. Likewise, McClelland and Frissell (1975) identified broken snags over 62 cm DBH were most commonly used for cavity excavation in Montana. Swallow et al. (1986) found similar results as probability of cavity excavation increased with snag DBH and top breakage in central New York.

Snag Decay

The visual appearance of a snag has been used to assess its structural condition. Cline et al. (1980) identified 5 stages of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) snag decay based on its structural appearance, wood deterioration, and relative time since tree death. Stage 1 snags, ranging from 1 to 6 years dead, are characterized by minimal sapwood decay and initial woodborer and bark beetle colonization that elicit woodpecker foraging. Stage 2 snags are characterized by extensive sapwood decay, top breakage and cavity excavation by hole-nesting birds. This stage ranges from 7 years post death to 18 years. The following three stages (3 through 5) include extensive bark sloughing, sapwood sloughing and continual top breakage as the snags crumbled from top to bottom over time. The ranges in temporal distribution among these later stages become increasingly variable. Cline et al. (1980) also suggested that these temporal transitions were dependent on snag size, as smaller snags deteriorate faster than larger snags.

Bull et al. (1997) provides a simplified system of snag transition using three classes of decay. Class 1 snags are characterized as recently killed snags retaining, bark, branches and tops. Woodpecker use of these snags is predominantly foraging. Class 2 snags show signs of bark sloughing, and top breakage with woodpecker use shifting to cavity excavation. Class 3 snags are severely decayed with broken tops, often used as nest sites by weak cavity excavators such as northern flickers (*Colaptes auratus* Linneaus) and Lewis' woodpeckers (*Melanerpes lewis* Gray) (Bull et al. 1997).

These classification systems suggest a transition in snag use by cavity nesters coincides with the structural transition of a snag. Upon tree death, snags provide subcortical insect prey for many species of woodpeckers. As these snags continue to deteriorate, woodpecker use may shift from foraging to cavity excavation.

Snag deterioration rates vary substantially among tree species. For example, ponderosa pine snags tend to uproot and fall sooner than Douglas-fir snags that tend to decay from the top of the snag downward, as pieces of the stem continually break (Dahms 1949). Likewise, the rate of snag decay varies among species due to percent sapwood and chemical constituents of wood. Douglas-fir sapwood is more resistant to brown rot fungi than ponderosa pine (Eslyn and Highley 1976). Brown rots utilize cellulose microfibrils, the major structural component of higher plants (Agrios 1988). In addition, ponderosa pine possesses a greater proportion of sapwood than Douglas-fir. Thus, ponderosa pine may experience a greater rate of wood deterioration in comparison to Douglas-fir. This information suggests that snag dynamics are not equivalent for all species and a better understanding of specific snag decay dynamics may be required for each tree species.

Factors responsible for tree mortality may also influence the decay rate of the snag. Keen (1955) suggested that fire-killed trees experience a reduced rate of decay because of "case hardening" of the sapwood and the lack of woodborer colonization. Littke and Gara (1986) were unable to isolate decay fungi (basidiomycetes) from wood samples taken beneath fire scars of lodgepole pine, thus providing some supportive evidence for Keen's (1955) statement.

The underlying mechanism of the effects of fire on decay may be understood through an examination of the tree defense system.

The induced resin system is a defensive mechanism possessed by members of the *Pinus* genus. Increased resin flow can be initiated by beetle attack, fungal inoculation, or mechanical wounding (Miller and Berryman 1985, Raffa and Berryman 1982b, Lombardero et al. 2000, Paine et al. 1997, Ruel et al. 1998). In this process, a resin soaked lesion is created around the wounded area that will repel and/or intoxicate beetles or halt fungal advancement (Miller and Berryman 1985, Nebeker et al. 1993). Fire may also trigger an induced response from wounding on the stem. Mechanical injury from the fire and exposure of xylem to airborne fungal spores or heat trauma may induce a localized, rapid production of resin (Geiszler et al. 1984). This finding is consistent with Santoro et al. (2001) who observed a linear increase in resin flow with stem charring from prescribed burning in a red pine (*Pinus resinosa* Aiton) forest in Minnesota. Santoro suggested that heat trauma from fire may result in an induced response similar to mechanical wounding.

The common use of prescribed burning coupled with the thousands of acres burned every year by wildfires in western North America suggests that fire-induced tree mortality will be a frequent component of these forested communities. Information regarding cavity-nester use of these snags relative to the structural transition may help to assess post-fire habitat suitability.

There were 2 objectives for this study: 1) Quantify the extent to which fire charring to the tree stem influenced snag decay rate, specifically top breakage and wood deterioration, and 2) Quantify woodpecker snag use of ponderosa pine trees that died post-fire, specifically the type of woodpecker bark foraging relative to subcortical insect type and woodpecker cavity excavation relative to snag characteristics (DBH, top condition, and decay rate).

MATERIALS AND METHODS

The study area was located on the Burns Ranger District in the Malheur National Forest in eastern Oregon. The study area (Lat 43° 54' N; Long 118° 45' W) consisted of 4 mixed-aged ponderosa pine timber sale units (DW14, DW17, DW26, and DW28) designated for prescribed burning. All stands were similar in age (80 to 100 years), aspect (SW), elevation (~1700 m), and mean annual precipitation (38 cm/year). Soils were primarily gravelly loam and clay loam. In 1995, all units were commercially thinned to basal areas of 18 m^2/ha and approximately 250 trees/ha. Site indices were similar for all stands, averaging 15.2 m (50 ft) at age 100. The sites were identified as being within the ponderosa pine/Idaho fescue (*Festuca idahoensis* Pavlick) plant association (PIPO/FEID) (Johnson 1998).

This research utilized a replicated, randomized complete block design that was implemented on the study area for a previous research effort by Thies et al. (1999). Investigators divided each timber sale unit (hereafter each will be referred to as a block) into three 12-ha sections (hereafter, treatment plot) for randomized treatment application. Each block consisted of three treatments: spring prescribed burn, fall prescribed burn, and no burn (control). Fall burns were conducted in October of 1997. Spring burns were conducted the following in mid June of 1998. Table 3.1 provides the conditions at the time of burn ignition.

Table 3.1: Conditions at the time of burning.

Block	Season of Burn	Temp (C°)	Relative Humidity (%)	Wind Speed (kmph)
DW14	fall	20	28	4.83
DW17	fall	19.5	25	4.83
DW26	fall	18.9	25	4.83
DW28	fall	20.5	26	6.44
DW14	spring	15.5	40	3.22
DW17	spring	19.5	30	4.83
DW26	spring	20	34	6.44
DW28	spring	20	34	6.44

Following burn application, six randomly selected circular sampling plots, 0.2 hectare in area (hereafter, sampling plots), were established in each treatment plot to monitor tree mortality and post-fire effects.

Circular sampling plot surveys

Surveys were conducted on the circular sampling plots in September 1998 after the 1st post-fire growing season. For all ponderosa pine (>15 cm dbh) in these plots, percent stem char height (average height of charring divided by the total height of the tree), tree height (m), dbh (cm), and mortality (live or dead) were recorded. Plots were monitored for mortality after the growing season each subsequent year following burn application. These data were recorded as part of a previous study (Thies et al. 1999) and the principal researcher permitted the use of it for the purposes of this research (Thies, unpublished data).

All ponderosa pine that died post-fire within the circular sampling plots were again surveyed in early June of the 3rd post-fire year. Variables recorded in these surveys included: woodpecker foraging evidence (present or absent; drilled, flaked, or both), woodpecker cavity excavation, top condition of the snag (intact or broken), and snag status (standing or collapsed). This survey was repeated in June of the 4th post-fire year.

Woodpecker snag use was classified as either bark foraging or cavity excavation. Two types of bark foraging were recorded during these snag surveys: (1) drilling, defined as small circular holes drilled perpendicularly into the bark not exceeding 1.5-cm in diameter (Figure 3.1) and (2) flaking, defined as a relatively uniform reduction of the bark thickness by the removal of bark plates (Figure 3.2). Cavity excavation was defined as a circular, perpendicular excavation of wood > 5 cm in diameter and extending at least ~ 7.5 cm into the sapwood of the snag

(Figure 3.3). Top breakage (Figure 3.3) was defined as a post-death severing of the snag stem occurring at a height greater than 2-meters and a diameter greater than 12-cm at the point of breakage.

Destructive sampling of snags

Randomly selected ponderosa pine snags were felled in the 4th post-fire year to record data for subcortical beetle (bark beetles and wood-borers) presence, woodpecker foraging type, and to obtain wood samples for laboratory analysis of wood deterioration. A snag for the purposes of this study was defined as any ponderosa pine greater than 15 cm DBH that died following the first growing season after burn application. Ponderosa pine trees killed outright by the fire were not examined in this study.

Two years of delayed tree mortality were examined (trees dying after the 1st and 2nd growing seasons after the fire) within each burn season (spring burn or fall burn). Snags could not be sampled from control treatment plots or for trees dying in the 3rd post-fire year because mortality was insufficient for random sampling. Therefore, a ponderosa pine snag could fall into four possible snag categories based on the burn treatment applied and year of tree death: fall burn treatment and 1st year death, fall burn treatment and 2nd year death, spring burn treatment and 1st year death, and spring burn treatment and 2nd year death. Two snags were randomly selected from each of these categories for all 4-blocks resulting in a total of 32 ponderosa pine snags (2 snags per category * 4 categories * 4 block = 32 snags).

Once the snags were felled, bark was removed at random points from the base up to a 12-cm top diameter using a hole-saw (92-mm diameter) and a cordless 12-volt power drill. The snag was divided into 3-m length sections from the base to the 12-cm top diameter. Within each of these sections, 4 bark samples were removed from the top side of the felled snag. This was done to ensure a relatively even distribution of sample taken along the bole of the snag. For each bark sample, 1) woodpecker foraging (external presence of bark flaking, drilling, or none), 2) beetle type (internal presence of bark beetle, woodborer, both, or none), and 3) the diameter and height of the sampling point on the snag were recorded.

Figure 3.1: Example of woodpecker drilling on ponderosa pine snag

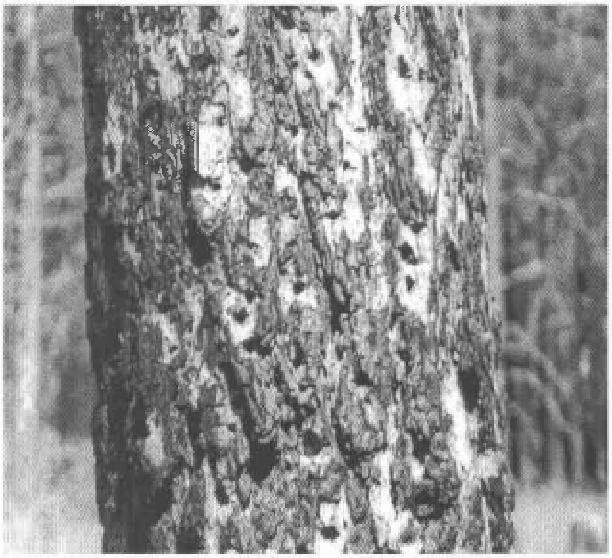


Figure 3.2: Example of woodpecker flaking on ponderosa pine snag

Figure 3.3: Example of broken top ponderosa pine snag with woodpecker cavity

Wood deterioration of snags

The rate of wood deterioration was determined through measurements of the Longitudinal Compression Strength (LCS) of wood samples extracted from randomly selected, destructively sampled snags. For each randomly selected snag, a 10-cm thick wood disc was taken every 3-meters along the stem of the snag starting at the base. For each disc, the bark condition (undisturbed or charred) and diameter were recorded. The wood discs were stored in a standard room (12% EMC) to increase the rate of drying and ensure uniform moisture content for all samples. After drying, wood plugs (2.54-cm in length and 0.95-cm in diameter) were extracted from the outer sapwood using a plug cutter from each wood disc. Three plugs were taken on equally spaced points around the circumference of each disc. Following extraction, each plug was saturated using an aspirator, cooled at 2° C for 24 hours, then compressed to determined LCS. The longitudinal compression strength (compression in a direction perpendicular to the grain of the wood) of these plugs was determined using an Instron testing machine equipped with a specialized jig (Smith and Morrell 1987). This machine measures the force required to compress wood to a standardized distance. The longitudinal compression strength (hereafter, LCS) was estimated as the force per unit distance of compression (expressed as kilograms/mm). The LCS of all three plugs were averaged to provide a single LCS measurement for each disc (hereafter referred to as "disc LCS").

The LCS was also calculated for the entire snag by averaging the disc LCS's taken from the base, 3-meters, and 6-meters height (hereafter, this will be referred to as "total snag LCS"). These data were used to provide supportive, numerical evidence for snag decay transitions (top breakage) identified from field data analysis.

Statistical methods

Woodpecker snag use

A Pearson's chi-squared test was used to determine if the type of woodpecker foraging was associated with the subcortical insect type for bark samples taken from the destructively sampled snags. Binary logistic regression (S-Plus 2000) was used to determine how snag characteristics (size, percent stem char, and top condition) affected the presence of woodpecker cavities.

Snag transition and wood deterioration

Binary logistic regression (S-Plus 2000) was used to determine which, if any, snag characteristics are related to top breakage. The binary response, "presence of top breakage", was regressed against DBH, tree height, percent stem char, and year of tree death.

The rate of wood deterioration as estimated by the longitudinal compression strength (LCS) was examined using analysis of variance (SAS Institute Inc. 1999) with a randomized complete block design. Using disc LCS taken from the 3-meter height section of each destructively sampled snag, variation of mean LCS was examined against time since tree death (3 years or 4 years) and bark condition (charred or uncharred). The variables, block and DBH were treated as random effects. Residual plots revealed that data transformations were unnecessary to meet normality assumptions.

Lastly, analysis of covariance (SAS Institute Inc. 1999) with a randomized complete block design was used to determine if the total snag LCS was influenced by the extent of stem charring. The response, total snag LCS was regressed against stem char height and time since death. Block and DBH were treated as random effects. Residual plots revealed that no data transformation was necessary.

PRELIMINARY FINDINGS

The two years after burning were characterized by substantial ponderosa pine mortality and immigration of several woodpecker species. The total number of ponderosa pine that died post-fire within the following two years (pines that died in the 1st and 2nd year following fire) was strongly correlated with the severity of the fire (Figure 3.4). Tree mortality had declined to near endemic levels (relative to controls) by the 3rd and 4th post-fire years. Woodpecker foraging was observed on nearly all ponderosa pine dying post-fire. Table 3.2 provides information regarding the presence and relative abundance of 4 woodpecker species observed on these study plots. These observations were made during annual mortality and snag surveys. There was no specific sampling method employed to collect these data and this information is strictly anecdotal.

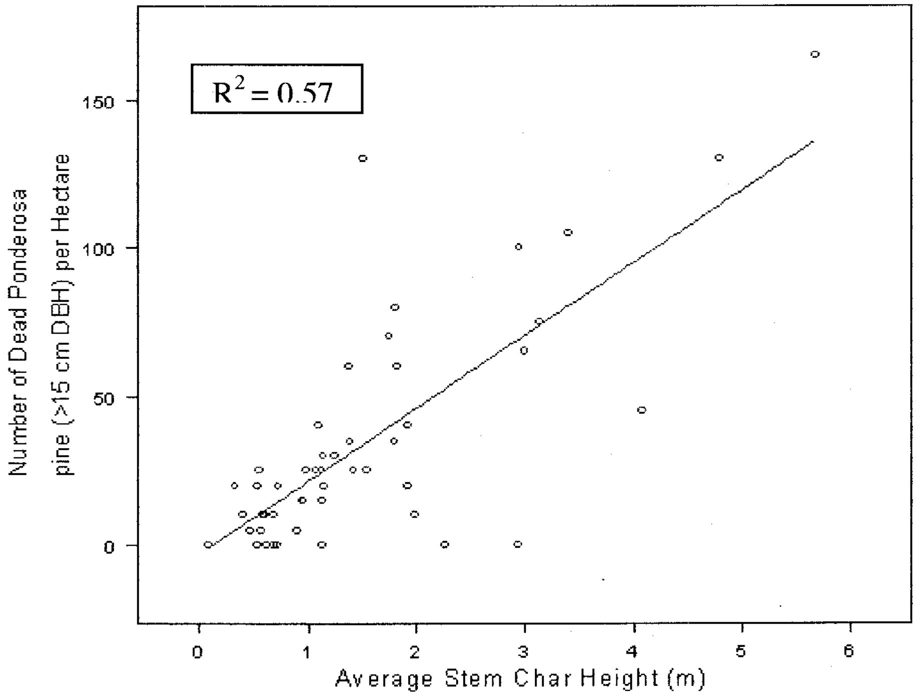
Table 3.2: Number of woodpeckers by species observed on treatment plots for 3 and 5 years post-fire.

	Woodpecker Species 3Years Post-Fire				
Burn Treatment	**Hairy**	**Black-Backed**	**White-Headed**	**Williamson's Sapsucker**	**Total**
fall	12	2	3	0	17
spring	3	2	1	0	6
control	1	0	1	0	2
Total	16	4	5	0	25

	Woodpecker Species 5 Years Post-Fire				
Burn Treatment	**Hairy**	**Black-Backed**	**White-Headed**	**Williamson's Sapsucker**	**Total**
fall	6	3	0	2	11
spring	2	0	0	0	2
control	2	0	0	0	2
Total	10	3	0	2	15

The number of ponderosa pine snags that collapsed (due to severe root decay and uprooting) became increasingly apparent by the 4th post-fire year. For all ponderosa pine dying post-fire on the circular sampling plots, 82.2% remained standing in 4th post-fire year. The following year, 65.1% of all trees dying post-fire remained standing (Table 3.3).

Figure 3.4: Ponderosa pine mortality as a function of stem char.



Snag stem breakage (from decay) and woodpecker cavity excavation became increasingly apparent by the 3rd post-fire year. Field observations revealed that top breakage of all snags appeared to have resulted from advanced decay caused by the basidiomycete, *Fomitopsis pinicola*. This is regarded as one of the most common decay fungi of dead conifers in western North America (Hennon 1997) and it is likely that this fungus is present in all snags found on these sites.

Figure 3.5: Average mortality for 4 post-fire years.

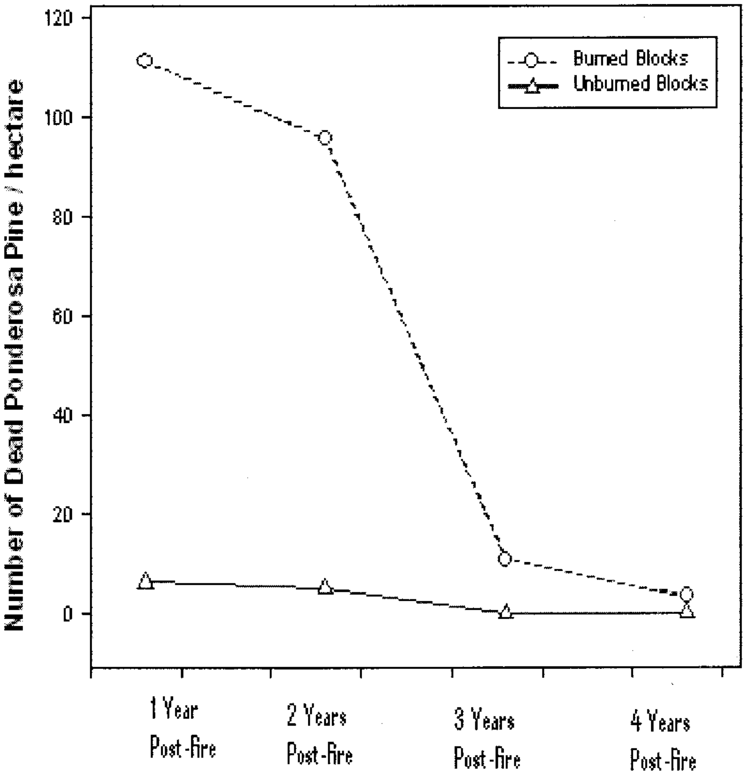


Table 3.3: Fall rates of snags by block and burn treatment.

Block	Burn Treatment	Total Dead by 2nd Year	Standing 4th Year	Standing 5th Year
dw14	fall	63	49 (77.7 %)	45 (71.4 %)
dw14	spring	5	5 (100 %)	5 (100 %)
dw17	fall	28	25 (89.2 %)	23 (82.1 %)
dw17	spring	33	31 (93.9 %)	27 (81.8 %)
dw26	fall	116	89 (76.7 %)	62 (53.4 %)
dw26	spring	4	3 (75.0 %)	3 (75.0 %)
dw28	fall	31	26 (83.8 %)	14 (45.2 %)
dw28	spring	18	17 (94.4 %)	15 (83.3 %)
	totals	**298**	**245 (82.2 %)**	**194 (65.1 %)**

STATISTICAL RESULTS

Woodpecker foraging

Of the 245 snags that remained standing by the 4th post-fire year, all but one snag had evidence of woodpecker foraging. Bark drilling was observed on 99.6 % (n = 244) of the surveyed snags. Bark flaking was recorded on 58.4 % (n = 143) of the snags.

Using the 192 bark samples removed from the 32 randomly selected snags, a Pearson's chi-squared test revealed that the type of woodpecker foraging was strongly associated with the taxa of beetles beneath the bark ($X^2 = 119.19$, $P = 0.001$, 3 df). Bark flaked by woodpeckers appeared associated with the presence of bark beetles (Scolytidae) whereas drilling was associated to the presence of woodborers (Buprestidae or Cerambycidae).

Table 3.4: Woodpecker foraging and beetle presence for bark samples from randomly selected snags

Beetle Type	Drilled bark	Flaked bark	Totals
None	1	0	1
Woodborer	116	4	120
Bark beetle	0	17	17
Both	15	39	54
Totals	132	60	192

Woodpecker cavity excavation

The 4th post-fire year survey revealed that 14 (4.94 % of the total snags) snags possessed at least 1 woodpecker cavity in ponderosa pine that died after the prescribed fire. One year later (5th year), a total of 17 (6.0 % of the total) snags possessed woodpecker cavities. Binary logistic regression revealed that DBH (P = 0.015, 280 df) and top condition (P = 0.014, 280 df) were significant variables for predicting the probability of cavity excavation. The probability of cavity excavation increased in a linear fashion with DBH. This probability was greatly increased if the snag possessed a broken top (Figure 3.6).

The binary logistic model for the probability of a snag possessing a cavity is:

$$Logit = -4.08 + 0.07*DBH + 0.83*TOP$$

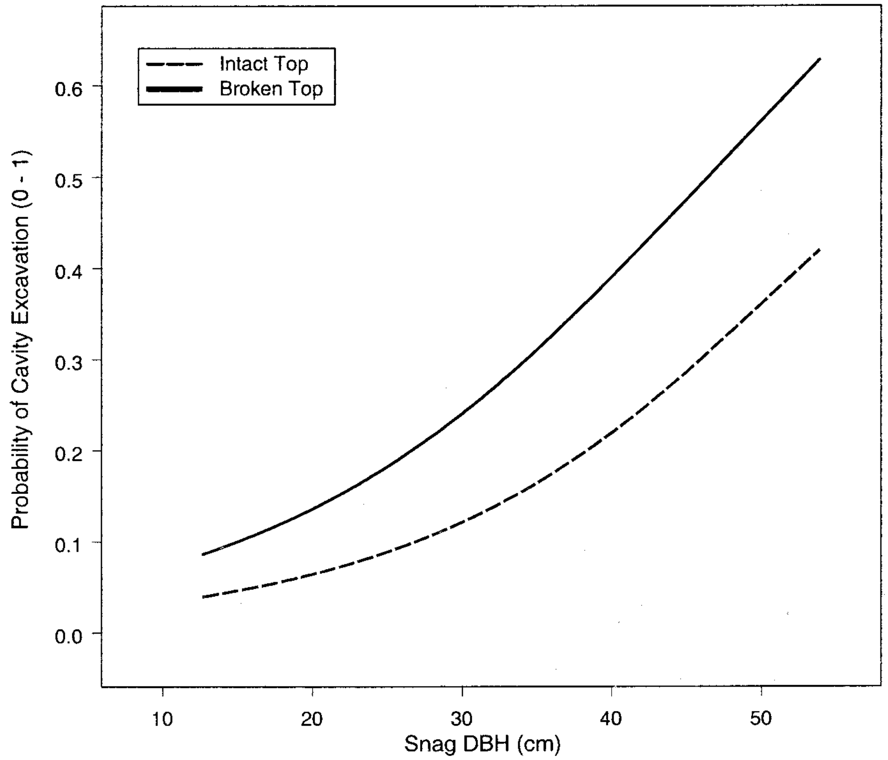
Where, TOP = 0 for Intact, 1 for Broken

DBH = diameter at breast height (cm)

$$Logit = (exp/1+exp)$$

Deviance = 12.5 280 df.

Figure 3.6: Probability of cavity excavation as a function of dbh and top condition (ponderosa pine dead for 4 years).



Snag transition

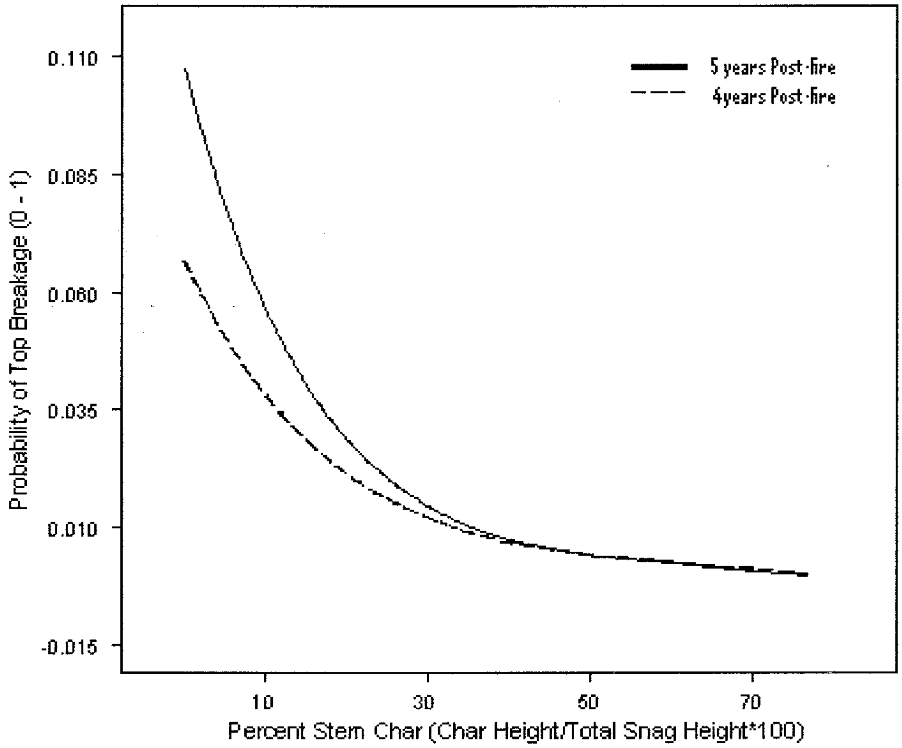
The 4th year survey revealed that 7 snags (2.47 % of the total snags surveyed) were identified as having a broken top due to the presence of internal decay. One year later (5th year survey), a total of 10 (3.53 % of the total snags surveyed) snags had broken tops.

Percent stem char and DBH were significant variables for predicting top breakage in sampled snags in the 5th post-fire year (P = 0.01 for DBH, and 0.03 for percent stem char). These two variables appeared weakly significant in the 4th post-fire year (P = 0.11 for DBH, P = 0.06 for percent stem char). The models for probability of top breakage as a function of percent stem char are:

$$Logit\,(\pi) = -2.67 - 0.06\,(\text{percent stem char})\ \text{for 4 years post-fire}$$

$$Logit\,(\pi) = -2.11 - 0.07\,(\text{percent stem char})\ \text{for 5 years post-fire}$$

Figure 3.7: Probability of top breakage as a function of percent stem char for ponderosa pine trees dead 4 and 5 years.

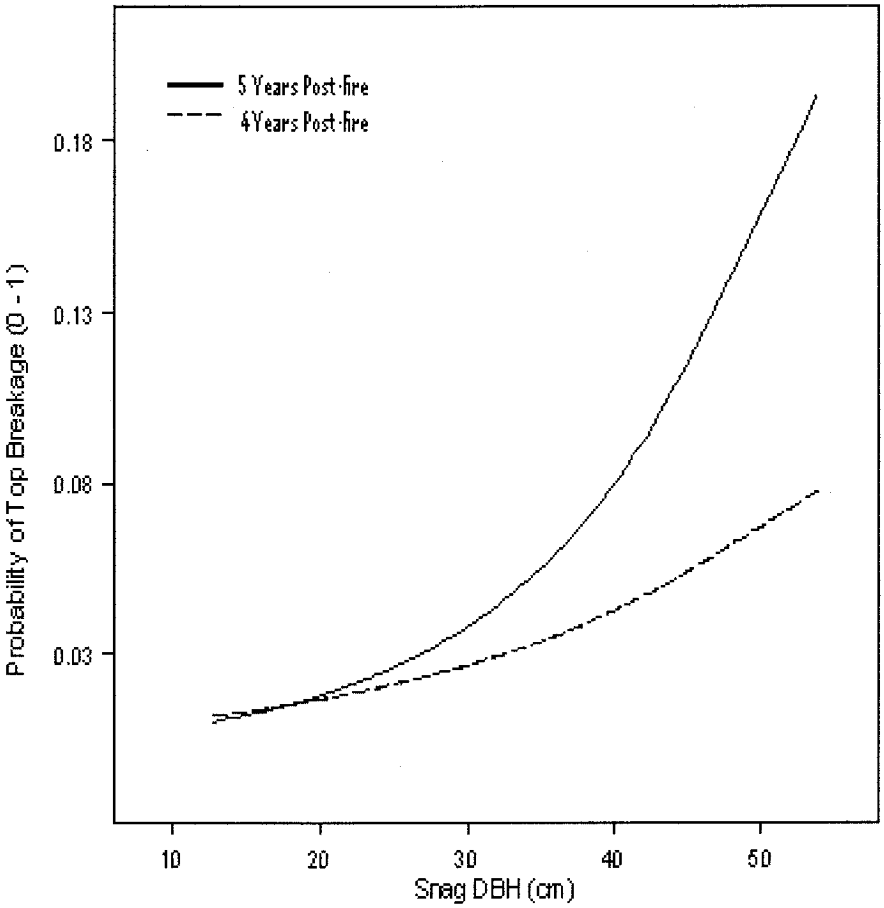


The probability of top breakage was inversely related to the percent stem char (Figure 3.7). As percent stem char increased, the probability of top breakage decreased. The opposite was true for DBH, where a positive relationship existed (Figure 3.8). The models for top breakage as a function of dbh are:

$$Logit\ (\pi) = -5.04 - 0.05\ (dbh)\ \textit{for 4 years post-fire}$$

$$Logit\ (\pi) = -5.54 - 0.08\ (dbh)\ \textit{for 5 years post-fire}$$

Figure 3.8: Relationship between snag dbh and top breakage for ponderosa pine trees dead 4 and 5 years.



Wood deterioration of snags

Differences in mean disc LCS taken from the 3-meter height were examined for bark condition (charred bark and uncharred bark) and year of snag death (1st or 2nd year post-fire).

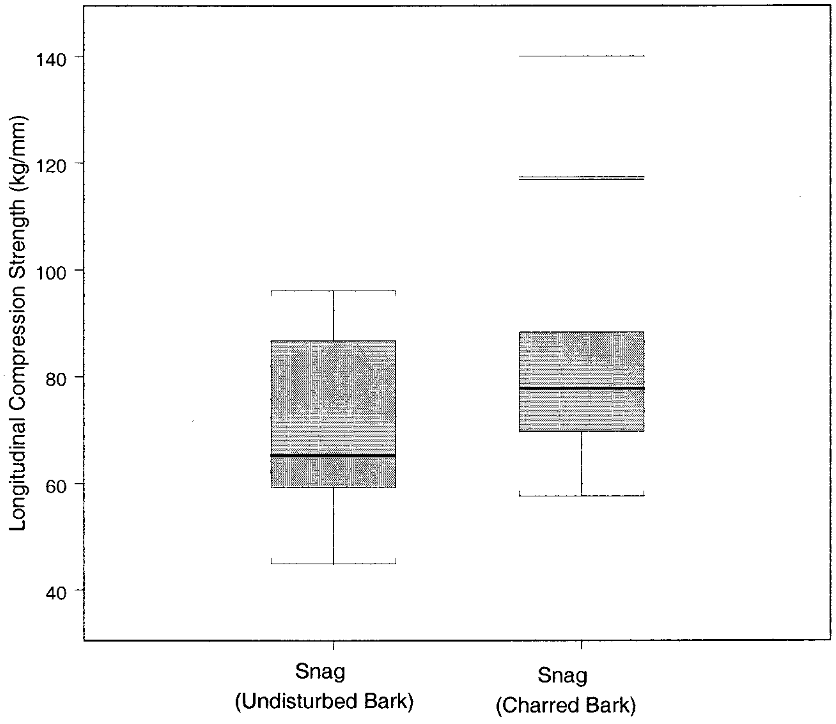
Longitudinal compression strength (LCS) differed significantly among wood samples extracted from beneath sections of trees with charred bark and undisturbed bark (uncharred) (F = 4.04, P = 0.05, 1, 23 df, Table 3.5). The time since death, (3 years or 4 years) and the interaction of bark condition and time since death were not significant variables for explaining observed differences in LCS (P = 0.84, and P = 0.95, respectively). LCS was greatest for charred bark and less for uncharred snags. The reduced force required to compress wood samples taken beneath uncharred bark is suggestive of an advanced state of deterioration (Figure 3.9).

Table 3.5: ANOVA results of disc LCS for bark conditions

effect	num DF	den DF	F-value	P-value
Bark Cond.	1	23	4.04	0.05
Year	1	23	0.04	0.84
Year*Bark Cond.	1	23	0.001	0.95
Block	3	23	x	x
DBH	1	23	x	x

Snag LCS was positively correlated with stem char height (P=0.003, Table 3.6), while time since death (Year) and the interaction of time since death and stem char height had no significant effect on LCS (P=0.13, P=0.12, respectively).

Figure 3.9: Effect of charring on LCS of outer sapwood removed from 3- and 4-year old ponderosa pine snags.



The increase in LCS as a function of stem charring indicates a reduced rate of decay (Figure 3.10). The linear equation for snag LCS is:

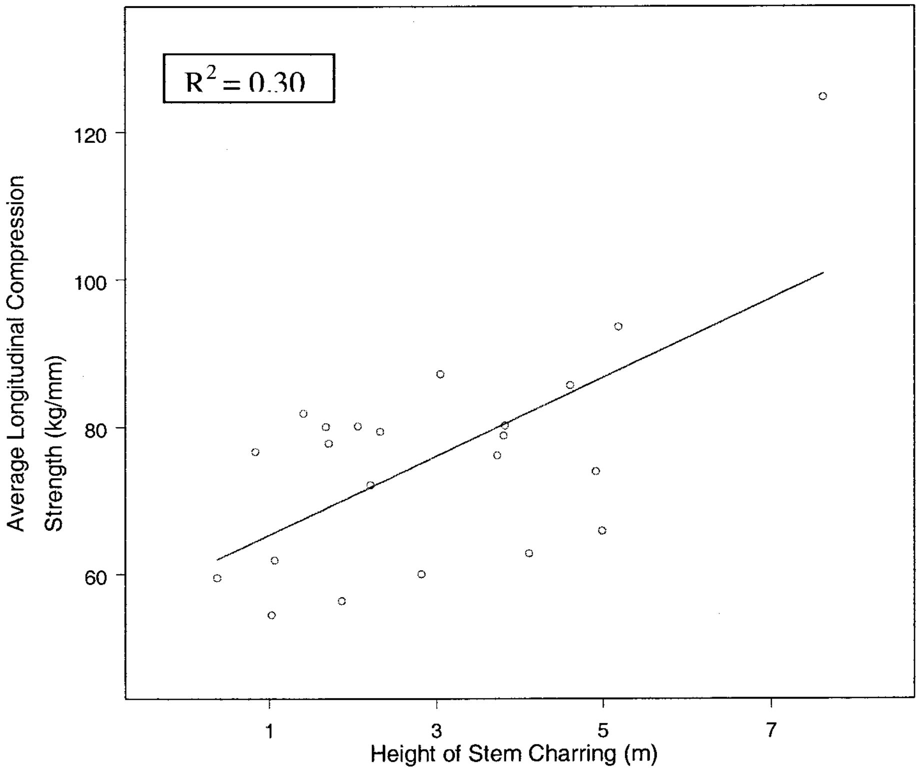
$$LCS\ (kg/mm) = 59.95 + 5.35*SCH$$

Where, SCH is Stem Char Height(m)

Table 3.6: ANCOVA results of snag LCS for stem charring

effect	num DF	den DF	F-value	P-value
Char Height	1	14	12.23	0.003
Year	1	14	2.61	0.13
Year*Char Height	1	14	2.7	0.12
Block	3	14	x	x
DBH	1	14	x	x

Figure 3.10: LCS for wood removed from the outer sapwood of 3 and 4 year-old ponderosa pine snags as a function of stem charring.



DISCUSSION

Woodpecker foraging

Woodpecker foraging was observed on 99.6% of the surveyed snags. The chi-squared test suggested a strong association between the type of bark foraging and the type of beetles present. This relationship supports observations reported in other studies that identify bark beetles and woodborers as important woodpecker prey sources (Otvos 1985, Kroll et al. 1980, Koplin 1970, Otvos 1970). Flaking of bark is most likely a function of woodpeckers searching for scolytid pupae and emerging adults as these beetles migrate from the inner bark region to the outer bark region as part of their development (Otvos 1970, Kroll et al. 1980). Drilling in the bark may result from woodpecker predation on woodborer egg clusters oviposited into the bark or developing woodborer larvae within the phloem region.

Since scolytid bark beetles and woodborers colonize trees at a point of severe stress or decadence (Furniss and Carolin 1977), it is suggestive that the greatest foraging opportunities occur at the time of tree death and shortly thereafter as beetle broods develop. However, this also suggests that as rates of tree mortality decrease (such as in the third post-fire year in this study), bark beetle and woodborer prey availability also decreases. This decrease in bark beetle prey may exclude woodpecker species that rely heavily on bark beetles and woodborers as a prey sources.

Nest site selection

A total of 14 snags (4.9% of the total snags) possessed woodpecker cavities in the third post-fire year. One year later, an additional 3 snags with cavities were recorded (totaling 17, 6.0%). Both top condition and snag size were significant variables in predicting the probability of cavity excavation occurring in a snag. The probability of snags having a cavity increased with DBH and if the snag had a broken top. These results are consistent with other studies that identify snag size and top condition as important characteristics of cavity nest trees (McClelland and Frissell 1975, Mannan et al. 1980, Bull 1983).

These results also suggest that shifts in snag use are closely linked to changing structural characteristics. Based on snag classification systems, cavity excavation occurs as snags progress toward more senescent decay classes. Top breakage is identified in stage 2 for systems presented by Bull et al. (1997) and Cline et al. (1980). The relationship between cavity excavation and snag decay may be attributed to: 1) greater wood deterioration associated with decay, and 2) behavioral instincts possessed by cavity nesters that prompt selection of snags with broken tops. This study cannot account for the latter of these two explanations, however, the structural deterioration of these snags can be assessed.

Snag decay

Percent stem char and top breakage was negatively correlated. As the percentage of stem char increased, the probability of top breakage decreased (see figure 3.7). In contrast, top breakage was positively correlated with snag size (figure 3.8). This observation is inconsistent with Cline et al. (1980) who suggested that smaller snags experienced faster decay transitions than larger snags. Therefore, percent stem char and DBH may be confounding variables. Percent stem char was calculated as the height of stem charring divided by the height of the tree prior to top breakage. This measurement is constant and does not change if the height of the snag decreases because of top breakage. However, the inverse relationship between top breakage and percent stem char could be an artifact of the snag size (DBH). Larger diameter snags are likely to be taller. Thus, for a given height of stem charring, a taller snag will have a lower percent stem char than a shorter snag. Therefore, it was important to examine the LCS differences based on snag size and stem charring to determine which of the two was more closely related to the probability of top breakage.

Longitudinal compression strength

The LCS results suggest that bark charring significantly reduced the rate of wood deterioration when accounting for DBH as a random effect. This was consistent for LCS estimates from 3-meter height sections as well as throughout the entire snag. Total snag LCS and stem char height showed a positive, linear relationship. As stem char height increased, the snag LCS increased, which suggests a slower rate of wood deterioration because a greater LCS means more force is required to compress wood samples to a standardized distance. This suggests that the relationship in top breakage and DBH is actually an artifact of the extent of stem charring sustained by the tree.

The inverse relationship between snag transition and stem char may result from internal responses of the tree following injuries sustained during the fire. Fire wounding on the stem may trigger an induced resin response that compartmentalizes invading organisms in a nutritionally deprived toxic environment (Nebeker et al. 1993, Miller and Berryman 1985). Specifically, the response consists of localized autolysis of parenchyma cells, tissue necrosis (lesion formation coupled with compounds toxic to the invading organism), secondary resinosis by adjacent secretory cells, and the formation of an impenetrable periderm can isolate and intoxicate invading organisms (Miller and Berryman 1985, Nebeker et al. 1993).

Mechanical injury from fire and exposure of xylem to airborne fungal spores or heat trauma may induce such a defensive response (Geiszler et al. 1984, Gara et al. 1986). Littke and Gara (1986) were unable to isolate decay fungi (basidiomycetes) from wood samples taken beneath fire scars of lodgepole pine. In addition, Santoro et al. (2001) observed a linear increase in resin flow with stem charring from prescribed burning in a red pine forest of Minnesota. This suggests that resinosis from fire wounding may reduce fungal advancement and inhibit deterioration on charred portions of the stem. This lends evidence to early observations by Keen (1955) who suggested that fire-killed trees may experience a reduced rate of decay because of "case hardening" of the sapwood and may explain the inverse relationship in top breakage and stem char reported here.

Snag decay, that may encourage cavity nesting, is inhibited by reduced wood deterioration from charring. In addition, my work and others show that ponderosa pine snag longevity appears to be short (Bull 1983, Dahms 1949). The percentage of snags still standing by the 4th post-fire year was 82%. This figure decreased to 65% by the following year, a 17% decrease in the number of available snags (Table 3.3). Likewise, the recruitment of snags decreased to near pre-treatment levels by the third post-fire year (relative to unburned controls experiencing minimal mortality) (Figure 3.5). This suggests that over a four-year period, attrition exceeds recruitment, snag deterioration is inhibited by stem charring and, woodborer and bark beetle prey availability becomes limited as mortality rates decrease over time. Thus, snag use and perhaps habitat use by woodpeckers shift from foraging to cavity excavation. Although the woodpecker abundance reported in this effort is anecdotal (table 3.2), the decrease in woodpecker abundance over time following a fire may be related to decreased availability of subcortical prey and relatively few cavities observed given the number of snags available.

In conclusion, these results illustrate that the factors contributing (fire injury and beetle attack) to delayed tree mortality exert a strong influence on the decay of snags and their use by cavity-nesters. Bark foraging by woodpeckers was strongly associated with the subcortical beetles that initially attacked and likely contributed to tree mortality. Cavity excavation was associated with the structural deterioration of the snags. In turn, the structural deterioration of these snags appear to be influenced by the effects of stem charring sustained prior to tree death.

Ultimately, the benefit of prescribed fire (and perhaps natural wildfires) to cavity-nesting birds depends upon the severity of the fire. The majority of delayed tree mortality occurred within the two years following fire. This mortality was directly related to the severity of the fire, measured as the average stem char height (Figure 3.4). Burning conducted under conditions that reduce fire severity will likely produce lower levels of tree mortality resulting in fewer foraging opportunities for subcortical insects and fewer snags available for cavity nesting in the following years.

MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH NEEDS

Management implications

Although delayed tree mortality following prescribed fire may conflict with burning objectives, the benefits of these dying trees to cavity nesting birds should be considered. Ponderosa pines dying post-fire appear to provide excellent sources of prey for woodpeckers. Fire injured ponderosa pine are likely candidates for woodborer and bark beetle colonization (Furniss and Carolin 1977, Rasmussen et al. 1996). Several studies have identified these invertebrates as important prey of woodpeckers (Koplin 1970, Otvos 1970, Otvos 1985, Murphy 1998), suggesting that foraging opportunities for these arthropod species are closely linked to tree mortality, and are therefore associated with the temporal patterns of tree mortality following disturbance. Decreased ponderosa pine mortality in the 3rd post-fire year suggests that prey abundance also decreases. The benefits of these snags as foraging sites for woodpeckers should be considered when determining if salvage logging is necessary. If the extent of post-fire mortality is minimal, or if the trees dying are of poor merchantable value due to size or branching form, these dead trees may best serve as foraging habitat for cavity-nesting birds.

Cavity excavation in ponderosa pine snags appears closely associated with structural transition and snag size. Additionally, snag transition or top breakage, is negatively influenced by the extent of stem charring. It appears that 4- and 5-year old ponderosa pine snags greater than 45 cm DBH with broken tops possess the greatest probability for cavity excavation. Thus, the sizes of trees dying post-fire and the extent of charring sustained to the stem should be examined when assessing nesting habitat.

Future research needs

The next logical step in this research would be to incorporate information pertaining to numerical responses and population dynamics of woodpeckers over time relative to the snag dynamics presented here. These results suggest that a shift in resources occurs in the four years following fire disturbance. The two years immediately following fire resulted in large amounts of prey availability. The next two years saw a shift from prey to nesting resources as beetles completed their development, tree mortality levels decreased, and snags progressively decayed. Determination of the corresponding shift in the avian community during this period would provide further insights concerning the temporal effects of prescribed fire on snag-dependent wildlife.

It is also unclear how these snags function as foraging sites after bark beetles and woodborers complete their development in the bark region of the tree. It is likely that a succession of insect communities occurs as these snags deteriorate through time. However, the insect species present, their abundance, and the utilization by insectivorous birds remain unclear.

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