ABSTRACT

Bark Beetle Activity in Douglas-Fir, *Pseudotsuga menziesii* var. *glauca* Mirb. (Franco), Following the 1994 Beaver Mountain Fire

by

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The 1994 Beaver Mountain fire ignited the canopies of subalpine fir, *Abies lasiocarpa*, and spread ground fire into adjacent Douglas-fir forests, *Pseudotsuga menziesii* var. *glauca*. Despite shorter flight seasons due to lower annual temperatures and persistent snow, the Douglas-fir bark beetle, *Dendroctonus pseudotsugae* Hopkins, attacked a range of moderately fire-injured host conifers. Logistic regression models illustrated that in 1995 associated bark beetles selected large diameter Douglas-fir with 60-80% bole char, 60-80% crown volume scorch, and 50-70% probability of mortality due to fire. In 1996 beetle preference shifted to smaller diameter trees with lighter fire injury. Tree size was less significant for predicted attack in 1996 because most large fire-damaged conifers were colonized by beetles in 1995. Beetle populations did not reach outbreak proportions outside the fire boundary, but 53 green trees were also infested in 1997 along the burn
perimeter.

Log linear tests conducted to quantify beetle emergence supported conclusions that beetles were not only attracted to mature, moderately fire-weakened conifers, but also produced greater brood numbers with up to 60-80 emergence holes/ 1800 cm². Fire-defoliated trees provided bark beetles with sufficient phloem and limited resistance, allowing beetles to aggregate on areas of viable stem tissue regardless of overall bole char extent.
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CHAPTER 1
INTRODUCTION

Empirical studies concerning the interaction of succeeding natural disturbance agents in the forest ecosystem are rare. Yet, multiple disturbances are critical to the functioning of many dynamic and sustainable forests. Jointly, these agents precipitate the regeneration of vegetative communities and are characteristic of most natural ecosystems. It is not adequate to study disturbance events in isolation. Rather, investigation of relationships between disturbances better predicts unique forest successional pathways. Subalpine fir, *Abies lasiocarpa* (Hook.) Nutt./Engelmann spruce, *Picea engelmannii* Parry, communities affected by dispersed colonization of the native associated bark beetle, *Dendroctonus rufipennis* Kirby (Coleoptera:Scolytidae), typically succeed to a different forest community than the same forest subjected to both fire and subsequent beetle activity (Veblen et al. 1991). Endemic populations of mountain pine beetle, *D. ponderosae* Hopkins (Coleoptera: Scolytidae), may become epidemic in multi-storied lodgepole pine, *Pinus contorta* Doug. ex Loud, forests that experienced a severe blowdown event, leading to eventual replacement of even-aged lodgepole pine stands (Stuart et al. 1989).

Different disturbance agents influence the severity and direction of future forest changes (Knight 1960; Franklin et al. 1987) that determine unique landscape patterns. Tree injury and death cannot be attributed entirely to activity of the most
recent, conspicuous disturbance agent. Drought may predispose a stand to budworm defoliation (Jenkins 1990), which in turn might render forests vulnerable to beetle infestation (Wright et al. 1984). Blowdown may predispose individuals to fungal growth in the living tissue. Beetle outbreaks may increase fuel loads on a slope and create potential fire danger in an entire community (Hadley and Veblen 1993; Hadley 1994), given appropriate fire weather. Fires can possibly kill or damage trees, leaving them susceptible to a variety of insects (Furniss and Carolin 1977). Together, multiple abiotic/insect/pathogen complexes reduce tree resistance and drive a process of gradual decline, leading to replacement of weakened trees (Schowalter and Filip 1993).

This study describes the interaction between fire and insect activity in an uneven-aged, upper-elevation *Pseudotsuga menziesii var. glauca* (Mirb.) Franco community on Beaver Mountain in northern Utah. For three consecutive years host selection of the Douglas-fir beetle, *D. pseudotsugae* (Hopkins), was evaluated following a specific fire event that occurred in 1994. Gara and others (1984) posited that fire may interact with bark beetles in a synergistic fashion to alter forest succession, while Miller and Keen (1960) argued that large beetle outbreaks effected by fire are rare and do not contribute to significant forest community changes. Empirical evidence suggests that *Dendroctonus* beetle-caused mortality is typically restricted to fire-damaged trees (Furniss 1941; Ryan and Amman 1996). However, higher levels of insect-related mortality have occurred in live conifers
within a 2-3 year period after some larger conflagrations (Rasmussen et al. 1996). Beetle-caused mortality of fire-damaged trees following the Tillamook fire of 1933 in Oregon resulted later in beetle colonization of non-fire-affected Douglas-fir that extended into five counties (Furniss 1941; Bevins 1980). Ryan and Amman (1996) suspected that delayed mortality in Douglas-fir following the Yellowstone Fire Complex of 1988 was partly due to a build-up of Douglas-fir bark beetles in fire-injured trees, which led to colonization of green Douglas-fir.

Conversely, Furniss (1965) suggested that larval development in fire-stressed hosts was precluded by a degraded food resource in the damaged phloem. Few callow adults in the northern Idaho 1964 Poverty Flat Burn perimeter emerged from fire-weakened trees to inhabit live host trees. Consequently, Douglas-fir bark beetle preference and success in fire-damaged host trees remains a controversial issue. The topic has not yet been extensively researched to draw any conclusions. Field research is especially lacking for smaller fires that might better replicate a prescribed burn and for higher-elevation sites where lower temperatures and persistent snowpacks might preclude the presence of insects altogether.

Understanding the synergistic effects of fire and insects is especially important to determining appropriate forest management practices, which condition the future appearance of our public lands. Fire suppression over the years has lengthened fire return intervals, resulting in greater accumulations of forest fuels and vegetation. Few forests have experienced regular fire intervals in the past 100
years (Jenkins 1990). Many conifer forests are primed for large conflagrations given appropriate fire weather. Early 1900's selective logging of valued pine species led to an abundance of shade-tolerant conifers, which have overwhelmed Rocky Mountain temperate forest ecosystems (Jenkins 1990). Current information about the physiological response of potentially fire-vulnerable trees to insect colonizers and insect attraction to these stressed trees may be helpful in management of fire and insect epidemics within their natural range of variability (Amman and Ryan 1991).

In this research, two central problems were explored that are critical to knowledge of how fire and phloem-feeding beetles interact in a Douglas-fir community. Answers to the following questions were sought. Would bark beetles select a high elevation stand of Douglas-fir conifers weakened by low-intensity surface fires? Would attacking adult beetles be successful in producing brood in these fire-injured trees? Following is a review of the biology and systematics of the host species, fire and its behavior in this fuel type, and bark beetles present in these Douglas-fir communities. Given that the relationship between bark beetles and Douglas-fir conifers is one of parasite and host, the term *attack* should be interpreted only as a means to most adequately express insect boring activity in Douglas-fir trees.
CHAPTER II
LITERATURE REVIEW

Douglas-Fir Ecology

Douglas-fir is a prominent conifer of the western United States, extending from Canada to Mexico City and from the Pacific Ocean to the eastern slopes of the Rocky Mountains, covering a distance of nearly 4500 km (Isaac 1963; Hermann and Lavender 1990). *P. menziesii var. menziesii* (Little) predominates in the Cascade Range and the Sierra Nevada mountains (Wright and Bailey 1982). The interior Douglas-fir, *P. menziesii var. glauca* (Beissn.) Franco, is widespread throughout the Rocky Mountains and into British Columbia. Both the Rocky Mountain and coastal Douglas-fir in the United States have been found at elevations ranging from sea level to 3300 m (Preston 1989; Uchytill and Crane 1991), but the interior species commonly inhabits slopes between 1800 and 2600 m (Wright and Bailey 1982; Hermann and Lavender 1990). The Rocky Mountain Douglas-fir grows in contiguous uneven-aged and even-aged stands in southern Idaho, northern Utah, and western Montana between the ponderosa pine, *P. ponderosa* Dougl. ex Laws. or *P. flexilis* James., forests and the spruce-fir zone (Hermann and Lavender 1990; Uchytill and Crane 1991). Douglas-fir is a moderately shade-tolerant conifer for as many as 10 subalpine communities in the Central Rocky Mountains (Furniss et al. 1981; Jenkins 1990). The variety *glauca*
is a principal species in three forest cover types: interior Douglas-fir, western larch
\((\text{Larix occidentalis} \text{ Nutt.})\), and grand fir \((\text{A. grandis} \text{ (Dougl.ex D. Don) Lindl.})\)
(Hermann and Lavender 1990). It is a minor species in Engelmann
spruce/subalpine fir, white fir \((\text{A. concolor} \text{ (Gord. &Glend.) Hildbr.})\), western white
pine \((\text{P. monticola} \text{ Dougl. ex. D.Don})\), aspen \((\text{Populus tremuloides} \text{ Michx.})\), and
lodgepole pine (Hermann and Lavender 1990). The Douglas-fir communities form
a broad belt above bunch grass, ponderosa pine, or limber pine habitat types at the
lower end of its elevational range (Daubenmire and Daubenmire 1968). At higher
elevations it is often replaced by subalpine fir \([\text{A. lasiocarpa} \text{ (Hook.) Nutt.}]\) or
grand fir (Wright and Bailey 1982; Uchytill and Crane 1991).

This highly adaptable species is found not only along an extensive elevation
gradient, but can also thrive on many aspects and soil types. Preferring the northern
exposures in moist, deep, porous soil with PH of 5-6 (Preston 1989; Hermann and
Lavender 1990), Douglas-fir also commonly occupy dry, rocky terrain on aspects
subject to drought (Jenkins 1990). Douglas-fir is a significant conifer in the wetter
forest zones where other drought-intolerant tree species can compete. \(\text{P. menziesii/}
\text{Carex geyeri-Symphoricarpos oreophilus}\) and \(\text{P. menziesii/C. geyeri-Artemesia}
\text{tridentata}\) are two examples of Rocky Mountain dry zone communities (Furniss et
al. 1981) where the interior species is a climax dominant. Soil substrates may be
shallow or rocky and comprised of granitic, volcanic, sedimentary, or metamorphic
parent material (Uchytill and Crane 1991).
*P. menziesii var. glauca* has a narrow pointed crown and evergreen flattened needles. A broad canopy and bushy conical silhouette with drooping lower branches distinguish this false fir from other conifer species. Douglas-fir also has unique cones with three-pronged bracts under the scales (Preston 1989). Younger trees have thin, smooth, grey-brown bark, becoming very thick, reddish-brown (1.7-6.8 cm), and furrowed for mature Douglas-fir (Preston 1989). The tree's rooting morphology varies with the nature of the soil. Generally Douglas-fir is considered a deep-rooting species (Hermann and Lavender 1990). Yet, Amman and Ryan (1991) suggested that interior Douglas-fir tend to have many lateral, surface roots that often are injured by ground fire. The size of the root system appears to be correlated to crown size. The proportion of root biomass may range from 50% at age 21 and decrease to less than 20% in 100-year-old trees (Hermann and Lavender 1990).

The stem's subcortical environment is divided into two parts, the inner xylem or wood and the outer phloem. The xylem tissues are composed of vertical trachaeids, as well as resin-producing horizontal ray parenchyma and epithelial cells (Raffa et al. 1993). Oleoresin is the “non-aqueous secretion of resin acid ... exuded from the intercellular resin ducts of a living tree” (Cates and Alexander 1982, p. 217). Young sapwood or outer xylem conducts water with nutrients from the soil from the roots and mychorrhizae to transpiring needles (Raffa et al. 1993). Aged xylem (heartwood) supports the trunk. Phloem tissue, arising from meristem
cells called vascular cambium (Raffa et al. 1993), conducts the flow of dissolved sugars and carbon created through photosynthesis. This energy-rich tissue is also the principal food resource for developing beetle larvae and adults (Furniss and Orr 1978). Lack of water uptake from the soil results in reduced transpiration and reduced photosynthesis of needles, conditioning a decreased allocation of carbon to the construction of phloem tissue. Therefore, the amount of soil water, the photosynthetic capacity of the crown, and the thickness of the phloem tissue are all proportional.

Douglas-fir trees are monoecious and begin producing strobili at 12-15 years of age (Hermann and Lavender 1990). Generally, flowering occurs in spring along with insect emergence (Uchytill and Crane 1991), but can happen as late as June in northern Idaho and the central Rocky Mountains (Hermann and Lavender 1990). Interior Douglas-fir trees produce seed prolifically in the late summer as cones develop. Seeds are wind-dispersed by fall. Total cone crop failures are rare. Large and medium-sized cone crops are produced every 6-10 years (Isaac 1963; Uchytill and Crane 1991). Red squirrels, chipmunks, voles, and shrews feed on these abundant seeds, reducing potential regeneration. Seedlings that do germinate, grow very little their first 3-4 years. After 5 years, growth begins to accelerate (Isaac 1963; Hermann and Lavender 1990). As a Douglas-fir tree matures, it begins to allocate less and less carbon to its leaves and to its apical growth. Rather, the conifer expends energy to maintain its stem and extensive root system. Growth for
Douglas-fir slows down dramatically past 200 years and trees rarely live beyond 400 years (Uchytill and Crane 1991). Adapted to a drier and colder climate, the Rocky Mountain species grows much slower than its coastal variety and seldom exceeds 40 m in height and 152 cm in diameter (Uchytill and Crane 1991; Hermann and Lavender 1990). Trees are decomposed by wood-staining fungi (usually Ceratocystis spp.), by ambrosia beetle activity (Wright and Harvey 1967), and by Fomes pinicola or red belt fungus (Wright and Harvey 1967).

Aging trees eventually weaken and decline, becoming more vulnerable to disturbances that act to maintain the dynamic forest. Insects effectively thin a crowded Douglas-fir stand, opening gaps for new seed establishment. Beetles and fire open the canopy and allow sunlight to reach newly photosynthesizing saplings that were previously unable to germinate because overhead light was <50% (Isaac 1963). Periodic fires combust thick duff, releasing more readily N, P, K, Ca, and Mn nutrients in decomposing logs (Edmonds and Englitis 1989). Meanwhile, severely weakened or dying fire-injured and/or insect-attacked trees become more receptive to saprophytic microorganisms and nitrogen-fixing bacteria (Schowalter and Filip 1993). These decomposing agents mineralize and slowly release bound nutrients for uptake by roots and mycorrhizae of younger trees. In fact, Douglas-fir tussock moth defoliation increases litter accumulation two-fold and raises N, K, and Ca in the soil by 20-30% (Edmonds and Englitis 1989), while pathogens aid in decomposing organic carbon. “Rather than threatening the forests... bark beetles,
fungi and pathogens interacting with fire have been instrumental in maintaining healthy conifer forests through natural thinning, nutrient-cycling and selection for site-adapted trees" (Schowalter and Filip 1993, p. 11).

**Fire Disturbance in Douglas-Fir Habitat**

The mean fire-return interval in Douglas-fir communities ranges from frequent, low-intensity surface fire to infrequent, severe canopy fires depending on habitat type, climatic conditions, and fuel loads (Arno 1976; Wright and Bailey 1982). Surface fires typically occur above decayed organic matter on the forest floor, in low brush, and in surface slash. These fires ignite every 15-30 years in young, productive Douglas-fir communities within the northern Rocky Mountains after a dry summer. The same forest stands may experience a high-intensity fire extending into the crown every 35-60 years (Arno 1976), depending on site conditions, elevation, and frequency of appropriate fire weather. On moist and high elevation sites, the fire return interval for ground fire can be as long as 45-50 years or longer, as was documented in southwestern Montana fire history (Arno 1976). Conversely, the drier Douglas-fir communities of the Northern Rockies may experience low to moderately intense ground fires at less than 30-year intervals (Arno 1980). The mean fire-return interval for the Bitterroot National Forest over the last 250-300 years on montane slopes between 1400-2067 m in Douglas-fir/ponderosa pine ranged from 2-48 years (mean 19 years). On the lower subalpine
slopes between 2,233 and 2,500 m in Douglas-fir/lodgepole pine, fire episodes ranged from 5-67 years with an average of 28 years (Arno and Petersen 1983).

Forest species composition and density, controlled in part by abiotic factors, play a role in determining the characteristic of fire and subsequent damage to the vegetative community. In *Pseudotsuga menziesii var. glauca* / *Pinus ponderosa* Laws. forests frequent ground fires every 10-15 years maintain open park-like stands of both larger fire resistant *P. contorta* Dougl. and thick-barked Douglas-fir, while propagating seral stands of fire-susceptible seedlings (Daubenmire and Daubenmire 1968). If Douglas-fir canopies become dense thickets, then these forests can become more susceptible to large, stand-replacing conflagrations (more common at the turn of the century). In 1933 the burn perimeter of the Tillamook fire in eastern Oregon Douglas-fir was equivalent in size and severity to the 1988 Yellowstone fire in predominantly lodgepole pine, reaching 98,000 ha in 1933. Later fires in 1939 burned 105,200 ha and in 1945, 36,000 ha (Bevins 1980).

There are three predominant ways in which fire injures conifers. The three primary components of fire stress imparted to Douglas-fir are crown scorch, bole char, and root damage (Ryan 1982a; Ryan et al. 1988).

Heat-caused injury to the canopy was found to be the most common source of tree mortality due to fire (Van Wagner 1972; Peterson 1985; Peterson and Arbaugh 1989). Crown fires are very intense, destructive disturbances that can defoliate an entire tree. Although Douglas-fir forests are more commonly subject to
ground fire (Arno 1980), dense uneven-aged Douglas-fir/subalpine fir forests can be susceptible to crown fires because the lower branches of young Douglas-fir and the crowns of succeeding true firs may create continuous ladder fuels (Ryan 1982a). Fire damage effects to the photosynthetic tissue of conifers vary, conditional upon the quantity of crown scorched, the type of live tissue heated, and the timing of the needle-torching event (Wagener 1961). Conifer mortality for mature Douglas-fir increases substantially as the percentage of crown volume scorched exceeds 60% (Van Wagner 1972), including both bud and needle kill (Ryan 1982a). Yet, young and vigorous trees could survive fire-effected defoliation of greater than 80%, if at least 20% of the buds survived (Ryan et al. 1994).

Fire season influences the degree of injury imparted to the photosynthetic tissue. Ignitions in August or September may not be as detrimental to tree foliage and bud survival as fires in the spring (Wagener 1961; Furniss 1965; Ryan 1982b). In early May young shoots are forming and trees produce new foliage from their food reserve. Buds are open and are more vulnerable to heat damage (Van Wagner 1972). By late summer the buds of the tree are set, growth is finished, and the needles are well protected (Ryan 1982a). After a fire, the live branches that were heated may immediately drop old needles and re-sprout during the growing season. Douglas-fir has slender twigs and small terminal buds, so the distinction between foliage and bud growth is slight. However, foliage death merely results in temporary loss of photosynthetic capacity, while bud loss precludes future growth
Scorch height of the canopy is the level at which a 60 °C lethal pulse of heat to the foliage causes drying and dying (Bevins 1980). Originally, this measure was used to indicate fire-caused crown damage. However, the percent of crown volume scorch (CVS) has been shown to be the best indicator of injury to photosynthetic tissue (Wagener 1961; Peterson 1985). Peterson (1985) gave three reasons for using CVS instead of scorch height. Scorch patterns are irregular around the tree because of the formation of vortices on the uphill or leeward side of the trunk (Gutsell and Johnson 1996). Tree species with open canopy growth habits experience lighter damage through the crown, whereas trees with denser crowns show greater heating. The upslope portion of the canopy will have greater damage due to the angle of flame and greater heat intensity on the stem’s leeward side (Peterson 1985).

Fire-caused injury to the cambium and roots may contribute to tree stress following low-intensity ground fires (Arno 1976; Ryan et al. 1988). Twenty minutes of exposure to a fire of average intensity can destroy the cambium under 1 cm of bark (Ryan 1982b). Ryan and others (1988), and Ryan and Amman (1994) speculated that conifers can survive up to 75% basal cambium kill with the absence of significant canopy damage. However, later studies conducted after the Yellowstone Fire Complex in Douglas-fir/lodgepole pine forests demonstrated that in a sample of 125 fire-affected Douglas-fir, the absolute basal girdling of surviving
trees was 59%, if they accounted for delayed fire mortality effects (Ryan and Amman 1996). Ryan and Frandsen (1991) asserted that mature conifers subject to over 50% basal cambial kill soon succumb to chronic moisture stress and die. This stress is observed when symptoms of greying tissue surrounded by concentrations of resin are seen.

In order to determine overall health for weakened conifers following ground fire, stem injury should be included in complete fire damage analyses. The most efficient measure of observed bole char is the percentage of scorch evident on the lower stem, including exfoliated bark and obvious root crown injury (Ryan 1982a). Cambial cores were taken in each of the four cardinal directions at the base of fire-damaged Douglas-fir trees for other fire field studies (Amman and Ryan 1991; Rasmussen and others 1996). However, these sample intensive measurements are site/time specific and still may not accurately assess the actual degree of stem damage (Ryan 1982b).

Damage to underground roots is the third most common cause of conifer fire-caused mortality (Ryan 1982a). Basal girdling by fire with extensive root damage may lead to moisture stress (Norum 1976; Ryan 1982b) and limited resistance to insects or disease (Furniss 1965). Shallow roots enable the tree to withstand drought during summer rain conditions, but an extensive lateral root system may make trees more susceptible to longer duration surface fires (Reinhardt and Ryan 1988). If fire burns intensely at the base of a maturing tree in organic
duff accumulations, then Douglas-fir's shallow lateral roots are likely to be vitally harmed (Ryan and Amman 1994). Root mortality due to fire is primarily correlated with duff depth, soil moisture, and fire consumption of the organic forest floor (Ryan 1982a; Reinhardt and Ryan 1988). These variables are a function of tree growth, annual precipitation, and fire behavior, respectively. Duff under prominent Douglas-fir trees is comparatively thick and carries slow, consuming fire that would heat the soil and roots at the tree's base (Furniss 1965). Further, duff consumption by fire is usually greatest in late August when fine fuels have dried sufficiently (Norum 1976), especially if the organic soil horizon is deep (Ryan 1982b).

Soil samples and fuel load inventories adjacent to burnt plots might be significant indirect indicators of fire intensity for low-intensity ground fire. Yet, post-fire recordings of soil heating or altered microbial composition assessed 2 years after this disturbance event would be inconclusive in accurately determining cambial or root damage.

Tree diameter size has been shown to influence individual tree resistance to fire and potential recovery from the fire. Diameter at breast height (DBH), taken at 1.5 m from the tree base, is perhaps the most critical and basic measurement for defining tree size. Small trees are rarely observed with fire scars or partial cambial charring. They are either completely crown defoliated by fire or their cambium is entirely scorched by fire (Gutsell and Johnson 1996). Young saplings are often
killed by surface fires due to their low-branching habit and closely spaced needles. Following a low-moderate intensity fire in Colorado, dead trees in a mixed-aged stand averaged 14.3 cm DBH and only 6.9 m in height (Uchytill and Crane 1991). Larger trees with thicker, more insulating, and furrowed bark are able to resist bole cambium charring (Ryan 1982b; Uchytill and Crane 1991). A twofold increase in bark thickness increases the fire resistance to cambial kill by a factor of four (Ryan 1982a). Further, a tree supporting a larger bole with a relatively smaller crown is usually less susceptible to crown scorch. Taller Douglas-fir typically self-prune to greater heights and have proportionally more foliage above the lethal scorch height (Reinhardt and Ryan 1989; Ryan et al. 1994; Wyant et al. 1986). Protection offered by thick bark and large tree size can, however, be offset by older, more flammable foliage (Uchytill and Crane 1991) and usually greater accumulations of basal duff (Norum 1976). If the duff becomes sufficiently dried, it provides excellent fuel for a longer duration fire at the root crown of the Douglas-fir, especially in a ground fire (Ryan and Frandsen 1991).

Although large diameter Douglas-fir trees are generally more resistant to ground fire and crown fires, larger trees are less likely to recover from fire injury if they become stressed. Mature Douglas-fir have more respiring tissue (a carbon sink) and relatively less photosynthetic biomass (carbon source) than younger and smaller diameter trees. As the individual tree approaches maturity, the growth curve flattens (Ryan 1982a). Older Douglas-fir allocate more energy to supporting the
large stem and extensive root system (Gutsell and Johnson 1996). If crowns of mature conifers become scorched, recovery is more difficult for them relative to smaller trees with greater photosynthesizing potential.

**Douglas-Fir Bark Beetle Development and Ecology**

The Douglas-fir beetle is one of 24 species in the genus *Dendroctonus*, a term that means literally "killer of trees." It is a native insect associated with both the coastal and interior varieties of Douglas-fir (Furniss 1941). Earlier this century, foresters considered the bark beetle a destructive forest pest to be managed through eradication. Furniss and Orr (1978) reported that *D. pseudotsugae* destroyed 7.4 billion board feet of timber from 1950-1969 in western Oregon and Washington during four separate outbreaks. During a 1966 epidemic in California, the beetle caused vital damage to 800 million board feet of Douglas-fir trees. In 1968 Idaho forests counted 109 billion board feet lost to this insect (Furniss and Orr 1978). Consequently, many entomologists in the 1960’s and 1970’s initiated a research campaign to understand the behavior and biology of this beetle for control purposes.

*D. pseudotsugae* adults are small, stout beetles with reddish-brown shield-like wing covers (Furniss and Orr 1978). The hatched larvae are legless, curved, pearly-white insects with shiny brown heads. They grow to 1 cm long throughout their four stages of developmental instars (Kimmey 1943). The beetle is uni-voltine and spends most of its existence beneath the bark of its host tree (Furniss 1965;
Furniss et al. 1981). Phloem is the principal food source for developing larvae and adults, who benefit from the tree’s store of nutritious starch and sugars (Raffa et al. 1993). Fortunately for the host, the nutrient content of their phloem is greatest in the late fall and winter when the insect larvae are no longer feeding. Phloem quality then declines rapidly in the spring when the adult beetles commence flight (Raffa et al. 1993).

The insect's adult life cycle can be segregated into four distinct stages: dispersal from the hibernation site, host selection, aggregation or mass colonization, and establishment or successful oviposition (Raffa et al. 1993). Adult beetles emerge from their overwintering site in early May to June when the maximum air temperature reaches 18.3-21.1 °C for several days (McMullen and Atkins 1962; Furniss et al. 1981; Lessard and Schmid 1990). Both Atkins’ (1966), and Schmitz and Rudinsky’s (1968) research confirmed that peak periods of host selection followed periods of sunny weather and air temperatures around 18.3 °C. Colonization dwindled with intermittent rain, clouds or temperatures below 10 °C. Conversely, atypical warm, dry weather led to prolonged flight periods (McMullen and Atkins 1962) where two flights per season were possible. Female adults could emerge to attack in early spring and reemerge to commence a second flight in late summer (Rudinsky and Vite 1956; Wood 1982). During the original period of host selection, primary female beetles identify potential hosts and taste the bark for suitability prior to colonizing the tree (Furniss and Orr 1978). If females deem the
host suitable for colonization, they send out aggregation pheremones to allure fellow beetles. The species-specific attractive pheremone plume is synergized by host resin chemicals, primarily conversions of host monoterpenes, like verbenone derived from alpha-pinene (Rudinsky 1966b; Furniss et al. 1981). Both males and unmated females sense the aggregation pheremone using their antennal chemoreceptors. However, the sex ratio of secondary beetles is usually two males to three females (Vite and Rudinsky 1957). High male mortality during flight possibly contributes to this disparity. Males spend more time exposed to the elements and predators than do females. They not only have to orient toward aggregation centers, but males must crawl around on the bark to search for a fresh entrance hole. Further, each male remains in the parent gallery no more than 2 weeks before setting out to find another female (Vite and Rudinsky 1957).

Once the female has found a mate, together they bore into the tree bark, trailing behind pitchy, reddish-orange frass (Rasmussen et al. 1996). In response, the host tree produces toxic monoterpenes, resin acids, and phenolics as chemical defense against invasion (Raffa et al. 1993). Sometimes the tree will even exude massive amounts of clear resin from the upper portion of the infestation zone (Furniss and Orr 1978). Healthy Douglas-fir may be suitable to beetle populations, but strong resistance to insect activity may deter their colonization. Conversely, stressed trees may not be capable of “pitching out” beetles, though few bark beetles are attracted to weakened conifers with less phloem. Host tree vigor and initial
insect density continually oscillate around an equilibrium point.

If bark beetles do not succumb to the tree's defense system, many females will aggregate on selected Douglas-fir and construct their own vertical, elongated egg galleries (Furniss 1941). Meanwhile, the male will pack the excreted frass behind his mate along the walls for warmth and protection. Optimal adult activity temperatures within the gallery have been reported between 26-28 °C (Furniss and Carolin 1977). Once impregnated, females lay eggs in niches on alternate sides of the gallery to maximize phloem resources (Furniss and Orr 1978). Marsden and others (1981) described the lateral egg galleries to be 15-20 cm long, with a density of 5-10 eggs per gallery at successful levels of colonization. In 1-2 weeks when eggs hatch, the larvae mine the phloem laterally and create double-fan-shaped (Furniss 1941) tunnels which effectively girdle the tree. Dusty bronze-yellow frass exuded from the tree positively identifies the presence of these feeding larvae laid in the host conifer by adults the previous flight season. Under ideal conditions larvae mine for 1 month (Marsden et al. 1981). After a short pupal stage of 9 days, adults begin to develop. Vite and Rudinsky’s (1957) study of 1,600 adults, and 8,900 total larvae and pupae in the laboratory found complete larval development from eclosion (or the egg state) to pupation in 30 days at 29-30 °C. Full development occurred only after 100 days at temperatures between 14-15 °C. Given those temperature requirements, nearly all brood subject to amiable temperature conditions create a pupal chamber and transform into callow adults by
fall (Furniss and Orr 1978). There they go into diapause and overwinter until the next spring flight season (Furniss 1964b; Furniss et al. 1981). While inside the pupal chamber, callow adults develop sex organs and a hardened skeleton to protect them against adverse cold and wet conditions or against predators (Rudinsky 1966a).

It is difficult for host trees, especially weakened Douglas-fir, to provide significant amounts of phloem resource year after year that is necessary for insect populations to increase substantially. Although the female beetle is capable of laying nearly 22 eggs per gallery (McMullen and Atkins 1961), egg survival can be as low as 45%, larval survival 33%, and pupal survival 13% (Fredricks and Jenkins 1988). Typical brood mortality in Fredricks and Jenkins’ (1988) analysis equated to a .52 emergence rate per female. Emerging insect sex ratio was recorded by Rudinsky (1966a) to be 1:1. In order to expand populations, beetles must seek healthier trees to colonize and risk being pitched-out by the resistant hosts.

The symbiotic relationship developed between bark beetles and fungi catalyzes a positive feedback loop that helps reduce Douglas-fir host resistance, enhancing bark beetle chances of colonizing relatively healthier trees. If the tree is successfully overcome by insects, bark beetle boring and associated blue-stain fungi create a reduction in oleoresin flow in the tree. Blue-stain fungi, traveling in the bark beetle mycangia, become inoculated onto the host tree xylem at the onset of beetle boring and effectively assist girdling the tree (Lewinsohn et al. 1994).
Conversely, intraspecific competition and interspecific competition between bark beetles, beetle predation, and parasite activity create a negative feedback loop in decreasing the bark beetle population. These biotic effects contribute to greater survival of trees from beetle colonization. Schmitz and Rudinsky (1968) suggested that competition for food and space is one of the more important factors limiting the rate of species multiplication. Rudinsky (1966a) reported that if successful Douglas-fir beetle attacks were greater than 8/2.7 m, then many larvae would die. In the spring, one female lays enough eggs to hatch as many as 22 brood in a viable egg gallery (McMullen and Atkins 1961). However, if female attack densities increase to 12 per 900 cm², the host becomes overcrowded and few larvae will survive (Lessard and Schmid 1990). If egg spacing is too close or if the larvae must mine around fungus-deteriorated phloem, then the larval tunnels begin to intersect and young instars will compete for food resources (McMullen and Atkins 1961; Furniss 1964b). Greater levels of larval mortality generally occur in the later instars because as the larvae grow their tunnel widens and their food requirements increase. One evolutionary bark beetle adaptation to intraspecific competition is the complex production of anti-aggregation pheremones. As a tree becomes too densely colonized, the males will elicit stridulatory sounds and induce their associated female to release anti-aggregation pheremones concentrated in beta-pinene (Rudinsky 1966a). This chemical plume effectively masks the attractive effect of other attractive pheremones and
aggregation is greatly reduced or ceases. Alternately, the female may reemerge and select another tree to lay her eggs. However, reemergence and flight are an additional drain on her lipid resources, so she is unlikely to be very successful (Atkins 1966).

Interspecific competition for similar resources and habitat can be another limiting factor to bark beetle population expansion, though not as critical for the Douglas-fir beetle. *Buprestis spp.* (Coleoptera: Buprestidae) emerge mostly in the springtime along with the Douglas-fir beetle, seeking newly weakened or dead Douglas-fir hosts. The adults, ranging from 12 to 20 mm long, are iridescent green or blue with “the margins of the electra bordered by copper” (Furniss and Carolin 1977; Mitton and Sturgeon 1982). The larvae’s heads are flattened, giving them the common name, flat-headed borer. Characteristic elliptical boring holes and flat masses of egg deposits positively identify the presence of *Buprestis spp.* in a host tree. Nutritional demand of the tree is apparently less for the Buprestid beetle than the phloem quality requirement of the *Dendroctonus* beetle (Kimmey 1943). As a result, they are not limited to live or only moderately damaged phloem tissue and they do not commonly overlap the Douglas-fir beetle’s niche. Female *Buprestis spp.* are able to lay their eggs in the crevices of the outer bark (Smith 1962). Larvae bore into the dying cambium region of the trunk, roots, and branches, and often mine the sapwood extensively (Mitton and Sturgeon 1982). *B. aurulenta* L. larvae typically bore in and around fire scars (Furniss and Carolin 1977).
Along with the *Buprestis spp.*, ambrosia beetles are the earliest colonizers of severely fire-damaged Douglas-fir. Following the 1933 Tillamook burn, they were the first to enter scorched wood (Furniss 1941). These small, cylindrical, dark, reddish-brown beetles construct simple short mines in the sapwood of unseasoned, downed timber (Furniss and Carolin 1977). The majority of ambrosia beetles associated with Douglas-fir, *Trypodendron lineatum* (Oliv.), begin to fly in early May (Rudinsky and Daterman 1964) and usually occupy windthrown or downed Douglas-fir. To locate their host, these insects first sense aggregation pheremone plumes and use other tactile and visual cues at closer range (Rudinsky and Daterman 1964). *Gnathotrichus spp.* Lee, another ambrosia beetle significant to *Dendroctonus* beetles, have a longer flight season which overlaps the Douglas-fir beetle’s flight. *Gnathotrichus spp.* aggregate toward the scent of the Douglas-fir beetle’s mass attraction pheremone or her borings (Rudinsky and Daterman 1964) and overwinter in *P. menziesii* stems. If piles of fine white boring dust can be found at the base of burnt trees, ambrosia beetles are active. The ambrosia beetles primarily feed on black-stain fungus (introduced fungal spores in the heartwood), so phloem food competition with Douglas-fir beetles is not a problem.

An array of other wood-boring beetles from the family Cerambycidae select fire-killed Douglas-fir. The Cerambycidae (long-horned or round-headed borers) are cambium wood feeders that construct long, irregular tunnels into the sapwood (Furniss and Carolin 1977). Like ambrosia beetle activity, Cerambycidae
Infestation does not result in tree mortality and does not directly influence Douglas-fir colonization. Rather, Mitton and Sturgeon (1982, p. 255) described the function of the borers in the forest ecosystem as decomposers that “... aid in the natural process of returning the deadwood to the soil.” Presence of woodborers in a depreciating tree have a significant impact on the decomposition rates of logs (Edmonds and Eglitis 1989). They effectively loosen the wood, allowing entrance of fungi and other pathogens into the heartwood of the tree (Kimmey 1943).

Insect parasites and entomophagous insects, on the other hand, can have a direct detrimental impact on Douglas-fir brood success (Furniss and Orr 1978). Marsden and others (1981) reported one significant insect parasite, *Coeloides vancouverensis* (Hymenoptera: Brachonidae) [Dalla Torre] (=brunneri Viereck), and two important clerid predators, *Enoclerus sphegeus* (Coleoptera: Cleridae) Fabricius and *Medetera spp.* (Coleoptera: Cleridae) Wheeler, for the Douglas-fir beetle in the Intermountain West. Because *C. vancouverensis* females deposit eggs singly via an ovipositor injected into the bark, most of these parasites were excluded from very thick-barked Douglas-fir trees beyond the length of the ovipositor, 4.6 mm. Yet, Bedard (1950) estimated that 29% of the Douglas-fir beetles in his sample were parasitized by this insect alone. However, *E. sphegeus* consume more bark beetle adults per predator per day than any other predator. These insects attack windthrown trees with the greatest densities of bark beetles, 61-70 beetles in 3.1 m of stem area (Cowan and Nagel 1965; Schmitz and Rudinsky
Entomophagous insects emerge in May and June, preying on bark beetles and laying eggs in masses under bark crevices. By the end of the summer their larvae hatch and enter bark beetle galleries, searching for viable larvae prey (Marsden et al. 1981). Theoretically, clerids consume 400 larvae in their lifetime, though overall they fail to have a major impact on Douglas-fir insect densities despite large beetle populations (Cowan and Nagel 1965). Temporally short cycles of Douglas-fir beetle infestation due to other exogenous factors protect isolated pockets of expanding bark beetle populations from much predatory influence.

In addition to predatory insects, woodpeckers prey on *Dendroctonus* beetle larvae and the buprestid beetle larvae living in the sapwood of Douglas-fir tree stems. Miller and Keen (1960) noted mortality of the western pine beetle larvae by native woodpeckers and up to 75% mortality of spruce beetle populations due to woodpecker activity. Yet, Furniss and Orr (1978) concluded that woodpeckers were an insignificant predator for Douglas-fir beetles, especially in the first years of colonization when woodpeckers were rare. Overall, Pasek and Schaupp (1995) recognized the concerted impact of biotic agents on brood production. Yet, they concluded that the relative influence of insect competitors, insect predators, and woodpeckers on the mortality of Douglas-fir beetle larvae is largely unpredictable and possibly irrelevant in most cases.
Factors Influencing Douglas-Fir Beetle Host Selection and Success

Four questions are important when considering Douglas-fir beetle host preference and relative brood production success. 1. Which Douglas-fir trees and what parts of the stem do these beetles selectively attack? 2. What cues do bark beetles use in choosing certain trees for colonization? 3. What factors affect bark beetle population densities and the dynamics of secondary host selection? 4. What makes an individual host tree more susceptible or more resistant to attack? The first three questions will be discussed at length here, whereas the last problem will be elaborated upon in the following section.

Progressively more mature, larger diameter trees with thicker phloem per square surface area to support larval populations (Furniss and Orr 1978) seem to be the beetle’s preferred food resource. Abundant resin production from these mature conifers might impede invasion. Yet, if these Douglas-fir are successfully colonized in greater numbers, then brood production can increase (Furniss et al. 1981). Amman and Ryan (1991) reported that most Dendroctonus beetles invariably infest larger diameter trees, possibly because thicker phloem correlates directly with the more successful development of larvae (Cole 1973; Cates and Alexander 1982).

Stand density, stand age, and proportion of host conifers in diverse forests also condition the vulnerability of Douglas-fir trees to beetle colonization (Furniss
et al. 1981). McMullen and Atkins (1962) noted that beetles do not colonize aged snags with desiccated phloem tissue. Furniss and Orr (1978) reported that overly dense stands of Douglas-fir are more susceptible to bark beetle epidemics. The literature supports the fact that *D. pseudotsugae* is a secondary agent of disturbance, infesting downed, damaged, or weakened trees (Wood 1982; Furniss et al. 1981; Fredricks and Jenkins 1988; Jenkins 1990; Stark 1993). Large-scale episodic disturbances have been reported to expand *Dendroctonus* spp. beetle populations (Hadley and Veblen 1993). Lightning-struck or recently windthrown trees (Wood 1982), slash from logging operations (Fredricks and Jenkins 1988), and boles broken from snow creep/avalanching (Coulson and Witter 1984, cited in Fredricks and Jenkins 1988) have been shown to be susceptible to *Dendroctonus* spp. beetle attack. By trapping *D. ponderosa* on window barrier traps, Gara and others (1984) found that during an outbreak more fire-scarred than unscarred trees were killed by the pioneering beetles. Would Douglas-fir bark beetles select fire-weakened trees to inhabit?

Douglas-fir bark beetles specifically colonize Douglas-fir trees almost 2 m up from the root crown because on the mid-bole there is more viable phloem space for the larvae to fan out and greater storage of the tree’s carbon resource (Heikkenen and Hrutfiord 1965; Cates and Alexander 1982). In Rudinsky’s (1966a) field evaluation of mature Douglas-fir, larvae mines were more abundant and longer egg galleries were located on the upper/mid-bole of selected mature
hosts. Field studies of Douglas-fir bark beetle activity in windthrown or downed
trees concluded that the middle zone of the tree bole exhibited the most dense, most
successful, and least variable insect infestation (Furniss 1964a; Schmitz and
Rudinsky 1968; Marsden et al. 1981). Occasionally the basal portion of the tree
from 5-10 meters was not attacked in large Douglas-fir. Rather, the lower bole was
infested only after several months following successful colonization of the middle
and upper stem (Furniss 1965). Excessive moisture beneath the bark at the tree’s
base likely contributed to unsuccessful beetle boring activity on the lower stem
(Bedard 1950). The average sizes of Douglas-fir measured for insect emergence on
Furniss’s (1964a) field site were over 35 m in height and 50 cm in diameter (Pasek
1990). However, given that tree height and variable phloem thickness along the
stem are generally correlated (Furniss 1965), a younger and shorter Douglas-fir tree
would likely experience bark beetle attack lower on the tree bole (Pasek 1990).

Researchers suspected that Douglas-fir beetles have developed particular
environmental cues to orient them toward viable hosts. The ability to find suitable
food and shelter for Dendroctonus spp. insects is the foundation of their
evolutionary success, “although, no definitive studies have been made that delineate
the complete basis for host selection by bark beetles” (Cates and Alexander 1982, p.
213). Future field work is needed to elucidate Douglas-fir bark beetle colonization
and exact mechanism of host selection. Primary attraction appears to result from
odors emanating from injured trees (Person 1931, cited in Stark 1993; Heikkenen
and Hrutfiord 1965). Weakened trees may emit volatile substances that subtly attract beetles. Rudinsky (1966b) demonstrated that *D. valens* were strongly attracted to volatile terpenes released in the oleoresin when the tree was injured or stressed. Treatment of *P. engelmannii* bark with 95% ethanol, a compound volatilized by the host species upon injury, induced *D. rufipennis* attacks (Moeck 1981). Heikkenen and Hrutfiord (1965) confirmed in laboratory studies that pioneer Douglas-fir bark beetles were attracted to alpha-pinene concentrations in the inner bark’s oleoresin, but repelled by high amounts of beta-pinene. Aggregation pheremones emitted by pioneering females are composed of unmodified plant compounds, primarily limonene and the conversion of host monoterpenes to verbenone, derived from alpha-pinene (Heikkenen and Hrutfiord 1965; Rudinsky 1966a). In nature beetles do not invade the crown, nor the bark on younger trees concentrated in beta-pinene (Heikkenen and Hrutfiord 1965), but aggregate instead toward stress resin exuded from damaged or aged cambium tissue (Furniss 1965).

In a later field report, Furniss and others (1981) found that the alpha-pinene component of oleoresin varied from 10-52% with the amount of oleoresin found in a tree bole exhibiting a specific physiological state associated with variable water stress. These discoveries led many entomologists to conclude that perhaps pioneering insects could sense a tree’s moisture condition. Disturbances in the tree-water relationship cause a subnormal physiological condition in the host, rendering
it more susceptible to beetle attack (Vite and Rudinsky 1957; Stark 1993). Water disturbance is best reflected in the turgor pressure of epithelial cells lining oleoresin conduits (Rudinsky 1966b). Therefore, oleoresin exudation pressure (OEP) is a good indicator of the resin-producing ability of Douglas-fir trees and perhaps of insect host selection. Larger diameter trees generally have a lower OEP because they are typically under more water stress, needing to support a larger stem.

Normally transpiring Douglas-fir needles secluded in a moist growing environment have high OEP and emit oils with a low alpha/beta-pinene ratio. In the heat of the summer, more exposed crowns of trees living under similar site conditions exhibit low OEP and rapidly volatilize attractive resin oils with higher ratios of alpha/beta-pinene (Heikkenen and Hrutfiord 1965). Interestingly, Douglas-fir trees with mature, damaged, or exposed canopies are preferred by bark beetles for attack (Furniss 1965). Though the insect’s flight season in late spring correlates with the greatest OEP in tree stems, the time of daily flights in the late afternoon coincides with the diurnal minimum OEP.

When pioneering female bark beetles colonize an individual tree, unmated females are attracted to the aggregation pheremones that these primary females produce upon initial boring. Discerning the cause of secondary invasion becomes difficult. “Once a standing tree is successfully attacked, it becomes the dominant attractant for other beetles into it and into boles of nearby un-infested trees because of locality” (Johnson and Belluschi 1969, p. 291). Dispersal tests of Douglas-fir
bark beetles later in the flight season suggest that OEP or alpha-pinene concentrations are not as important in determining secondary host selection. Density of beetles and the rapidity of mass invasion become important (McMullen and Atkins 1962; Rudinsky 1966b; Furniss 1965). Therefore, a study of host selection would be incomplete without mention of the biological and environmental factors that control concentrated bark beetle populations. These primary factors include: adult female lipid content upon emergence and flight capacity, regional weather and climatic conditions, and the nature of host disturbance that sufficiently weakens a stand of Douglas-fir. All of these variables play a role in determining successive bark beetle population densities, and therefore secondary host selection.

Lipid content of emerging callow adults is a function of the quality of phloem tissue in the host, intraspecific competition, and other factors that would contribute to the relative health of this second generation adult. Newly emerged beetles are phototropic, but reverse their light response and seek new hosts before fat content is depleted (Atkins 1959a; Atkins 1966). Greater flight time reduces lipid content (Atkins 1959b), so it is desirable to colonize nearby hosts. Bark beetles that remain phototropic for a longer time do not respond immediately to nearby attraction centers. Rather, they migrate to remote locations, selecting new susceptible hosts (Atkins 1966). These females are critical to ensuring the continuance of populations when infestation centers are bereft of suitable host material (Atkins 1959a). Rudinsky and Vite (1956) documented that the Douglas-
fir beetle can fly for 3 days for at least 4 hours daily and cover at least 48 km in active flight. Therefore, the possible range of flight could maintain a viable population, if large stands of weakened Douglas-fir could be found on a continual basis within this range, and if the females’s capacity for flight is not restricted by limited lipid reserves.

Climatic conditions during the flight season and at the time of larval development also contribute to establishment of secondary bark beetle populations. Callow females fly within a restrictive band of temperatures. Between 18-20 °C, flight attempts are spontaneous (Rudinsky and Vite 1956). If the flight is late in the season, larval development is delayed and young, vulnerable instars may be forced to overwinter (Johnson 1967; Johnson and Belluschi 1969). However, if colonizing females emerge early in spring due to favorable light conditions and preferred temperature regimes of 60 °C, then the potential for larval success is greatly increased (Atkins 1966a). When 3 weeks of cold and moist conditions follow a period of warmth that elicited emergence, the frequency of female boring is usually reduced or terminated. This reduced activity is generally due to activated resinosis or an increase in the host’s OEP under these moist circumstances (Rudinsky 1966b). Would temperature-sensitive insects still be attracted to and successfully establish brood in trees at a cool, higher elevation site? Amman and Ryan (1991) suggested that later beetle flights and higher rates of larval mortality occurred at high elevation sites. Even if the food resource is adequate, beetles may not colonize sites in the
northern latitudes where colder temperature are common throughout the year and persist into the summer months (Johnson 1967; Rudinsky 1966b).

The type of disturbance events preceeding beetle host selection might also impact bark beetle boring activity and population growth in Douglas-fir communities. Bark beetle infestation centers are usually small and dispersed in conifer stands subject to windthrow because this disturbance event typically affects the largest, most mature individual trees scattered throughout the forest (White 1979). Conversely, an entire contiguous stand of Douglas-fir may become susceptible to water stress given an extensive period of spring drought and allow colonization of larger bark beetle populations (McMullen and Atkins 1962). During and after defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata* McD. (Lepidoptera: Lymantriidae), a number of host conifers were colonized by beetles that experienced 90% leaf-loss (Wright et al. 1984). Yet, after Douglas-fir crowns regenerated lost photosynthetic tissue, resistance to insect attack increased and populations of the beetle decreased (Johnson 1967; Wright et al. 1984). Consistent with McMullen and Atkins's (1962) findings, Furniss (1965, p. 9) stated that "the incidence of Douglas-fir beetle attack increased with the degree of crown injury...but declined abruptly in [completely] defoliated trees."

The seasonality of a disturbance might also condition population densities because the bark beetle’s life cycle is univoltine and emergence happens in the spring (Furniss and Orr 1978). A fire event in late summer that might sufficiently
cure wood by the beetle’s following flight period may no longer be desirable, especially for less fire-resistant and thin bark trees (Veblen et al. 1991). Conversely, an avalanche disturbance may deposit fresh host material, immediately preceding the beetles’s emergence in spring.

**Host Susceptibility and Resistance to Beetle Activity**

When bark beetle boring into the Douglas-fir stem commences, the tree initiates one of two distinct defense mechanisms against parasitic colonization, necrosis or resinosis. Necrosis, the conifer’s induced defense mechanism, inhibits beetle colonization and fungal spread at the time of attack (Johnson 1967). Initiation of this defense response demands that large amounts of carbon energy be expended to synthesize terpenes and phenolic compounds. In a necrotic reaction, first the tree removes all nutrients and water from the cells surrounding the infestation in attempts to nutritionally deprive the invading beetles and to compartmentalize associated fungus (Vite and Rudinsky 1957; Miller and Keen 1960; Wood 1982; Lorio 1993; Raffa et al. 1993). Second, the host mobilizes toxins to the wound site (e.g., poisonous monoterpenes, acetates, phenol, alkaloids and pyrethrines) to impact the metabolism of feeding-insects, and to restrict the growth and spread of fungi (Lorio 1993).

Resinosis is the preformed, short-lived resinous flow (Rudinsky 1966b) of toxic monoterpenes, resin acids, and phenolics (Raffa et al. 1993) that physically
expels beetles and prohibits fungal spread. Many plant physiologists consider the energy expensive resinosis reaction the most important factor influencing the impact of beetle activity (Rudinsky 1966b). Resinosis interferes with species-specific pheremone solicitation, it repels beetles from further attack, and it precludes beetle gallery construction (Raffa et al. 1993). In resinosis, the vertical parent gallery becomes flooded with resin from the entrance of the gallery. Beetle gallery construction is impeded because beetles are either pitched-out by resin or poisoned by the resinous monoterpene vapors (Rudinsky 1966a; Nebeker et al. 1993). Generally, this defense mechanism causes the clogging of bark beetles’ spiracles and they die of suffocation.

The tree’s capacity for resinosis and necrosis depends primarily on the water condition of the host, its photosynthetic capacity, and on the amount of available soil nutrients (Nebeker et al. 1993). A relatively healthy tree is able to generate greater amounts of oleoresin. If oleoresin exudation pressure (OEP) is high in an individual tree, then the capacity for necrosis/resinosis increases and bark beetles are repelled by the tree at short distance or are intoxicated. Interestingly, oleoresin in the living parenchyma of the sapwood is attractive to Douglas-fir bark beetles in higher alpha-pinene, limonene, and camphene fractions (Heikkenen and Hrutfiord 1965). Further, lower OEP correlates with higher alpha-pinene fractions. Female beetles begin colonization and emit pheremones to attract secondary female colonizers when alpha/beta-pinene ratios are high (Rudinsky 1966a). The ability of
a host conifer to withstand bark beetle boring activity and associated fungal inoculation is linked also to the amount of carbon that can be utilized directly for defensive wound reactions (Cates and Alexander 1982). “Any environmental factor that restricts the size of the canopy or its photosynthetic efficiency can weaken the tree’s resistance [to beetle colonization]” (Christiansen et al. 1987, p. 101). If an individual host stands in a dense forest and must compete for light, water, and nutrients, then resistance to insect colonization decreases because the photosynthetic capacity of a tree is proportional to light, water, and soil nutrient availability. If individual conifers are overly mature and cannot assimilate enough water, nutrients, or carbon resource to support their stems and create defense toxins, then host vulnerability to insect colonization increases (Cates and Alexander 1982). Extended drought and fire-caused or insect-effected defoliation deter photosynthesis and generally force trees to allocate carbon for recovery from a weakened state, rather than hold energy resources in reserve anticipating insect invasion (Christiansen et al. 1987).

**Evaluating Bark Beetle Activity in Fire-Damaged Conifers**

For many years researchers believed that practically all fire-killed Douglas-fir trees were selected by the Douglas-fir beetle (Kimmey 1943). “Burnt trees offered no resistance to beetle attack and yet provided a super-abundance of nutritious food, creating the best breeding ground for the Douglas-fir beetle”
Beetles allegedly colonized all burnt trees, loosening the bark, allowing wood borer access and fungal inoculation. Further, insects were believed to initiate this concerted boring during their spring flight seasons for 1 to 3 years after all late summer fires (Kimmey 1943). The 1933 Tillamook fire provided the foundation for these mid-1900 assertions about Douglas-fir bark beetle activity following fire disturbance. One to 2 years after the 1933 fire, bark beetles colonized almost all fire-killed trees (Kimmey 1943) and became epidemic as beetle populations infested 600 km of Douglas-fir (Furniss 1941; Bedard 1950).

Furniss (1941) asserted that the incredible size of the Tillamook Burn uniquely contributed to substantial Douglas-fir bark beetle activity by creating much viable host material for beetle populations to expand and thrive in healthy trees. As a result, renewed interest arose to study the interaction of fire and the Douglas-fir bark beetle. Contemporary researchers agreed that increasing beetle population densities and the potential for insect outbreaks following fire depend on the frequency, size, and intensity of a particular fire event. A smaller fire would not create enough host material necessary to precipitate an epidemic in the same way as a large fire (Furniss 1965). More frequent, less intense fires might provide ample viable food resource on an on-going basis to allow for continued (albeit patchy) bark beetle presence. The physiological response of Douglas-fir to a variety of crown and surface fires, as well as the relationship between these fire-stressed trees and future insect colonizers, has been little studied (Ryan and Amman 1994).
entomological research conducted later in the century following the Clover Mist fire, the Lowman fire, the complex of Yellowstone fires, and the Poverty Flat fire have contributed to science’s incomplete knowledge of Douglas-fir bark beetle activity in fire-damaged Douglas-fir forests.

The Clover Mist fire ignited in August of 1988 on the Shoshone National Forest in Douglas-fir, Engelmann spruce, and lodgepole pine. Aerial surveys taken after the fire detected 5,600 Douglas-fir killed by fire in 1990 and 3,000 suffering fire-caused delayed mortality in 1991 through 1992 (Schaupp and Pasek 1993). Following the Clover Mist fire, November 1992 evaluations of overwintering brood densities of the 1992 through 1993 Douglas-fir beetle generation averaged 29.6 insects per 90 cm² bark sample (Schaupp and Pasek 1993). These figures suggested a seven-fold brood population increase, which may have indicated a bark beetle epidemic capable of exceeding the fire boundary. However, caution must be taken to extrapolate these findings in the Douglas-fir community. Pasek (1990) speculated that 2,000 trees were likely infested with bark beetles by the year 1990, but did not pursue extensive surveying of beetle populations with ground truthing in fire-damaged, fire-killed, or un-injured Douglas-fir. Brood survival in trees of varying fire damage and host selection of fire-stressed trees were only minimally studied and of slight interest to the research team. Schaupp and Pasek (1993) were primarily interested in studying the variation of emergence timing and the overwintering stages of larvae influenced by winter weather conditions. Further, the on-
going 7-year study of brood production utilized only 8-12 selected trees per year (Schaupp and Pasek 1993). Continued measuring on a larger, more random sample would be necessary to confirm their results.

In contrast, Weatherby and others (1993) conducted a 3-year field study on the Boise National Forest following the 1989 Lowman Fire Complex and were interested primarily in the significance of bark beetle colonization of fire-damaged Douglas-fir experiencing delayed fire mortality. With a resulting 185-tree sample due to extensive logging, they confirmed that the likelihood of attack was initially low with lightly scorched trees, increased with moderate to heavy defoliation, and usually declined with complete crown defoliation (Miller and Keen 1960; Furniss 1965; Weatherby et al. 1993). More precisely, given their biological evaluation of tree survivorship, beetles overcame host conifers with an average crown volume scorch (CVS) of 48% and avoided trees with over 75% CVS (Weatherby et al. 1993). Relevant to their original research goal, they discovered that live fire-damaged Douglas-fir, averaging 62.5 cm in size, were most likely to be killed by insects. Consequently, the original Probability Mortality Equation (Ryan et al. 1988) tended to underpredict actual mortality of larger Douglas-fir trees following the Lowman fire disturbance. The equation did not include insect preference for fire-damaged trees, especially those larger diameter host conifers.

After the Yellowstone fire, where many kilometers of lodgepole pine/Douglas-fir forests at 2000-2500 m suffered various degrees of fire damage,
bark beetles first selected moderately fire-stressed Douglas-fir and later mass colonized few green trees. Most of these beetle-affected Douglas-fir sampled in 1989 had 50% of their bole charred and less than 75% CVS (Amman and Ryan 1991), but 16.3% of those trees were un-injured (Ryan and Amman 1994). Generally, Douglas-fir hosts with no cambial fire-caused mortality and light crown scorch were not selected by beetles. One year following this fire complex, 15% of the 446 fire-damaged Douglas-fir measured were colonized by associated bark beetles (67 trees). In 1991 these Douglas-fir bark beetles were observed inhabiting 76% of the remaining 125 fire-injured trees sampled (Amman and Ryan 1991). Later in 1992, 12% of the un-injured trees examined were selected by Douglas-fir bark beetle for colonization, documenting an increase from previous seasons of nearly 7% (Amman and Ryan 1991). Perhaps imminent fire-caused mortality much later in Yellowstone Douglas-fir trees, accounting for 31.7% of species death in 1990-1991 (Rasmussen et al. 1996), precipitated a more substantial attack of significantly weakened hosts the second year. Prior success of first generation beetles on a few heavily infested trees in 1989 seemingly allowed even this slight increased insect effect. Yet, their populations soon plummeted, possibly as weakened host resources declined.

Yellowstone’s fire complex encompassed unusually large crown fires, atypically associated with Douglas-fir forests. The Douglas-fir communities are generally subject to more frequent surface fires. Investigation of bark beetle activity
following smaller fires and adjacent ground burns in Douglas-fir communities might be more practical to forest managers. Malcolm Furniss (1965) earlier surveyed 328 Douglas-fir trees in southern Idaho a year after the smaller 3,800 km\(^2\) Poverty Flat burn. He found as well that 1 year after the summer fire, bark beetles invaded 228 (70%) of the 328 sample of trees. Numbers of preferred insect hosts increased with larger diameter trees and greater degree of fire damage, but declined in trees outright killed by fire (Furniss 1965). Successful brood establishment occupied 88% of the trees at low populations. However, only 17% of those attacked exhibited great emergence densities. Contrary to Robert Furniss’s (1941) original suppositions for larger conflagrations, Furniss (1965) predicted that beetle densities in fire-damaged trees would plummet in a short time due to indigestible sour sap conditions of the charred phloem. Necessarily, bark beetles later aggregated toward healthier trees. However, green conifers could only be overcome by a massive, synchronized insect attack. Relatively smaller fires with lesser amounts of weakened host material would prohibit expansion and infestation of live trees essential to the bark beetle’s continued existence (Furniss 1965; Furniss et al. 1981). Unfortunately, Furniss (1965) terminated the study too early to confirm his hypothesis concerning sour sap and brood survival with field documentation.

The evaluation of Douglas-fir bark beetle activity following the 1994 Beaver Mountain fire, discussed in the following chapters, adds valuable insight to the discussion of host selection and brood success in fire-damaged Douglas-fir
communities. Unlike the Lowman and Yellowstone fires, no insect activity was detected within or adjacent to the Beaver Mountain fire boundary. Prior to the Lowman fire, four consecutive years of drought caused water stress in the forest trees. Aerial detection surveys from 1989 in that area plotted 53 Douglas-fir mortality centers (ranging from 10-700 trees per center) within the Lowman fire boundary (Weatherby et al. 1993). Amman and Ryan (1991) admitted that significant numbers of Douglas-fir beetles were present on site subsequent to the Yellowstone fire event. Rasmussen and others (1996, p. 12) stated, “It can’t be said with certainty that insects built up in [Yellowstone’s] fire-injured trees and caused a subsequent infestation in uninjured trees.” Therefore, initial host selection of fire-damaged over non-damaged trees due to fire remains inconclusive in these two studies and aggregation or survival of bark beetles to fire-stressed forests remains undetermined.

Limited logging operations on the Beaver Mountain field site assured a relatively pure sample population. On the Lowman fire site, the Forest Service continued selective logging operations throughout the course of their insect surveying. In 1990, 14% of the fire-affected forest (578 trees) was logged. In 1993, 11% was harvested (435 trees), leaving a total of 187 Douglas-fir trees as available samples for the study.

Most important, the Beaver Mountain study was original in its intent to investigate the effect of relatively more severe climatic conditions evident at higher
elevations on the success of bark beetles in Douglas-fir communities previously subject to ground fires. Does fire change the structure of Douglas-fir forest communities such that fire-weakened trees indirectly provide a sink for expanding bark beetle populations, or do fire-damaged conifers provide a viable food resource to allow epidemic beetle populations? Continued research on different field sites following a variety of fire events is necessary to gain a fuller understanding of the factors and mechanisms responsible for projecting insect populations outside their natural range of variability. More field work is needed in fire ecology and insect biology to investigate whether these beetles are merely opportunists on a severely fire-stressed stand and/or are aggressors who effectively contribute to host senescence in and around a moderately fire-damaged community.
CHAPTER III
FIELD EXPERIMENT TESTING DOUGLAS-FIR BEETLE ATTACK
OF FIRE-DAMAGED HOST TREES

Introduction

On August 16, 1994 a lightning-ignited crown fire spread in the subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., forest on Beaver Mountain. The fire burned 247 ha of land from the mid-slope above Franklin Basin to the upper northwestern aspect of the mountain and became a surface fire as it entered the multistoried Douglas-fir stands along the edge of the main fire front. Embers produced from the fire ignited spot ignitions in five additional Douglas-fir stands on the ridge and surrounding the peak (Appendix B).

Prior to the fire, endemic populations of Douglas-fir bark beetles were detected on Beaver Mountain. During the 1995 spring flight season, the beetle population increased substantially in the fire-damaged Douglas-fir stands. Aerial detection surveys for the Douglas-fir beetle in Logan Canyon identified beetle activity since 1986 northeast of Temple Peak surrounding Temple Aspen Spring. Researchers speculated that the increased number of these insects in the Temple Spring area was attributable to extended periods of drought from 1988-1992 and previous defoliation by the western spruce budworm, *Choristoneura occidentalis* Freeman, (Lepidoptera: Tortricidae). Bark beetle populations became epidemic by
1993 in this location and probably served as the greatest source population for the Beaver Mountain outbreak.

The objective of this research was to explore whether bark beetles preferred fire-damaged over non fire-damaged and fire-killed host trees. Public land managers are concerned with Douglas-fir beetles attacking live, fire-injured trees and establishing successful brood to later overcome green conifers adjacent to scorched stands.

Materials and Methods

Study Area and Sample. The Beaver Mountain peak (2699 m) is located in the Bear River Range of northern Utah (Appendix A). The study area was located between 2500 and 2622 m in elevation (Appendix B) and included Douglas-fir trees on seven plots near the central ignition point that experienced low-moderate fire injury. Habitat type, aspect, and distance from the central fire were assessed for each plot. Plot boundaries were delineated in Douglas-fir stands by observing blackened surface fuels, charred bark, torched branches, and heated needles of individual trees.

On each of the seven plots varying in size from 2-5 ha, all Douglas-fir trees greater than 30.5 cm in diameter at breast height (DBH) were sampled. Furniss (1964a) established that beetles generally attack only larger diameter trees with enough phloem to support colonization. Given these criteria, 997 individuals were
evaluated. Each sample tree was tagged with a discrete number for identification and re-location. A few fire-killed individuals were harvested in 1995 before the study was conducted. However, the sample population of trees over the course of the field research was not significantly biased by salvage logging.

**Fire.** Fire incident records from 1994 were helpful in evaluating fire intensity specific to the Beaver Mountain incident (Appendix A). The degree of damage caused by the 1994 fire on individual Douglas-fir trees was quantified by measuring percent of crown volume scorch (CVS), and percent of bole char. Probability mortality due to fire, ranging from 0-1 (Reinhardt and Ryan 1989), was also calculated. The diameter of each sample tree at breast height was measured to the nearest 0.1 cm because DBH is perhaps the single most important factor for analyzing an individual's resistance to fire (Ryan 1982a). CVS was estimated as the proportion of crown foliage and buds scorched, relative to the amount of pre-fire live photosynthetic tissue (Ryan 1982a; Peterson 1985). Different observers are capable of consistently quantifying the affected crown within 10% measurements (Ryan 1982a), so CVS was categorized into 10% increments. Different stem scorch heights typically correlate with the intensity of the fire at the base of individual trees, resulting in varying duff consumption and root crown/stem damage (Norum 1976). Therefore, the extent of bole injury from the base of the tree up to 5 m was also estimated, accounting for obvious root and cambial death exhibited by exfoliated bark (Ryan 1982a). Field work on Beaver Mountain measuring fire-
caused damage to the crown and cambium was planned in the summer of 1996. Fire data collection was purposely scheduled after the second growth season following the fire event because fire-caused mortality is best observed after two spring seasons, while the tree attempts recovery of its lost energy-fixing tissue and when delayed cambial injury is apparent (Ryan and Amman 1994).

Scorching the stem’s dead outer bark may not necessarily be damaging to the tree in all cases (Ryan 1982a). Therefore, indirect means of analyzing crown and bole injury combined were also performed in the analysis. Reinhardt and Ryan’s (1989) revised Probability of Mortality fire effects equation, 

\[ PM(0-1) = \frac{1}{1 + e^{(-1.94I + BF + CF)}} \]

was used to calculate fire injury for each of the 997 sample trees and to confirm results for the measured fire damage variables. The components of the equation were: Bark factor (BF) = 6.316\{1-e^{\text{exponent}:-0.3937BT}\}, BT = bark thickness (cm); crown factor = -0.000535CVS; and CVS = the crown volume scorched (%). The model used bark thickness derived from DBH, adjusted specifically for Douglas-fir (Monserud 1979), and CVS estimations to determine crown mortality.

**Bark Beetles.** Aerial insect detection surveys between 1986-1995 were attained to locate source bark beetle populations (Appendix C). Bark beetle host selection for 1995, 1996, and 1997 on Beaver Mountain was documented by evaluating Douglas-fir beetle activity in this forest community. Symptoms of bark beetle attack were recorded beginning in the summer of 1996. Visual inspection of
insect activity on the entire lower bowl was sufficient for identifying bark beetle invasion (Pasek 1990; Rasmussen et al. 1996). Crown fade, dried pitch, yellow frass masses, and emergence holes distinguished 1995 insect activity from 1996 insect activity. In the northern Rocky Mountains, Douglas-fir trees retain their red foliage for one year after the callow adult beetles emerge (Belluschi and Johnson 1969). The canopy then slowly fades to grey, becoming difficult to discriminate from fire-torched needles. Dry, yellowish frass masses observed on Beaver Mountain's Douglas-fir trees either reflected larval mining of the first successful brood or confirmed an invasion by the preceding adult population in 1995 (Furniss and Orr 1978). Small and circular emergence holes indicated successful adult emergence from 1995 attacked trees. Entrance holes were not likely to be confused with emergence holes because females typically bore into their host under the bark furrows and cover the entrance with frass. Successful current year beetle activity was identified by pitchy, red/orange-colored boring dust at the base of the host tree. Conversely, fresh and clear pitch reflected unsuccessful bark beetle attempts to colonize trees during the recent flight. Beetle activity limited to a section of the tree left other parts of the bole vulnerable to further strip attack and insect colonization the second season.

**Statistical Analysis.** A series of chi-square analysis independence tests was performed comparing counts of positive and negative beetle attacks in fire-damaged, fire-killed, and non fire-affected trees. Separate tests for each field season
from 1995 through 1997 were conducted for three levels of fire damage to determine annual beetle host selection. Each year the same host population was measured, but previously insect-affected trees were eliminated. Alpha values were adjusted for multiple simultaneous inference. Significant relationships between fire damage and binomial insect attack response were measured at the <0.001 p-value.

Log-linear modeling of the data from 1995 through 1997 was employed to further evaluate the extent and type of fire injury that attracted the greatest insect activity, as well as to include other host characteristics that might additionally condition an attack response. The generalized linear model was expressed as,

\[
\log\left( E[Y_i] \right) = B_0 + B_1X_{i1} + B_2X_{i2} \ldots + B_{p-1}X_{ip-1},
\]

such that \( E[Y_i] = e^{(B_0 + B_1X_{i1} + B_2X_{i2} \ldots + B_{p-1}X_{ip-1})} \)

and by definition \( e^{B_0}e^{B_1X_{i1}}e^{B_2X_{i2}} \ldots e^{B_{p-1}X_{ip-1}} = e^{(B_0 + B_1X_{i1} + B_2X_{i2} \ldots + B_{p-1}X_{ip-1})} \)

\( E[Y_i] \) was analyzed as the expected count of the response variable for each ith observation in the field study. \( B_0 \) was evaluated as the overall adjusted average of scaled deviation not explained by the other linear components in the equation. \( B_1X_{i1} \) was calculated as the multiplicative effect of the \( X_1 \) explanatory variable and the coefficient representing its relative effect on the response, given the unique combination of explanatory factors for each ith observation (Knoke and Burke 1980). Values were first analyzed on the log scale in order to protect against
negativity in the results, then converted back to the numeric scale and recorded as probabilities. A one-unit increase in $X_{i1}$, $X_{i2}$ ... corresponded to an $e^{B_1}$ unit increase in the bark beetle positive attack response (Feinberg 1980). A particular form of general linear models, the log regression model, was used to analyze the data. Logistic regression related the log of the odds of bark beetle attack to a linear combination of explanatory variables or host characteristics (Feinberg 1980) and took the form $\log \left( \frac{E[\Pi/1-\Pi]}{1-E[\Pi/1-\Pi]} \right) = B_0 + B_1 X_{i1} + B_2 X_{i2} + \ldots + B_{p-1} X_{ip-1}$ (Knoke and Burke 1980).

A series of logistic regression models was created to employ stepwise regression and to determine significant host characteristics that explained the attack response, such as DBH, CVS, or bole char. Differences in scaled deviance between the associated full models and more parsimonious models measured the relative importance of each host characteristic. Corresponding figures illustrated the changing probability of beetle attack given a range of values for each relevant host characteristic. Individual trees strip-attacked in a previous year were removed in order to avoid biasing the effect response due to unmeasurable bark beetle aggregation pheremone plumes (McMullen and Atkins 1962; Atkins 1966).

**Results**

Aerial detection surveys conducted in the Logan Canyon area documented that Douglas-fir bark beetle populations were at endemic levels on Beaver Mountain.
before the 1994 August fire (Appendix C). However, in spring of 1995 beetles inhabited a range of live, fire-weakened Douglas-fir trees in the area. Over three beetle flight seasons (1995-1997), 39% (389 trees) of 997 potential host trees observed 1995-1997 were not affected by fire, 43% (429 trees) were damaged by fire, and 18% (180 trees) were fire-killed. Figure 1 illustrates the relative distribution of bark beetle attack for the three categories of fire effect from 1995 (top) to 1997 (bottom). Beetle colonization was most common in moderately fire-damaged trees the first 2 years after the fire. Beetles invaded 257 fire-weakened Douglas-fir in 1995 and 91 fire-affected host trees in 1996 (Fig.1). In 1997, insect host preference shifted. Green Douglas-fir (53 trees) with no fire injury were colonized by the third generation of bark beetles (Fig.1). These results were consistent with the findings of Furniss (1941), Furniss (1965), Weatherby and others (1993), and Ryan and Amman (1996). Further, chi-square analysis confirmed dependence between fire damage and bark beetle host selection in 1995 ($\chi^2 = 244.062$ with a p-value < 0.001). Similar tests conducted for the 1996 and the 1997 data also depicted a significant relationship between host fire injury and subsequent insect attack (p-value < 0.001). However, the $\chi^2$ statistic for 1996-1997 decreased from 165.620 to 15.720 with two degrees of freedom. These results meant that in the third season following the fire event bark beetle attack response did not depend greatly on relative fire damage.

Fig. 1. Distribution of bark beetle attack for variously fire-affected Douglas-fir host trees.
host characteristics that explained the beetle attack response for each year. In 1995 DBH, CVS, bole char, and PM were highly significant (p<0.001) in conditioning the dependent beetle response when each term was subtracted from its associated full model (Table 1). As DBH increased, attack probability rose invariably in graphs depicting bole char and CVS fire damage variables against DBH for 1995 colonization (Fig. 2). In fact, the likelihood of attack approached 100% as DBH increased to 80 cm for a wide range of PM due to fire (Fig. 3). However, fire-caused defoliation (CVS) and calculated PM due to fire were both highly important in explaining 1995 beetle attack response (Table 1). Plotting CVS, PM, and bole char against DBH illustrates that beetles primarily selected moderately fire-damaged, mature Douglas-fir trees in 1995. Larger diameter trees, exhibiting 60-80% bole char or (more significantly) 60-80% CVS were highly preferred by beetles for colonization (Fig. 2). The three-dimensional surface for PM and DBH also reflects a 45% probability of beetle attack even for the smaller-sized trees calculated at 60% PM (Fig. 3).

Beetle-affected trees from the previous year were extracted to comprise the 1996 tree sample of 635 Douglas-fir. Logistic regression analysis for the 1996 data demonstrated again that CVS, bole char, and PM were significant host characteristics explaining beetle host selection (Table 2). CVS and PM exhibited highly significant scaled deviance differences for 1996 (Table 2). However, the relative importance of all tested independent variables determining beetle attack in
Table 1. 1995 Logistic Regression Models. Testing for significant continuous and quadratic effect variables explaining Douglas-fir bark beetle attack response for that year.

<table>
<thead>
<tr>
<th>Logistic Regression Model</th>
<th>Df</th>
<th>Scaled deviance</th>
<th>Df difference</th>
<th>Scaled deviance difference</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBH+Bc+Cvs+Bc²+Cvs²+Plot</td>
<td>985</td>
<td>1024.6226</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DBH+Bc+Cvs+Bc²+Cvs² (Plot)</td>
<td>991</td>
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<td>6</td>
<td>8.178</td>
<td>p&gt;0.05 Ho</td>
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<td>DBH+Cvs+Cvs² (Bc+Bc²)</td>
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<td>p&lt;0.001 Ha</td>
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<td>DBH+Bc+Bc² (Cvs+Cvs²)</td>
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<td>1192.6326</td>
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<td>159.832</td>
<td>p&lt;0.001 Ha</td>
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<td>Bc+Cvs+Bc²+Cvs² (DBH)</td>
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<td>25.895</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>DBH+Pm+Pm² (Plot)</td>
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<td>15.142</td>
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<td>DBH+Plot (Pm+Pm²)</td>
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<td>122.294</td>
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<td>Pm+Pm²+Plot (DBH)</td>
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<td>81.677</td>
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Fig. 2. DBH and fire damage logistic regression model for 1995 bark beetle attack. Log (Attack Response/1-Attack Response) = DBH + Bc + Cvs + Bc^2 + Cvs^2. DBH*Bc^2 multiplier effect (top). DBH*Cvs^2 multiplier effect (bottom).
Fig. 3. DBH and probability mortality logistic regression model for 1995 beetle attack.
Probability mortality = \( \frac{1}{1 + e^{-1.941 + \text{bark factor} + \text{crown factor}}} \) due to fire injury.
\[
\log \left( \frac{\text{Attack Response}}{1 - \text{Attack Response}} \right) = \text{DBH} + \text{Pm} + \text{Pm}^2 + \text{Plot}.
\]
DBH* Pm^2 multiplier effects overlaid.
Table 2. 1996 Logistic Regression Models. Testing for significant continuous and quadratic effect variables explaining Douglas-fir bark beetle attack response for that year. 1995 attack trees eliminated from the sample.

<table>
<thead>
<tr>
<th>Logistic Regression Model</th>
<th>Df</th>
<th>Scaled deviance</th>
<th>Df difference</th>
<th>Scaled deviance difference</th>
<th>P-value</th>
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<td>8.967</td>
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<td>DBH (Pm+Pm²)</td>
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<tr>
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this year decreased overall from the previous flight season. In fact, an insignificant
scaled deviance value was reported for DBH when subtracted from the full PM
model (Table 2). Three-dimensional surfaces illustrate bole char/DBH and
CVS/DBH multiplier effects for the 1996 data (Fig. 4). Unlike trends in 1995, in
1996 there was a downward quadratic trend in probability of attack for measured
fire damage effects as tree size increased (Fig. 4). However, the likelihood of beetle
activity still increased for hosts experiencing moderate fire injury up to 50% bole
char or 50% CVS (Fig. 4). In a separate logistic regression equation of PM, the
probability of beetle host selection for fire-weakened Douglas-fir in 1996
substantially rose for a range of moderately fire-affected trees. PM peaked at less
than 50% PM opposed to 60% PM in 1995 (Fig. 5).

Results from 1997 evidenced a complete deviation from bark beetle attack
response in either 1995 or 1996. Bark beetle colonization behavior could not be
explained by variation in bole char or tree size (Table 3). The quadratic terms for
CVS and PM were significant in the 1997 data analysis at p-value < 0.001 (Table
3). Fig. 6, relating PM to beetle attack odds, shows the decrease in number of
potential fire-damaged host trees and the decline in the scale of attack odds each
subsequent year following the fire event. The probability of attack was highest in
host trees exhibiting no fire effect and decreased exponentially as PM fire injury
rose (Fig. 6). Whereas 70% of the beetle-affected Douglas-fir in 1995 and 1996
exhibited some degree of fire damage, 80% (53 trees) of the 66 trees invaded by
Fig. 4. DBH and fire damage logistic regression model for 1996 beetle attack. 1995 bark beetle invaded trees removed from the sample. 
\[
\log(\text{Attack Response}/1-\text{Attack Response}) = DBH + Bc + C_{vs} + Bc^2 + C_{vs}^2. \\
DBH^*Bc^2 \text{ effect overlaid (top). } DBH^*C_{vs}^2 \text{ effect overlaid (bottom).}
\]
Fig. 5. Probability mortality logistic regression model for 1996 beetle attack. 1995 bark beetle invaded trees removed from the sample. 

Log (Attack Response/1-Attack Response) = Pm+Pm². 
Probability mortality= 1/ (1+e^(-1.941+bark factor+crown factor))

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Fig. 6. Probability mortality logistic regression model fitting DBH+Pm+Pm2+Plot to show the sample frequency distribution of fire-damaged trees for 1995, 1996, 1997 respectively (top to bottom).
bark beetles in 1997 were non fire-affected (Fig. 7). These results proved to be consistent with direct field observation and further confirmed host selection of healthy green trees 3 years after the fire event (Ryan and Amman 1996).

Plot location for both measured fire-damage and PM logistic regression models, using 1997 data, reported to be the most important host characteristic with scaled deviance differences of 31.121 and 30.617, respectively (Table 3). Though the location of the Douglas-fir hosts in 1995 did not impact insect colonization, probability of attack among the seven field plots became increasingly divergent as time passed (Fig. 8). Plots A1, A3, and F closest in proximity to the main fire front and on the northwest aspect showed higher probabilities of beetle boring activity in 1997 up to nearly 25% (Fig. 8).

**Discussion**

The Douglas-fir beetle commonly exhibits patchy, periodic, and episodic population density cycles. Less aggressive *Dendroctonus* beetles generally aggregate toward mature and weakened hosts, but seem to have limited success in expanding their populations. However, Ryan and Amman (1996), and Rasmussen and others (1996) suggested that bark beetles are capable of establishing healthy brood populations in contiguous stands of weakened Douglas-fir and later expanding their population to colonize healthier trees. Immediately proceeding the August 1994 Beaver Mountain fire, Douglas-fir bark beetles had already flown for
Fig. 7. Percentages of Douglas-fir trees attacked by bark beetles for each of the three years that insect activity was observed.
Annual Plot Effect on Insect Attack

Fig. 8. Frequency of predicted values for insect attack given plot. 1995-1997.
that season, although the following spring/summer of 1995, female beetles located moderately fire-weakened Douglas-fir trees. Colonization of these trees allowed an increase of bark beetle populations that year. Emerging brood caused further infestation in recovering fire-damaged host trees in 1996 and previously resistant green trees in 1997.

Annual host selection was conditioned by both the available phloem resource given tree size and site location, and the relative extent of fire injury to Douglas-fir trees. A significant scaled deviance value calculated for DBH (Table 1) and results reported for logistic regression models of 1995 data (Figs. 2, 3) confirmed the aggregation of insects toward predominantly larger hosts (ranging between 120-140 cm). Conversely, the recorded insignificance of DBH in the PM model of 1996 data (Table 2) suggested that female beetles bored into smaller trees only because mature Douglas-fir had been colonized in 1995 and beetles had no other viable host alternative. Douglas-fir beetles first preferred larger trees in 1995 with generally thicker phloem, allowing greater brood survival. In addition, larger trees were already predisposed to insect attack due to their massive allocation of carbon resources necessary to maintain root water conductivity supporting the stem and slowly depreciating photosynthetic tissue (Christiansen et al. 1987).

Additional fire-caused defoliation of mature conifers was especially debilitating, forcing Douglas-fir to recover from a weakened state rather than to create a carbon reserve to ward off insects (Vite and Rudinsky 1957; Wright and
Harvey 1967). Douglas-fir beetles selected larger, moderately fire-weakened hosts with both ample food and reduced defense response capability in 1995 (Figs 2, 3). The relative significance of all fire damage variables conditioning beetle attacks declined (Table 2). In addition, the highest range of probable attack calculated using both bole char and CVS shifted from 60-80% in 1995 to 50-60% in 1996 for larger-diameter trees and calculated using PM decreased to 35-50% the second season (Figs. 4). However, beetles still selected moderately fire-weakened trees, demonstrating their incredible ability to sense weakened host condition and undeniably strong preference for colonizing these Douglas-fir. Ninety-one trees of the resulting 171 non beetle-attacked fire-injured Douglas-fir were attacked the second season following the fire event (Fig. 1). In addition, 80 remaining fire-damaged trees not recorded in the 1996 sample were mildly strip-attacked both years. Therefore, total attack densities in 1996 for fire-weakened trees slightly under-estimated actual host selection.

Amman and Ryan (1991) similarly concluded that female bark beetles selected mature host conifers suffering 50% or greater basal cambial damage (not to exceed 80%). Following the 1989 Lowman fire complex, Weatherby and others (1993) reported that Douglas-fir bark beetles were discovered in the study area colonizing trees that exhibited above 48% CVS. After the Yellowstone fires, insects were also found to attack host trees with moderate crown heating not in excess of 80% CVS (Amman and Ryan 1991). Biologically, the attraction of bark
beetles to weakened Douglas-fir seems plausible. An injured tree with reduced photosynthetic capability is less able to allocate carbon to its roots, decreasing water uptake capacity (Nebeker et al. 1993). In addition, as the oleoresin exudation pressure (OEP) decreases in the stem tissue, a tree’s overall ability for resinosis and necrosis declines (Lorio 1993). Further, Heikkenen and Hrutfiord (1965) discovered that reduced OEP correlates with higher concentrations of alpha-pinene in the tree’s resin. Interestingly, bark beetle aggregation pheromones derived from the host tree’s monoterpenes are high in alpha-pinene and have seemingly evolved to select weakened host conifers (Rudinsky 1966a).

Excessively-high scaled deviance differences for CVS in logistic regression models for data in 1995 (Table 1) and in 1996 (Table 2) confirmed the relative importance of damage to the crown, rather than injury to the stem, in conditioning a beetle attack response. PM, primarily a function of crown damage for larger, more attractive hosts, also reported a highly significant variation in scaled deviance from the main model in logistic regression models for data in 1995 and again in 1996 (Tables 1, 2). Heat-caused injury to the photosynthetic crown has been widely accepted by fire ecologists as the most common source of conifer injury and mortality due to fire (Wagener 1961; Petersen 1985; Petersen and Arbaugh 1986). Bole char may be restricted to part of the stem and only slightly impact the beetle resistance capability of the tree or its health. A tree with fire scarring to the cambium precludes the conductance of water and nutrients through that stem area
and carbon through that phloem tissue. Yet, fire-caused defoliation reduces the overall ability of trees to produce carbon necessary to maintain root and stem vigor, and to defend itself against bark beetles (Christiansen et al. 1987; Raffa et al. 1993). Field observation on Beaver Mountain supported the fact that bark beetles aggregated specifically toward crown-damaged trees and were further attracted to areas on the bole adjacent to damaged sections that exuded resin with high concentrations of alpha-pinene (Miller and Keen 1960; Furniss 1965).

Host conifers on Beaver Mountain that evidenced crown and stem injury greater than 80% by the 1995 flight season were not generally attacked in 1995 through 1997. However, in 1995 females aggregated toward small, live stem surfaces on 74 large host conifers observed to have suffered certain delayed fire mortality. The thicker-bark on large trees likely insulated sections of the cambium from extensive heating, delayed complete drying of the stem, and protected pockets of the phloem resource. Conclusions drawn by Furniss (1965) following the Poverty Flat fire supported the fact that successful Douglas-fir beetle colonization densities rose as host crown injury increased, but declined dramatically in completely defoliated trees. In 1996 and in 1997, fire-killed Douglas-fir were observed with exfoliated bark and dry phloem, prohibiting beetle colonization. Conversely, only 31 non fire-affected live trees were attacked in 1995 and 32 in 1996 (Fig. 1). Green Douglas-fir have nutritionally high-quality phloem (McMullen and Atkins 1962; Furniss 1965), but also possess the capacity for necrosis and resinosis which enables
potential hosts to isolate or "pitch-out" beetles, respectively (Nebeker et al. 1993; Lorio 1993).

In 1997 beetle host selection shifted on Beaver Mountain (Fig. 6) and plot location became a marginally important term in explaining beetle attack preference for 1997 (Table 3). Both small and large diameter, fire-weakened Douglas-fir were selected out of the 1997 sample. Therefore, brood populations were forced to aggregate in large numbers on fewer (53) relatively vigorous host trees. Small infestation centers of green Douglas-fir developed along the perimeter of plots A1, A3, and F most likely for two reasons (Fig. 9). First, these plots were on northwest and western aspects where amiable site conditions contributed to greater numbers of pre-fire, vigorous, thick-phloem host conifers (Appendix B). Second, significantly more beetle-preferred fire-damaged trees were in these field locations opposed to sites farther from the main fire source.

Although attack preference shifted in the third season toward green host trees, fewer trees were attacked. The decline in the number of beetle-affected conifers was partly due to the greater densities of bark beetles necessary to mass colonize healthier conifers, but other exogenous and endogenous factors also contributed to reduced insect activity in the third season.

Limited, yet significant, 1997 brood success in Beaver Mountain's green Douglas-fir was possibly due to the relatively small number of mature and fire-weakened host trees affected by the fire, colonization patterns given the endemic
source population of beetles in the area prior to the fire event, and other exogenous factors. Combined, 348 fire-damaged trees were attacked between 1995 and 1996 (Fig. 1). Although bark beetles seemed keenly attracted to weakened Douglas-fir, there simply were not enough moderately fire-weakened trees in the Beaver Mountain area to precipitate epidemic insect populations. Second, the small source population of insects attracted to Beaver Mountain strip-attacked many mature, moderately damaged Douglas-fir instead of mass colonizing these trees in the first season. This initial small population of beetles contributed to less brood production in 1996. Further, rejuvenation from immediate fire damage effects in 1996 probably inhibited successful strip-attack of fire-damaged conifers in the second season. Smaller diameter trees selected in 1996 with lighter fire damage were best able to recover from the effects of fire and effectively “pitched-out” bark beetles. Wagener (1961) concluded that Douglas-fir needed only 40% live crown to recover sufficiently from fire injury. Perhaps similar to the temporal effects of budworm defoliation (Wright et al. 1984), now vigorous photosynthetic tissue of previously injured Douglas-fir trees on Beaver Mountain deterred extensive bark beetle colonization in 1996. Third, once substantial prey populations developed, hairy woodpeckers, *Picoides villosus*, and other biotic agents may have also contributed to substantial decline in the population of the 1997 bark beetle generation. Predator and parasite activity generally lags behind a few seasons after prey populations have increased. Fourth, the relatively harsh climate in these Douglas-fir communities
likely contributed to unfavorable flight conditions and lower rates of brood survival. Douglas-fir beetles are typically active when temperatures reach 18.3-21.1 °C for several days (McMullen and Atkins 1962; Furniss et al. 1981; Lessard and Schmid 1990). Upper elevation forests in the Bear River Range reached highs of 20.3 °C only in July for 1995 and for 1996 (Appendix D). Temperatures for high-elevation Douglas-fir forests even plummeted to -1.7 °C in June of 1995, joined by intermittent rain and clouds. On Beaver Mountain during the prime flight season, 11.2 cm of precipitation fell in May and 6.4 cm fell in June, 1995 (Appendix D). Delayed flight of female beetles in the first season was likely due to these predominating low temperatures (Rudinsky and Vite 1956; Vite and Rudinsky 1957; Rudinsky 1966a). Many larvae may not have completed their natural growth cycle from first vulnerable instar to hard-shelled pupae by the fall season (Johnson 1967).
CHAPTER IV
FIELD EVALUATION OF BROOD PRODUCTION IN
FIRE-DAMAGED TREES AND UNDAMAGED TREES

Introduction

Information about Douglas-fir beetle host selection may help forest managers identify susceptible trees, but research focused on bark beetle brood production is also important from a population dynamics standpoint. Understanding how fire damage contributes to insect population increase is critical for prevention of beetle epidemics. Some beetle-attacked Douglas-fir trees were able to “pitch-out” insects and prohibit the further construction of beetle galleries or larval tunnels. Conversely, other Douglas-fir unable to inhibit beetle colonization allowed successful brood development and emergence. Large conifers may have thicker phloem for feeding larvae, but also greater ability to resist bark beetle boring activity. Additional fire damage of especially large diameter Douglas-fir may affect host defense mechanisms and permit greater colonization. The objective of this study was to quantify brood emergence in Beaver Mountain Douglas-fir forests for each beetle-attacked tree following the August 1994 fire.

Materials and Methods

Quantifying Douglas-Fir Brood Success. Douglas-fir on Beaver Mountain
attacked by Douglas-fir bark beetles in 1995-1996 were re-located in July 1997. The resulting sample size used for analysis included 343 conifers exhibiting at least one emergence hole on the lower bole. Emergence holes were small, circular openings from the phloem tissue to the outer bark that were constructed by emerging bark beetles and indicated successful brood development. Two 900-cm$^2$ sections on the lower stem of each beetle-selected Douglas-fir tree were chosen and the number of emergence holes was visually counted. The average length of viable parent egg galleries for Douglas-fir beetles is 21.3 cm (Schmitz and Rudinsky 1968), so this size sample likely included entire single vertical galleries and associated lateral larval tunnels. Emergence holes were mapped on a clear sheet with a dry-erase pen. Any evidence of successful emergence within the bark furrows was included. Bark chips in the sample area were not removed, making measurement especially difficult for larger, thick-barked trees. Douglas-fir bark beetle exit holes are unique and were not confused with elliptical flat-headed borer holes, larger round-headed borer holes, nor smaller ambrosia beetle pin holes also observed on the host bark surface. Obvious fire scars on the stem of sample trees were avoided for measurement.

Generally, the north and south aspects of the tree were sampled. Furniss (1964a) concluded that although beetle attack density was greatest on the northern aspect of the stem, many Douglas-fir were observed to have greater brood production on the southern exposure. The two count samples on each tree were
averaged and used in the analysis, rather than compared or evaluated separately.

The resulting sample area for calculated brood density was 1800 cm² for each Douglas-fir.

Schmitz and Rudinsky (1968) concluded that colonizing Douglas-fir bark beetles showed little preference for any particular portion of the tree from the lower to the upper bole. Therefore, the lower stem was selected as an acceptable and efficient region to quantify brood success (Pasek 1990; Lessard and Schmid 1990). For mountain pine beetle in maturing lodgepole pine forests, sampling limited to the lower portion of the bole "satisfied the requirements of efficiency and reliability in reproducing the character of the host population" (Carlson and Cole 1965, p. 1). Ground fire affecting the root crown and lower tree bole also possibly attracted greater numbers of bark beetles to that section of the stem. Though Douglas-fir bark beetles will not colonize dead cambium, the insects generally first occupy areas immediately adjacent to scorched bark (Miller and Keen 1960).

**Brood Production and Emergence Hole Correlation.** Additional analyses were conducted in 1997 to ensure that the number of emergence holes counted on the larger (343) sample of successfully colonized trees accurately reflected brood survival. Cages measuring 900 cm² were placed randomly on 31 tree boles that evidenced previous beetle attack in the 1996 flight season. These mesh enclosures were stapled to a smoothed bark surface, similar to the method described by Lessard and Schmid (1990). Cages were tightly sealed to prohibit random escape and the
bottom ends were fastened together to form a funnel, which was secured to a plastic tube. A no-pest insect strip with Vapona as its active lethal ingredient deterred escape from the tube following capture. Emerging adults from the area of tree stem were collected, separated from other entrapped insects or moist frass, and counted in the laboratory. Mesh cages were removed from the tree and emergence holes were counted with a permanent marker in the same sample space used to trap emerging insects. Thick bark was smoothed to reveal all possible beetle holes against a flush surface.

**Statistical Analysis.** Log-linear modeling was employed in this study to evaluate brood emergence density for each successfully beetle-attacked Douglas-fir in the sample population. The observed density of emergence / 1800 cm² was equated to a linear combination of significant host characteristics, such as DBH, CVS, PM, and bole char. The model was expressed,

\[
\log (E[Y_i]) = B_0 + B_1 X_{1i} + B_2 X_{12} + \ldots + B_{p-1} X_{ip-1},
\]

such that \( E[Y_i] = e^{(B_0 + B_1 X_{1i} + B_2 X_{12} + \ldots + B_{p-1} X_{ip-1})} \)

and by definition \( e^{B_0 \cdot e^{B_1 X_{1i}} \cdot e^{B_2 X_{12}} \ldots \cdot e^{B_{p-1} X_{ip-1}}} = e^{(B_0 + B_1 X_{1i} + B_2 X_{12} + \ldots + B_{p-1} X_{ip-1})} \).

\( E[Y_i] \) was analyzed as the expected count of emergence holes / 1800 cm² for each ith observation in the field study. \( B_0 \) became the overall adjusted average of scaled deviation not explained by the host characteristics fit into the equation. \( B_1 X_{1i} \) was
the multiplicative effect of the $X_i$ explanatory variable (or host characteristic) and the coefficient representing its impact on the predicted emergence hole count response (Knoke and Burke 1980). Values were evaluated first on the log scale in order to protect against negativity in the results, then were converted back to the numeric scale. A one-unit increase in $X_{i1}, X_{i2} ...$ corresponded to an $e^{B_i}$ unit increase in the expected count response (Feinberg 1980). The relative impact of each significant host characteristic in determining the density of emergence was first quantified by subtracting a series of parsimonious models from the full model. Second, variation in the predicted emergence count was graphed according the changes in each relevant host characteristic isolated on its own axis.

Separate log linear statistical analyses for the 900-cm$^2$ caged sections of selected trees regressed actual emergence with the density of emergence holes. A correlation coefficient for emergence holes and actual brood production evaluated the trend and the strength of association between the two variables in this subsidiary 31-tree sample. Bark beetle emergence could then be accurately calculated from counts of emergence holes in the larger (343) sample exhibiting successful brood production.

**Results**

**Quantifying Douglas-Fir Brood Success.** DBH, bole char, crown damage, calculated PM, and plot location were each significant terms in affecting the
predicted values for relative brood success at p-value <0.001 (Table 4). Yet, bole char displayed the lowest scaled deviance difference (Table 4). Plot and DBH host characteristics demonstrated great divergence from both the full $DBH + Pm + Pm^2 + Plot$ model and the full $DBH + Bc + Cvs + Bc^2 + Cvs^2 + Plot$ model (Table 4). Invariably, predicted emergence density increased as diameter size increased, regardless of which fire damage multiplier effect was graphed against DBH (Figs. 9, 10). Neither stem damage, crown injury, nor PM effects for smaller diameter trees showed significant predicted emergence densities of bark beetles in either 1996 or in 1997 flight seasons. The seven plot locations fit to predicted density further demonstrated that successful population growth occurred in plots A1 and A3 along the main fire flanks and on the northwest exposure (Fig. 11).

Figure 9, isolating the multiplier effect for bole char (top) and for crown damage (bottom) against DBH, illustrates opposing trends in predicted density for those significant measured fire damage variables. Figure 9 (top) shows the greatest emergence density occurring for large trees experiencing no bole-charring effect or severe damage observed to the lower stem. Predicted densities were higher than 60 beetle exit holes/1800 cm$^2$ bark surface at either end of this bole-charring spectrum (Fig. 9, top). Conversely, large Douglas-fir exhibiting moderate CVS (45-70%) recorded the largest density of emerging insects (Fig. 9, bottom). Nearly 80 beetle exit holes/1800 cm$^2$ were predicted for individual hosts with 70% crown damage (Fig. 9, bottom). PM (as a primary function of crown damage for large Douglas-fir)
Table 4. Log Linear Models testing for significant continuous and quadratic effect variables impacting the density of Douglas-fir bark beetle brood success on individual hosts. The number of emergence holes on an 1800 cm² area of bark surface were counted. Non-attacked trees were eliminated from the sample.

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Fig. 9. DBH and fire damage log linear model for quantitative analysis of 1995-1996 bark beetle brood success by measuring density of emergence. All non-attacked Douglas-fir trees were removed from the sample. Log (Density) = DBH + Bc + Cvs + Bc^2 + Cvs^2 + Plot. DBH*Bc^2 multiplier effects overlaid (top). DBH*Cvs^2 multiplier effects (bottom).
Fig. 10. DBH and probability mortality log linear model for quantitative analysis of 1995-1996 bark beetle brood success by measuring density of emergence (1800cm² area).

Probability mortality = \frac{1}{1 + e^{(-1.941 + \text{bark factor} + \text{crown factor})}}.

\log (\text{Density}) = \text{DBH} + P_m + P_m^2. \text{DBH and } P_m^2 \text{ multiplier effects overlaid.}
Fig. 11. Full log linear model illustrating the plot location effect on the predicted bark beetle emergence density response.
reflected the general orientation of the CVS quadratic with slightly lower values, accounting for additional cambial damage.

Results for the subsequent test correlating 1997 emerged beetles and emergence holes demonstrated that actual emergence was only mildly and positively associated with the density of emergence holes measured on each 900-cm\(^2\) caged area. Correlation coefficients reported values of 0.74 (Pearson) and 0.67 (Spearman) at <0.001 alpha levels. Log-linear modeling of actual beetle emergence data showed that as the number of emergence holes increased, the number of 1997 emerged bark beetles increased (Fig. 12). Although the trend in number of actual beetles emerged was nearly 1:1 for low emergence densities, the increased slope in the curve suggested that more than one beetle emerged from the same exit hole for heavily colonized host trees (Fig. 12). Actual data points graphed in Fig. 12 further illustrated a significant divergence above the regression line for infested trees. A spread of values below the regression line apparent on the lower end of the emergence density scale indicated possible adjacent or overlapping strip-attack for 1995-1996.

Discussion

Moderately fire-damaged trees were not only highly desirable for attack by bark beetles, but they were also colonized at higher densities than other potential host conifers. Results of log linear models for quantitative brood emergence
Fig. 12. Log linear model for Douglas-fir bark beetle emergence hole count and actual emergence on 900 cm² bark surface for 31 samples.
demonstrated that both available phloem resource, given tree vigor, and variable resistance to colonization, given different degrees of fire damage, influenced brood survival.

Tree size and site quality likely reflected relative vigor for Douglas-fir trees. Great differences in scaled deviance values for the tree size explanatory variable in the log linear emergence density response model illustrated the significance of DBH in conditioning brood emergence (Table 4). Regardless of fire injury on individual hosts, as tree diameter increased, the predicted density of surviving brood rose to between 50-80 exit holes/1800 cm$^2$ for the largest conifers measuring 120-140 cm (Figs. 9, 10). Generally, larger diameter trees harbor a thicker reserve of phloem food resource per unit area to support larger numbers of maturing larvae and allow for greater brood survival (Furniss 1964a). In addition, great quantities of carbon resource are necessarily allocated to supporting large stems and would be unavailable to resist boring insects. Aspect, a major factor in vegetative growth and stand density, possibly contributed to the spatial extent of the fire-insect complex. Colonized forested stands that were oriented northwest permitted vigorous tree growth prior to the fire event. Trees located on these mesic sites likely maintained greater phloem reserves for feeding larvae than host conifers subject to less ideal site conditions (Furniss et al. 1981). Results from the parsimonious log linear models confirmed the significance of plot location in affecting the predicted degree of emergence (Table 4). Plots A1 and A3 with the highest predicted response
values were closest to the main fire front and were located on northwest exposures (Fig. 11).

The greatest predicted density of emerging beetles was determined for large trees, subjected to 50-70% crown damage and calculated for 45-65% PM (Figs 9, 10). Beetles thrived on the thick phloem and were best capable of colonizing moderate fire-injured trees due to reduced host defense. However, the measured bole char three-dimensional surface for emergence density contradicted the results reported for the above fire damage variables.

A few explanations may account for this divergence from previously graphed trends. First, the graph supports the substantial increase in brood production for larger diameter trees, but results showed a difference of 10 emergence holes between moderately stem-injured Douglas-fir and no bole char or extensive bole char. Biologically, it makes sense that non fire-affected stems would allow greater brood survival and emergence. A vigorous tree (assuming light fire defoliation, as well) would have greater resistance to insect boring activity, necessitating larger attack densities (Christiansen et al. 1987). Thick and nutritious phloem would also become available to developing larvae if mass colonization was sufficient to overcome the tree’s defense mechanisms. Conversely, it does not immediately seem reasonable that bark beetles would propagate large numbers of brood in severely fire-weakened tree hosts. Yet, it is possible that mature individual trees, suffering severe delayed mortality effects, maintained sufficient phloem
resources to permit congregations of bark beetles on limited sections of the tree bole in 1995. These small pockets of bark beetle activity were likely recorded on severely damaged host trees because the sampling method used purposely avoided areas of the lower bole with exposed and dry cambium charred by surface fire effects. A tree with a greatly reduced crown may still have provided ample phloem resource for regenerating bark beetle populations on part of its stem or on the entire bole, especially if they were drawn to live cambial tissue adjacent to fire scars (Miller and Keen 1960).

It is most reasonable to conclude that measured bole char alone really did not condition the density of beetle emergence, as was probably also the case for annual bark beetle attack data. Most likely the extent of stem scorch observed from the base of the tree to 5 m (the lower bole) overestimated actual cambial damage to the entire tree stem for larger diameter trees. These host conifers had thick bark to insulate the cambium from fire injury, making visual assessment difficult. The calculated PM equation that indirectly quantified extent of cambial damage probably better explained the relative density of beetle emergence. Besides, symptoms of cambial scorching may have been restricted to only a portion of the bole, whereas photosynthetic crown loss affected overall tree vigor and probably became the primary attractant for bark beetles, as well as the determinant for relative brood production.
In addition to different host characteristics that determined predicted densities of beetle emergence, a number of other endogenous and exogenous factors likely contributed to the overall restricted success of the Douglas-fir bark beetle in these moderately fire-damaged Douglas-fir communities. Intraspecific competition, predation, and harsh climate possibly inhibited the establishment of epidemic brood populations. It is difficult to assert with certainty that intraspecific competition among bark beetles played an active role in limiting their reproductive success. Yet, mature, moderately fire-damaged host conifers supported large brood populations one year following the 1994 Beaver Mountain fire. Perhaps these colonizing beetles became overcrowded and competed for limited phloem resources. Intraspecific competition likely resulted in shorter parent galleries, reduced number of eggs laid, and higher female mortality due to continued re-emergence (McMullen and Atkins 1961). McMullen and Atkins (1961) concluded that the lowest percent of annual brood mortality occurred in habitat where there were only 5 attacks/900 cm². Reported emergence densities for the Beaver Mountain study of up to 60-80 holes/1800 cm² suggested 10 or more attacks per/1800 cm² on some heavily colonized trees.

Predation by other beetles or woodpeckers possibly had a delayed effect in slightly reducing 1996 brood production for these Douglas-fir forests. Marsden and others (1981) reported one significant insect parasite, Coeloides vancouverensis (Hymenoptera: Brachonidae) [Dalla Torre] (=brunneri Viereck), and two important
clerid predators, *Enoclerus sphegeus* (Coleoptera: Cleridae) Fabricius and *Medetera spp.* (Coleoptera: Cleridae) Wheeler, for the Douglas-fir beetle in the Intermountain West. Neither *Enoclerus sphegeus* nor *Medetera spp.*, nor *Coeloides vancouverenis* was located in any of the Beaver Mountain study plots. Hairy woodpeckers became especially active at the field plots in spring 1997. However, their impact was largely unpredictable and likely irrelevant in influencing beetle populations (Weatherby et al. 1993; Pasek and Schaupp 1995).

Finally, higher elevation host sites on Beaver Mountain contributed to later beetle flights and probably restricted larval success due to cold temperatures, wetter spring seasons, and persistent snow (Amman and Ryan 1991). The 1995 and the 1996 beetle flights were observed in Beaver Mountain’s Douglas-fir forests as late as June for both years (Appendix D) because average monthly temperatures fell below 18-20 °C through late spring. Beetle flight was observed to be even later in 1997. Precipitation for June 1997 measured 45.21 cm (Appendix D), while the residual accumulated snow pack was greater than 2.5 m in May 1997 due to cold temperatures and heavy winter snowfall. Bark beetle populations thrive if flight is early, and if callow adults gain sex organs as well as hardened skeletons by the time reduced fall temperatures necessitate overwintering (Rudinsky and Vite 1956; Rudinsky 1966b; Johnson 1967). Furniss and Orr (1978) observed that eclosion to pupation increased dramatically to 100 days for lower temperatures between 14-15 °C. Each Douglas-fir brood generation possibly developed slowly and few beetles
likely entered diapause as young larvae (Rudinsky and Vite 1956; Johnson 1967) because monthly averaged maximum temperatures never exceeded 22.81 °C between 1995-1997 on Beaver Mountain (Appendix D). Perhaps mature and fire-damaged hosts colonized in 1995 would have precipitated viable infestation centers in green mature trees, if climate had not been an added deterrent to brood development.

Actual beetle emergence showed a trend of almost 1:1 with the number of exit holes counted for 31 trials. Outlying observations underneath the regression line suggested that closely neighboring or nearly overlapping strip-attack is possible, though not common (Fig. 12). Exit holes counted after the 1997 flight possibly included 1995 exit holes that were constructed in close proximity to 1996 pupal chambers. Further, all circular holes sized to this specific bark beetle were counted, so a few adult reemergence exits and ventilation holes were likely measured as well. These unavoidable errors in sampling may have slightly overestimated the number of emergence holes (Schmitz and Rudinsky 1968). Conversely, some observations on 900 cm² surface areas that had 20-40 emergence holes quantified nearly twice as many emerging beetles per exit hole (Fig. 12). If Douglas-fir beetle attack densities were relatively high in host trees, then intraspecific competition among adjacent larvae could have partly regulated mining patterns and precipitated larval mortality (McMullen and Atkins 1961; Schmitz and Rudinsky 1968). Mountain pine beetle emergence from the identical exit hole by
more than one young adult insect is possible for similarly mass-colonized lodgepole pine (Cole and Amman 1980). Therefore, surviving Douglas-fir larvae may create closely neighboring pupal chambers and encourage overlapping brood emergence. If this was the case, then actual brood production in moderately crown-damaged, mature host trees was exponentially higher than the results reported for associated emergence density log linear models.
CHAPTER V

SUMMARY

Additional research is needed to investigate the possible interaction of fire and insects that contributes to the succession of particular forest ecosystems. The conclusions drawn from this study provided a useful prognosis of bark beetle activity in fire-scorched Douglas-fir communities at an upper elevation field site. Douglas-fir beetle host preference for 1995 through 1997 and quantitative brood survival for 1995 through 1996 for Beaver Mountain confirmed that the most viable hosts for colonization were moderately fire-damaged trees. Given a scarce source population of beetles and patchy fire-injured Douglas-fir forests, insects were still successful in causing the mortality of many fire-damaged Douglas-fir from 1995 through 1996 and 53 mature green hosts in 1997. However, the 1994 low-intensity surface fire in these conifer forests failed to precipitate associated bark beetle infestation beyond the established fire boundary.

The research conducted on Beaver Mountain in fire-affected Douglas-fir forests was predominantly analyzed using explanatory log linear modeling techniques in order to explore the dynamics between bark beetles and fire in the associated communities. This information might contribute to the Forest Health Protection project on developing a landscape-scale rating system for *Dendroctonus* beetle activity in the Rocky Mountains. Forest fire managers could use this analysis
of subsequent beetle colonization in fire-stressed Douglas-fir trees to determine appropriate conditions for prescribed burning. Most importantly, these studies were conducted and the descriptive analyses presented to further the evaluation of multiple disturbance agents in wildland forests. Most critical to the work of disturbance ecologists is exposing others to the awesome and essential function of disturbances in forest ecosystems. Biotic and abiotic disturbances protect the processes that balance vegetative communities within their natural range of variability.

Traditionally, these agents of accelerated forest succession were restricted to solitary exogenous impacts acting on a vegetative community (White 1979). Now, scientists are beginning to realize that multiple disturbance regimes, ranging from individual to large-scale community change, both alter vegetation and are incited by particular characteristics of the forest (Hadley and Veblen 1993; Hadley 1994). It necessarily follows that our management of the forest must be based on an ecological understanding of these processes and of the dynamic relationship between natural disturbances. Tree mortality is an ongoing, gradual phenomenon of the forest. Many species depend on the structural dynamics of a forest ecosystem for continued survival. Bark beetles and fungal pathogens interacting with fire have been instrumental in sustaining healthy coniferous forests (Belluschi et al. 1965). They aid nutrient cycling, natural thinning, and selection for site-adapted species (Lorio 1993). Insect activity and fungal decomposition add to the basic ingredients
that are necessary for forest regeneration (Franklin et al. 1987), maintaining the long-term productivity of forest ecosystems (Christiansen et al. 1987). “Temporally and spatially heterogeneous environments are important to bio-diversity and inevitable evolution” (White 1979, p. 230).
LITERATURE CITED


Gutsell, S.L., and E.A. Johnson. 1996. How fire scars are formed: Coupling a


Van Wagner, C. E. 1972. Height of crown scorch in forest fires. *Canadian Journal*


Appendix A. Beaver Mountain Fire Incident, 1994
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**IDENTIFICATION**

1. Region/Forest/District ID and SO Fire Number: 04/12/06/055
2. Protecting Agency at Origin: USF
3. Ownership at Origin/State at Origin: 2/UT
4. Fire Management Analysis Zone: 12
5. Adjoining Forest Report Number (if applicable): 00/00/00/000

**OCCURRENCE**

6. Point of Origin lat= 41 58.0 long= 111 35.0
7. Time of Origin: 08/16/94/0900
8. Time of Discovery: 08/16/94/1604
10. Statistical Cause: fire
11. Unplanned Ignition Designated as a Prescribed Fire: N

**ACTION**

12. Initial Suppression Strategy: 3
13. Escaped Fire: Y
14. Time of Initial Action: 08/16/94/1640
15. Time Final Suppression Strategy Attained: 08/23/94/1800
16. Time Fire Out: 09/23/94/1000
17. Forces Used: H2/C/ 2 D2/C/ 2 E2/C/ 1
Up to Time of: D1/C/ 3 C2/C/ 3 A1/F/ 4
Attainment of: C2/F/ 4 P1/C/18 / /
Initial Strategy: P1/F/40 E6/C/ 2 / /
or Escape: H3/C/ 2 E7/C/ 2 / /

**DESCRIPTION**

18. FFF Cost ($): 7000
19. FMAZ NVC per Acre (whole $): 1
20. NFS Acres (Reporting Forest Only): 142.4
21. Other Acres Inside: 475.0
22. Other Acres Outside: .0

Total Acres = 000617.4

23. Fire Intensity Level: 5
24. Representative Weather Station: 420201
25. NDRS Fuel Model/Cover Type: B/22
26. Aspect: 7
27. Elevation (feet): 7500 origin

**OPTIONS**

28. Special Code: / / /

**Remarks**

Submitted/s/J.BRUNNER /d/082994Approved/s/F.WIGGINS /d/091294
Fire Narrative

Beaver Mountain Incident

The first report of a wildfire on Beaver Mountain was received from the ski area owner/permittee Ted Seeholzer by Logan District dispatch at 1604 hours August 16, 1994. The cause was identified as a lightning strike from an early morning thundershower. Fuels were mostly subalpine fir timber and grass with scattered aspen (Fuel Models 2 and 10). Elevation varies from 7400 feet to 8853 feet (Beaver Mountain summit). District personnel Mike Van Horn and Craig Pettigrew responded, ordering engines and a helicopter. Initial reconnaissance by the helicopter indicated 30-50 acres in heavy timber involved. Additional resources ordered were an air tanker, 3 hand crews, and two large bulldozers. Suppression actions were directed towards structure protection, notably the ski lodge and associated buildings.

By 1830 hours, the first air tanker was on scene and began retardant drops. A second tanker was requested and made available for the fire. Bulldozers began to arrive on scene and started construction of line on nearby ridges. VFD's arrived on scene providing structure protection. By 2400 hours approximately 70 personnel were assigned or enroute to the fire. The fire slowed down but continued active burning during the night.

Fire activity increased during daylight August 17. At 0900 hours an overhead team was requested to take over management of the fire. The Southern Interagency Blue Team was diverted from the Tin Cup fire.

Initial arrival and briefing of the Blue Team was conducted at Logan District Headquarters at 1745 hours August 17. Estimated fire size at that time was 1000 acres. With heavy retardant drops (a total of 17) and helicopter support, the fire slowed its rate of spread. It was mostly torching out, throwing sparks starting new spots which water drops from helicopters were helping to contain. Dozers had nearly completed indirect line construction on adjacent ridges.

At 0600 August 18, the Blue Team formally assumed command of the incident. The fire was broken into three divisions, three more hand crews and two additional helicopters were ordered. Initial efforts were directed towards reinforcing existing lines and direct lining the fire with dozer lines. Initial reconnaissance flight of the fire put acreage at 720 acres.

Base Camp and the Incident Command Post were set up at Beaver Mountain Ski Area. Primary incident objectives were: 1. Provide for firefighter safety; 2. Protect private structures, especially the ski lodge and related buildings and equipment (valued in excess of $2 million); 3. Protect domestic livestock, wildlife and cutthroat trout habitat; and 4. Keep costs to a minimum.

By 1800 August 18, 193 personnel were assigned to the incident, 468 chains of line (primarily dozer line) had been built and the fire was 35% contained. Continued helicopter drops helped cool down hot spots and kept spotting to a minimum allowing the fire to burn out to the lines. Approximately 250 chains
of line, primarily hand line, remained to be built in steep, rocky terrain. Weather conditions became more moderate -- temperature low 80's, RH 25%, winds 15 mph.

August 19. With the ski area owner's permission, the ski lift was activated to move firefighters to the ridgetop. This greatly sped up transportation and saved firefighters a long, bumpy ride and hike. Efforts were devoted to handline construction with good progress along the front slopes and connecting dozer lines in steep areas. Fire was declared 50% contained at 1800 hours.

On August 20, the forest rehabilitation specialist arrived to develop the fireline rehabilitation plan. Use of GPS and field checking firmly located all bulldozer lines and firebreaks. The recomputed burn acreage was reduced to 617 acres -- 475 (77%) state lands, 142 (23%) federal lands. Hose lays were initiated from drop point 1 to speed mopup with plans to expand to additional areas. Total personnel on fire were 205.

August 21. Rehabilitation of dozer lines on ski slopes was completed with seed, netting and straw ordered. IR flight identified 20+ hotspots which were located for mop-up by crews and water drops. Water source near highway 89 was discontinued due to traffic safety concerns. A hose lay from Beaver Mountain was begun to reach interior spots. Containment estimated at 85%. A short, strong thunderstorm moved through camp and over the fire at 2130 hours causing minor damage but no change to the fire.

August 22. Xedar flight identified 20-25 spots to work. Crews made good progress in direct mop-up of these spots. Total containment of fire was declared at 1800 hours. Initial demobilization of crews is underway with most crews scheduled to be released August 24 leaving only National Guard crews.

August 23. Evening August 22 IR flight showed far fewer hot spots. Xedar flight at 0900 confirmed the reduced activity. Crews were aware of all spots and actively mopping up. Total control is expected at 1800 hours. Wasatch Regulars were sent to assist on a lightning strike fire on Logan Mountain at Logan District's request. Crews and all personnel have been notified of the scheduled demobilization of the incident at 0800 hours on August 24.

Injuries on the incident have been fairly minor -- blisters, allergic reaction to bee stings, colds and mild dehydration. Two more serious injuries were a crew member being too close to a water drop and receiving back muscle strains, and a backwards fall with possible head/back injury requiring medivac from the incident.

Total cost of the incident was estimated at $700,000. Costs were higher than initial projections due to additional work done -- 100% mop-up of fire and rehabilitation of bulldozer lines. Management of the incident was formally turned over to the Logan District Office at 1300 hours August 24.
Beaver Mtn. Incident

1600 HRS 8/18
FWD Road   ---
OPEN Fireline  \\
Dozer Line   xxx
Hand Line    HHH
Helibase
WATER Source
ICP
Base
Scale -1" = 2000'
Appendix B. Fire-Affected Douglas-Fir Communities
Appendix C. Aerial Bark Beetle Detection Surveys (1980-1995)
1987 Western Budworm Douglas-fir MORTALITY

R. 41 E.  R. 42 E.  R. 43 E.
1989 Western Budworm
Douglas-Fr Mortality

[Map of the area showing the distribution of Western Budworm in the Douglas-Fr region]
1990 Western Budworm
Douglas-Fir Mortality
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