ATTACK AND BROOD PRODUCTION BY THE DOUGLAS-FIR BEETLE (COLEOPTERA: SCOLYTIDAE) IN DOUGLAS-FIR, *PSEUDOTSUGA MENZIESII* VAR. *GLAUCA* (PINACEAE), FOLLOWING A WILDFIRE

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ABSTRACT.—In 1994 ground fire ignited in forests of Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco, on Beaver Mountain, Utah. The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, attacked a range of moderately fire-injured host conifers in 1995. Logistic regression models run for 1995 data illustrated that 1 year after the fire event the Douglas-fir beetle selected and attacked 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, because most large, fire-damaged conifers were colonized by beetles in 1995. Although beetle populations did not reach outbreak proportions outside the fire boundary, host selection shifted to green trees in 1997 along the burn perimeter. Log linear analysis indicated that increased brood production was conditioned by increased diameter and moderate fire damage to the trees.

Key words: *Douglas-fir, bark beetles, wildfire, disturbance ecology.*

Relatively few empirical studies concerning the interaction of wildland fire and bark beetle colonization have been conducted (Weatherby et al. 1993, Ryan and Amman 1996, Bebi et al. 2003). Yet, multiple disturbance agents are critical to the functioning of most dynamic, sustainable forest ecosystems. Interior Douglas-fir is a prominent conifer of the western United States that extends throughout the Rocky Mountains and into British Columbia. This species covers a distance of nearly 4500 km (Hermann and Lavender 1990). Public land managers are concerned with Douglas-fir beetle attacking live, fire-injured trees and establishing successful brood, which later overcome green Douglas-fir trees adjacent to scorched stands. Understanding how fire damage contributes to increasing the insect population is critical for preventing beetle epidemics (Jenkins 1990). Although information about Douglas-fir beetle host selection may help forest managers identify susceptible trees, research focused on bark beetle brood production is also important from a population standpoint. Some beetle-attacked Douglas-fir trees on Beaver Mountain, Utah, were able to repel attacking beetles with resin flow. Conversely, other Douglas-fir trees, unable to inhibit beetle colonization, allowed successful brood development and emergence. Fire damage of especially large-diameter Douglas-fir may affect host defense mechanisms and permit greater colonization.

On 16 August 1994 a lightning-ignited crown fire spread in a forest of subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae), 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 multi-storied Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco (Pinaceae), stands along the edge of the main fire front. Prior to the fire, endemic populations of Douglas-fir beetles were detected on Beaver Mountain. During the 1995 spring flight season the beetle population increased substantially in the fire-damaged Douglas-fir stands.

The 1st objective of this research was to explore whether bark beetles prefer fire-damaged over non-fire–damaged and fire-killed host trees. The 2nd objective was to quantify brood emergence in Beaver Mountain Douglas-fir forests for each beetle-attacked tree following the August 1994 fire.

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MATERIALS AND METHODS

Study Area and Sample

Beaver Mountain peak (2699 m) is located in the Bear River Range of northern Utah. The study area was located on this peak between 2500 m and 2622 m in elevation (41′58″N, 111′33″W) and included Douglas-fir trees on 7 plots. Plots were selected in 7 areas where low-intensity, surface spot fires resulted in low to moderate fire injury to Douglas-fir. Plot boundaries were delineated in Douglas-fir stands by observing blackened surface fuels, charred bark, torched branches, and fire-damaged needles of individual trees.

On each of the 7 plots varying in size from 2 ha to 5 ha, all Douglas-fir trees greater than 30.5 cm in diameter at breast height (dbh) were sampled. Furniss (1962) established that beetles generally prefer to attack larger-diameter trees. Given this criterion, 997 individual trees were evaluated. Each sample tree was tagged with a unique number for identification and relocation. A few individual fire-killed trees were harvested in 1995 before the study was conducted. However, the number of sample trees in the population over the course of field research was not reduced by salvage logging.

Fire-caused Injury

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 of mortality (PM) due to fire ranging from 0 to 1 (Reinhardt and Ryan 1989) was also calculated. 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). We estimated CVS 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% (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 visually by the extent of black-

ened bark surface and obvious root and cambial death exhibited by exfoliated bark (Ryan 1982a). We scheduled fire-data collection on Beaver Mountain for the summer of 1996 after the 2nd growth season following the fire event. Fire-caused mortality is best observed after 2 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 damage the tree in all cases (Ryan 1982a). Therefore, an indirect means of analyzing both crown and bole injury was also performed in the analysis. Reinhardt and Ryan's (1989) revised PM fire effects equation,

$$[PM = 1/(1 + e^{(-1.941 + BF + CF)})], \qquad (1)$$

was used to calculate fire injury for each of the 997 sample trees and to confirm results for the measured fire damage variables. Components of the equation calibrated for Douglas-fir were as follows:

$$\text{Bark factor (BF)} = 6.316(1 - \exp[-0.3937BT]), \quad (2)$$

where BT = bark thickness (cm) and CF = crown volume scorched (%). Bark thickness was calculated from dbh adjusted specifically for Douglas-fir (Monserud 1979).

Bark Beetle Attack Behavior

Beginning in the summer of 1996, we inspected all plot trees after adult flight for insect activity on the lower bole to a height of 10 m to determine bark beetle invasion (Pasek 1990, Rasmussen et al. 1996). Bark samples were removed on attacked trees to confirm that damage was caused by Douglas-fir beetle. Crown fade, dried pitch, and emergence holes distinguished 1995 insect activity from 1996 insect activity. 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 beetle activity in the current year 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 attack and insect colonization during the 2nd season.

Quantifying Douglas-fir Brood Success

A subset of host trees attacked by Douglas-fir bark beetles in 1995–1996 was relocated in July 1997. The resulting sample size used for this 2nd analysis included 343 trees exhibiting ≥1 emergence hole on the lower 5 m of the tree bole. Two sections 900 cm^2 (30 cm × 30 cm) on the lower stem of each beetle-selected Douglas-fir tree were chosen, and we counted the number of beetle emergence holes. Douglas-fir beetle exit holes are aligned with pupal chambers and were not confused with ventilation holes, which are formed in the egg gallery. We also observed wood borer and smaller ambrosia beetle pinholes on the host bark surface. We avoided measuring obvious fire scars from previous fires, which are devoid of bark and cambium.

Generally, the north and south aspects of the tree were sampled. Furniss (1962) 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 2-count samples on each tree were pooled and used in the analysis, rather than compared or evaluated separately. The resulting sample area for calculated brood density was 1800 cm^2 for each Douglas-fir.

Schmitz and Rudinsky (1968) concluded that colonizing Douglas-fir bark beetles show little preference for any particular portion of the tree from the lower to the upper bole. Therefore, breast height was selected as an acceptable and efficient region to quantify brood success (Furniss 1962, 1965, Lessard and Schmid 1990, Pasek 1990). Ground fire affecting the root crown and lower tree bole also possibly attracted greater numbers of bark beetles to that section of the stem. Although Douglas-fir beetles will not colonize dead cambium, these insects generally first occupy areas immediately adjacent to scorched bark (Miller and Keen 1960).

Emergence Hole Count and Actual Brood Production

Additional analyses were conducted in 1997 to ensure that the number of emergence holes counted on the larger sample (n = 343) of successfully colonized trees accurately reflected brood survival. We placed square cages measuring 900 cm^2 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). We sealed cages tightly to prevent escape, and the bottom ends were fastened together to form a funnel secured to a plastic tube. A no-pest insect strip with Vapona® as its active lethal ingredient was placed in the container to kill collected insects and to prevent consumption by other collected organisms. We collected emerging adults weekly and counted them in the laboratory. Mesh cages were removed from trees and emergence holes were counted. Thick bark was smoothed to reveal all possible beetle holes against a flush surface.

Statistical Analysis

Chi-square analyses were performed comparing presence and absence of beetle attacks in fire-damaged, fire-killed, and non-fire–affected trees for each field season 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. Chi-square values with probabilities <0.001 were considered statistically significant.

We used stepwise logistic regression (Hamilton 1992) to analyze annual beetle attack behavior data, relating the log of the odds of bark beetle attack to a linear function of dbh, and quadratic functions of CVS, bole char, and PM. Terms were added to the equation if reduction in deviance was statistically significant given the change in degrees of freedom, similar to the calculation of adjusted R^2 in multiple linear regression.

Log linear regression (McCullagh and Nelder 1989) was used to analyze emergence hole density for each successfully beetle-attacked Douglas-fir in the sample population. Terms were tested for significance by calculation of adjusted reduction in deviance. Additional log linear regressions were calculated on the caged sections of trees to estimate number of beetles emerging as a function of emergence hole density. Total brood production could then be estimated as product of emergence hole density and beetle emergences per hole.

RESULTS

Fire Damage

A total of 997 potential host Douglas-fir trees were inventoried in the study area; 389 (39%) were not fire damaged, 429 (43%) were damaged but not killed by fire, and 180 (18%) were killed by fire.

Annual Beetle Host Selection

In the spring of 1995, beetles inhabited a wide range of Douglas-fir trees in the area (Fig. 1A). Beetle colonization was most common in fire-damaged trees ($\Pi^2_{2\,df} = 244.062$, $P < 0.001$), but also included 74 fire-killed trees presumably because sufficient phloem resources existed the 1st spring after the fire. Beetle preference for fire-damaged trees persisted the 2nd year ($\Pi^2_{2df} = 165.6$, $P < 0.001$; Fig. 1B), although an increasing number of non-damaged trees were selected. By 1997 beetles selected mostly non-fire–damaged trees, as most fire-damaged trees had been colonized during the previous 2 seasons.

In 1995 the probability of beetle attack was significantly correlated ($P < 0.001$) with dbh, CVS, bole char, and PM (Fig. 2). Beetles primarily selected moderately fire-damaged, large Douglas-fir trees, with probabilities approaching 1 for selected trees. Beetle-affected trees from the previous year were removed from the sample for 1996, leaving 635 potential host trees. Again, the probability of attack was correlated with CVS, bole char, and PM, but effects were smaller than in 1995, with probabilities approaching 0.50 for selected trees (Fig. 3). Tree diameter was negatively associated with probability of attack in combination with bole char (Fig. 3A) or CVS (Fig. 3B) and was statistically insignificant in combination with PM (Fig. 3C), reflecting the low availability of suitable large trees after the 1st year. Beetle-affected trees were again removed from the sample for 1997. Only CVS and PM were significantly correlated with colonization for 1997, and both exhibited exponentially decreasing probabilities as fire damage increased. Neither bole char nor dbh was significant. Plot location, simply measured as the distance in meters to the main fire front, was not significant in 1995 or 1996 but emerged as an important variable in predicting colonization in 1997.
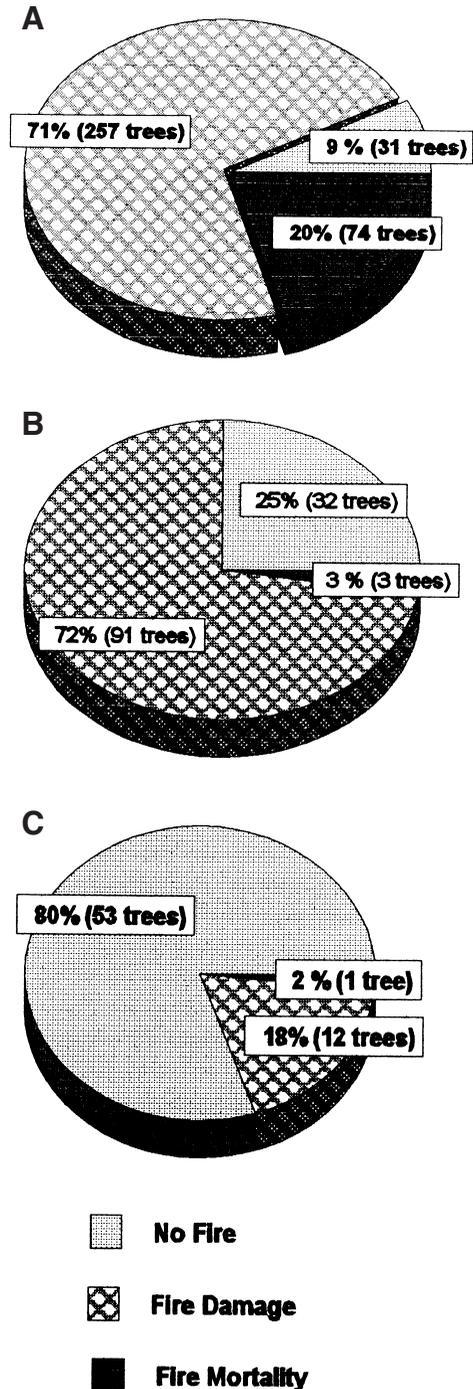

Fig. 1. Distribution of *Dendroctonus pseudotsugae* attack on Douglas-fir trees by fire damage classes in 1995 (A), 1996 (B), and 1997 (C).
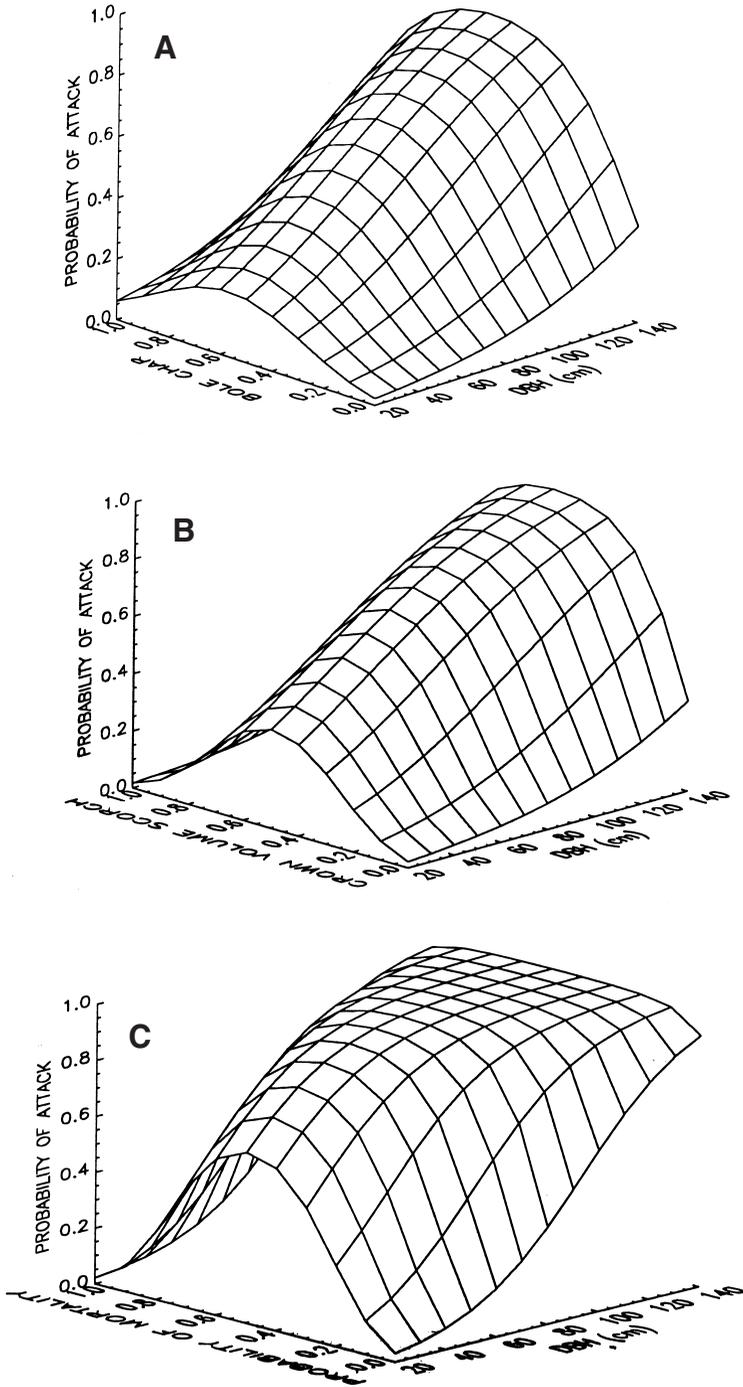
Fig. 2. Logistic regression model for 1995 *Dendroctonus pseudotsugae* attack data for bole char (A), crown volume scorch (B), and probability of mortality (C).
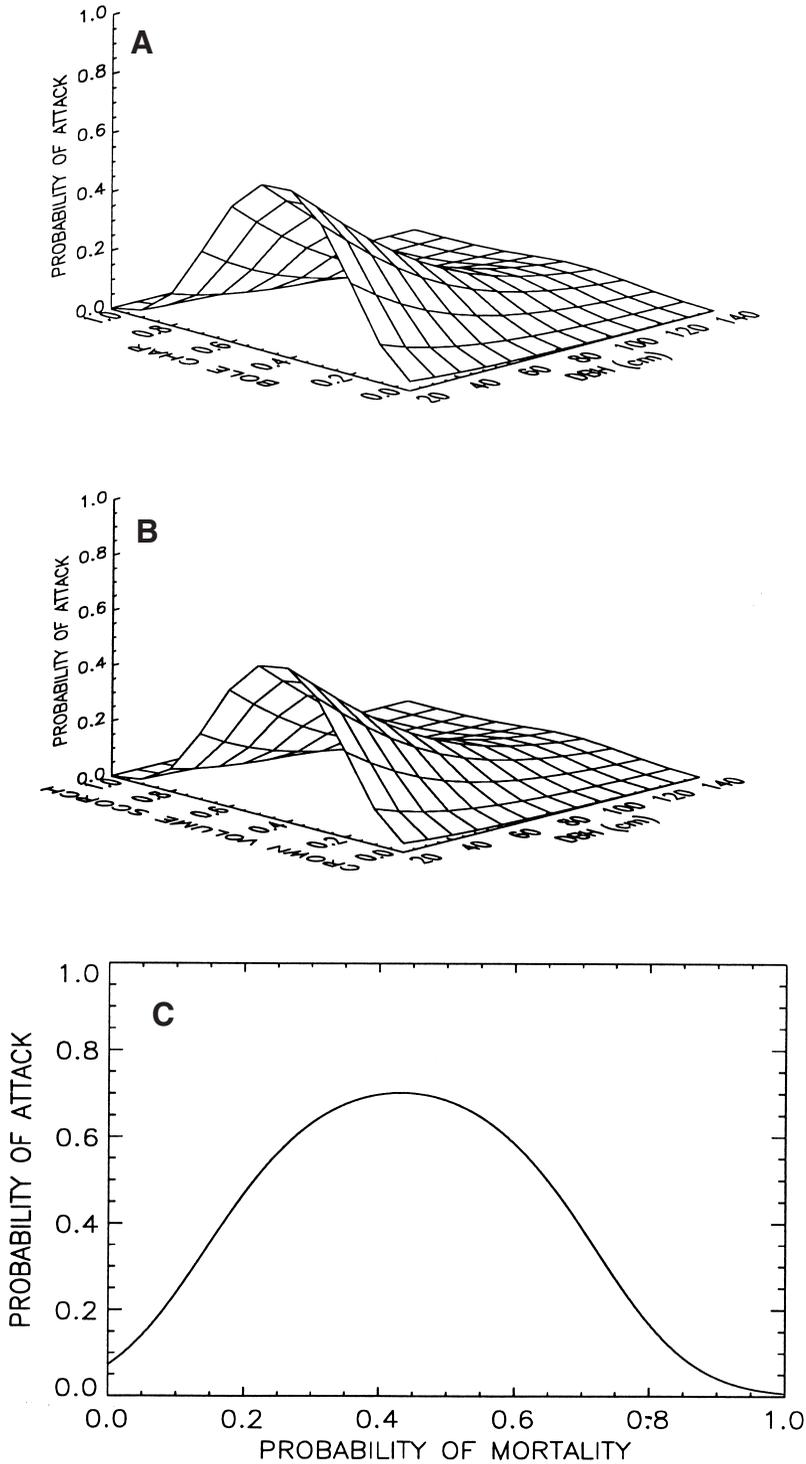
Fig. 3. Logistic regression model for 1996 *Dendroctonus pseudotsugae* attack data for bole char (A), crown volume scorch (B), and probability of mortality (C).
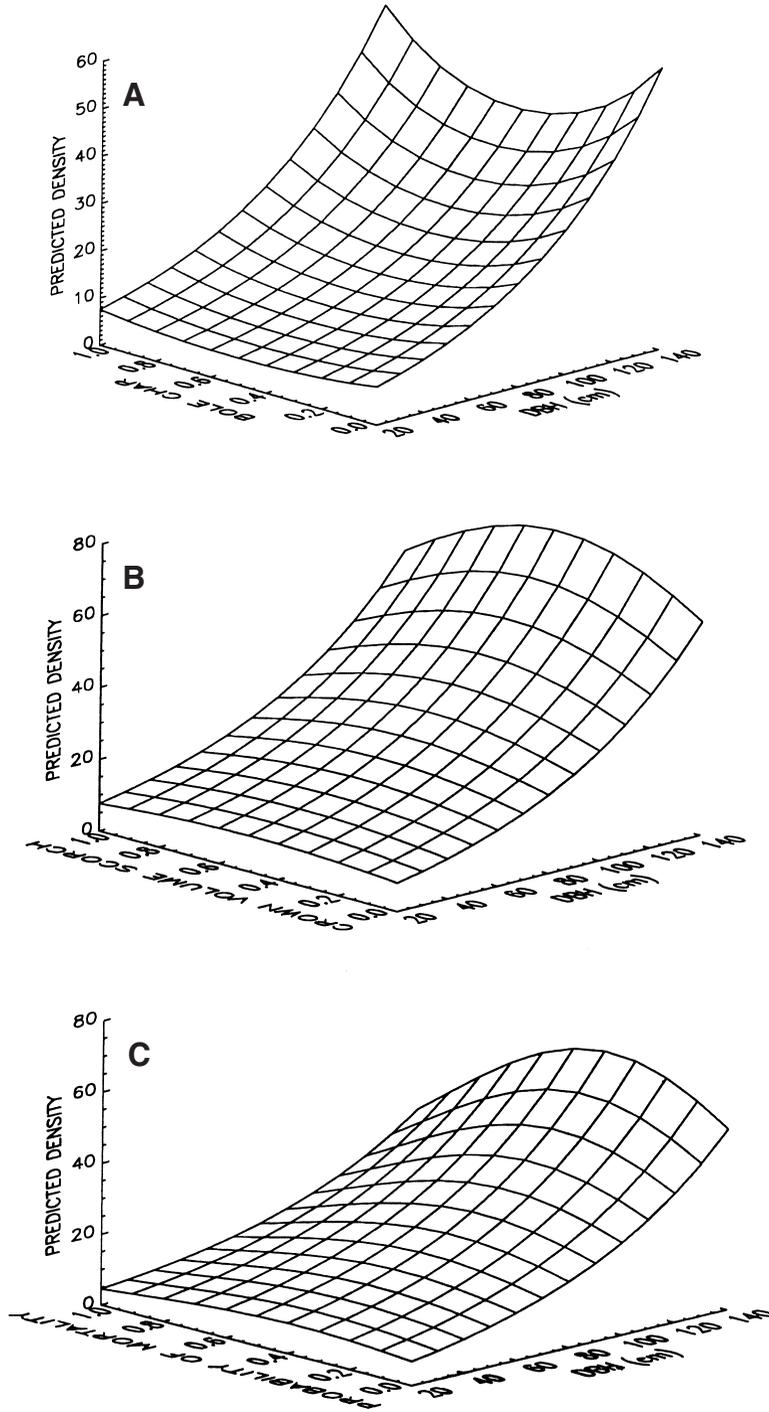
Fig. 4. Log linear model of *Dendroctonus pseudotsugae* brood emergence as indexed by density of emergence holes for bole char (A), crown volume scorch (B), and probability of mortality (C).

Quantifying Douglas-fir Brood Success

Bole char, dbh, CVS, PM, and plot location were all statistically significant variables in predicting brood emergence, with dbh showing the most significant effects. Opposing trends in predicted emergence were observed for bole char versus CVS or PM (Fig. 4A vs. Figs. 4B, 4C). Maximum emergence is predicted for large trees with moderate CVS (45%–70%), with predicted emergence densities of nearly 80 exit holes · 1800 cm^{-2}. Number of beetles emerging per emergence hole increased significantly with increasing emergence hole density (Fig. 5).

Fig. 5. Log linear model for *Dendroctonus pseudotsugae* emergence holes · 1800 cm^{-2} and actual adult emergence ($n = 31$).

DISCUSSION

Annual host selection was conditioned by both tree size and relative extent of fire injury to Douglas-fir trees. A significant effect for logistic regression models of 1995 data (Fig. 2) confirmed the aggregation of Douglas-fir beetles on predominantly larger hosts (ranging between 120 cm and 140 cm). Conversely, recorded insignificance of dbh in the PM model of 1996 data suggests that beetles attacked smaller trees only because most mature Douglas-fir had already been colonized in 1995.

In 1996 the highest probability of attack calculated for bole char and CVS shifted from 60%–80% in 1995 to 50%–60% in 1996 for larger-diameter trees. The highest probability of attack calculated using PM decreased to 35%–50% (Fig. 3). Relative significance of all fire-damage variables conditioning beetle attack declined from 1995 to 1996. However, beetles still selected moderately fire-weakened trees in 1996, demonstrating their ability to sense altered host condition. Amman and Ryan (1991) similarly concluded that female bark beetles selected mature Douglas-fir exhibiting ≥50% basal cambial damage (not to exceed 80%). Following the 1989 Lowman Fire Complex, Weatherby et al. (1993) reported that Douglas-fir bark beetles were discovered in the study area colonizing trees that reported ≥48% CVS. After the Yellowstone fires, bark beetles were also found to attack host trees with moderate crown heating not greater than 80% CVS (Amman and Ryan 1991).

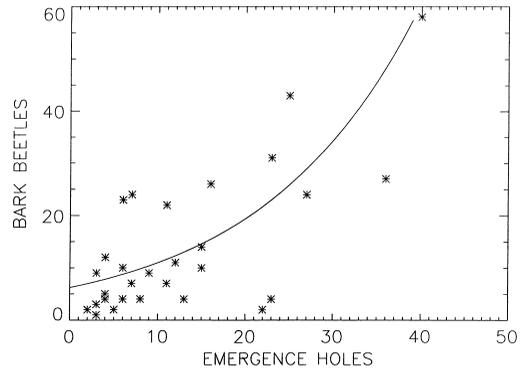Highly significant effects for CVS in logistic regression models for data in 1995 and in 1996 confirmed the greater relative importance of damage to the crown, rather than injury to the stem, in conditioning a beetle attack response. Primarily a function of crown damage for larger, more attractive hosts, PM also exhibited a highly significant effect in 1995 and 1996. 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, Peterson 1985, Peterson and Arbaugh 1986).

Conclusions drawn by Furniss (1965) following the Poverty Flat Fire demonstrated that beetle attack densities rose as host crown injury increased, although successful Douglas-fir beetle colonization declined dramatically in completely defoliated trees. Host conifers on Beaver Mountain that evidenced crown and stem injury >80% by the 1995 flight season were not generally attacked in 1995–1997. However, in 1995 females aggregated on the surviving stem surfaces on 74 large host conifers that were observed to have suffered 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. In 1996 and 1997, fire-killed Douglas-fir, exhibiting exfoliated bark and dry phloem, were not colonized by beetles.

By 1997 both small- and large-diameter, fire-weakened Douglas-fir had already been killed by beetles, and beetle host selection on Beaver Mountain shifted, making plot location a marginally important term in explaining

beetle attack preference. Therefore, emerging beetles were forced to aggregate in large numbers on fewer ($n = 53$) relatively vigorous host trees. Small infestation centers of green Douglas-fir developed along the perimeter of certain plots on northwestern and western aspects. Significantly more beetle-preferred, fire-damaged trees were in these field locations than on sites farther from the main fire source.

Moderately fire-damaged and large-diameter trees were not only highly desirable for attack by Douglas-fir beetles, but they were also successfully colonized at higher densities than other potential hosts. Results of log linear models for quantitative brood emergence demonstrated that both tree diameter and different degrees of fire damage influenced brood survival.

Regardless of fire injury on individual hosts, the predicted density of surviving brood rose as tree diameter increased. The largest trees measuring 120–140 cm recorded 50–80 exit holes · 1800 cm^{-2} (Fig. 5). The greatest predicted density of emerging beetles was established for large trees, subjected to 50%–70% crown damage or 45%–65% PM (Fig. 4). However, the relationship between bole char and emergence density contradicts the results reported for the other fire-damage variables. The graph supports the substantial increase in brood production for larger-diameter trees, yet results show a reduction in emergence holes with moderately stem-injured Douglas-fir. Biologically, it makes sense that non-fire–affected stems would allow greater brood survival and larger emergence densities. Conversely, it does not immediately seem reasonable that large brood densities would be supported in severely fire-weakened tree hosts. Yet, it is possible that large-diameter trees suffering severe delayed mortality effects maintained sufficient resources to permit aggregations of bark beetles on limited sections of the tree bole in 1995. These small pockets of bark beetle attack were likely recorded on severely damaged host trees, because the sampling method 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 resources for regenerating bark beetle populations on part of its stem or on the entire bole adjacent to fire scars (Miller and Keen 1960).

Actual beetle emergence showed a trend of increasing emergence with the number of exit holes counted for 31 trials. All circular holes sized to this specific bark beetle were counted. A few adult reemergence exits and ventilation holes were likely measured as well. These errors in sampling may have slightly overestimated the number of emergence holes (Schmitz and Rudinsky 1968). Conversely, some 1800-cm^2 surfaces with 20–40 emergence holes exhibited nearly twice as many emerging beetles (Fig. 5). If Douglas-fir beetle attack densities were relatively high in host trees, then intraspecific competition among adjacent larvae could have partly regulated mining patterns (McMullen and Atkins 1961, Schmitz and Rudinsky 1968). Mountain pine beetle emergence by >1 young adult insect from a single exit hole is possible for similarly mass-colonized lodgepole pine (Cole and Amman 1980). Therefore, surviving Douglas-fir larvae may create closely neighboring or coalesced pupal chambers and encourage overlapping brood emergence. If this was the case, then actual brood production in moderately crown-damaged, large-diameter host trees was significantly higher than the results reported for the emergence density log linear models.

Although attack preference shifted in the 3rd season toward green host trees, fewer trees were attacked. The decline in the number of beetle-affected conifers in 1997 may have been partly due to greater densities of bark beetles necessary to mass colonize healthier conifers.

This paper provides information useful in selecting trees for sanitation and salvage based not only on direct fire mortality, but also on the likelihood that injury will result in beetle colonization and mortality. Early postfire removal of non-fire–damaged, bark beetle–susceptible trees may decrease colonization, brood production, and subsequent beetle mortality.

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