Predicting postfire Douglas-fir beetle attacks and tree mortality in the northern Rocky Mountains

Sharon Hood and Barbara Bentz

Abstract: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were monitored for 4 years following three wildfires. Logistic regression analyses were used to develop models predicting the probability of attack by Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins, 1905) and the probability of Douglas-fir mortality within 4 years following fire. Percent crown volume scorched (crown scorch), cambium injury, diameter at breast height (DBH), and stand density index for Douglas-fir were most important for predicting Douglas-fir beetle attacks. A nonlinear relationship between crown scorch and cambium injury was observed, suggesting that beetles did not preferentially attack trees with both maximum crown scorch and cambium injury, but rather at some intermediate level. Beetles were attracted to trees with high levels of crown scorch, but not cambium injury, 1 and 2 years following fire. Crown scorch, cambium injury, DBH, and presence/absence of beetle attack were the most important variables for predicting postfire Douglas-fir mortality. As DBH increased, the predicted probability of mortality decreased for unattacked trees but increased for attacked trees. Field sampling suggested that ocular estimates of bark char may not be a reliable predictor of cambium injury. Our results emphasize the important role of Douglas-fir beetle in tree mortality patterns following fire, and the models offer improved prediction of Douglas-fir mortality for use in areas with or without Douglas-fir beetle populations.

Résumé : Des douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) ont été suivis pendant 4 ans à la suite de trois incendies de forêt. Des analyses de régression logistique ont été utilisées pour élaborer des modèles de prédiction de la probabilité d'une attaque du dendroctone du douglas (*Dendroctonus pseudotsugae* Hopkins, 1905) et de la probabilité que le douglas de Menzies meure dans les quatre années suivant un feu. Le volume de cime roussi, les dommages au cambium, le diamètre à hauteur de poitrine (DHP) et l'indice de densité du peuplement de douglas de Menzies étaient les variables les plus importantes pour prédire les attaques du dendroctone. Une relation non linéaire entre le roussissement de la cime et les dommages au cambium a été observée, ce qui signifie que les dendroctones n'attaquent pas de préférence les arbres qui ont à la fois le maximum de dommages à la cime et au cambium mais plutôt un niveau intermédiaire quelconque. Les dendroctones étaient attirés par les arbres avec un degré élevé de roussissement de la cime mais sans dommages au cambium, un et 2 ans après un feu. Le roussissement de la cime, les dommages au cambium, le DHP et la présence ou l'absence d'attaques du dendroctone étaient les variables les plus importantes pour prédire la probabilité que le douglas de Menzies meure après un feu. La probabilité estimée de mortalité diminuait avec l'augmentation du DHP chez les arbres qui n'avaient pas été attaqués alors que la probabilité qu'un arbre meure augmentait avec l'augmentation du DHP chez les arbres qui avaient été attaqués. Des échantillons prélevés sur le terrain indiquent que l'estimation oculaire d'une couche superficielle d'écorce carbonisée pourrait ne pas être un prédicteur fiable de dommages au cambium. Nos résultats font ressortir l'importance du rôle que joue le dendroctone du douglas dans les patrons de mortalité après un feu et les modèles offrent de meilleures prédictions de la mortalité du douglas de Menzies dans les zones avec ou sans populations de dendroctone.

[Traduit par la Rédaction]

Introduction

Tree mortality following fire is influenced by multiple factors. Many coniferous species have life-history traits and characteristics that can greatly enhance their resistance to fire. These traits include a deep root system, thick bark, and distinctive crown features such as large buds or protective woody structures around buds. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* (Dougl.) ex P. & C. Laws.), for example, are known for their fire tolerance, which is in large part due to thick, insulating bark that develops with age and protects the inner cambium from heat injury (Fowler and Sieg 2004). Mortality following fire depends not only on species-specific traits and tree age, but also on the type and degree of fire-caused injuries, initial tree vigor, and the postfire environment (Ryan and Amman 1996). One important component of the postfire environment that often confounds predictions of delayed tree mortality is phloem-feeding bark beetles that are attracted to fire-injured conifers. Trees that are only moderately injured by fire and capable of recovery can be subsequently attacked and killed by bark beetles (Furniss 1965).

Bark beetles within the genus *Dendroctonus* (Coleoptera: Curculionidae, Scolytinae) require live phloem for success-

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ful brood production. When beetle population densities are high, the defenses of healthy host trees can be overwhelmed by the attack of many beetles simultaneously (Wood 1982; Raffa and Berryman 1983). At low population densities, trees stressed by a variety of factors are initially attacked (Wood 1973), and some species, including the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), preferentially attack downed trees (Schmitz and Gibson 1996). Following fire, several *Dendroctonus* species are often found colonizing thick-barked trees that have been physiologically stressed by a variety of fire-caused stem, root, and crown injuries. For example, western pine beetles (*Dendroctonus brevicomis* LeConte) preferentially attacked ponderosa pine with moderate levels of fire-caused crown and bole injury (Miller and Patterson 1927; Peterson and Ryan 1986; McHugh et al. 2003; Wallin et al. 2003), and Jeffrey pine beetles (*Dendroctonus jeffreyi* Hopkins) colonized Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) with moderate levels of fire-caused injuries (Bradley and Tueller 2001). Attraction of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) to fire-injured lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and ponderosa pine appears to be weak (Amman and Ryan 1991; Safranyik et al. 2001; Elkin and Reid 2004), although successful attack and reproduction have been observed in lodgepole pine with moderate fire injury (Geiszler et al. 1984). The Douglas-fir beetle has been consistently associated with fire-injured trees, often attacking larger trees with moderate to high levels of basal bole injury (Furniss 1965; Rasmussen et al. 1996; Weatherby et al. 2001) and light to moderate levels of crown injury (Peterson and Arbaugh 1986; Ryan and Amman 1994; Weatherby et al. 2001; Cunningham et al. 2005), with attacks declining only in completely defoliated trees (Furniss 1965).

Knowledge of the effects of fire injury on tree survival is imperative for prescribed fire planning and postfire management, including salvage, following both wildfires and prescribed fires (Covington et al. 1997; Fowler and Sieg 2004). A large body of research describing the complex interactions among fire injuries and tree survival exists, and has been used in the development of predictive models for a variety of tree species. Tree size and heat-caused crown and cambium injury have been found to be the most significant factors for predicting tree mortality following fire, with the levels varying among tree species (Wagener 1961; Ryan and Reinhardt 1988; McHugh and Kolb 2003). Several studies also attributed observed bark beetle attacks after fire to an increase in delayed tree mortality (Peterson and Arbaugh 1986; Bradley and Tueller 2001; McHugh et al. 2003). Using data from a wildfire in Utah, Cunningham et al. (2005) correlated fire-injury variables with Douglas-fir beetle attack. No models have been developed, however, for predicting the probability of delayed Douglas-fir tree mortality that include the interaction of fire injury and Douglas-fir beetle attack. This information is important because trees that are only moderately injured by fire and capable of recovery can be subsequently colonized by bark beetles and killed, confounding predictive models that do not include this second-order fire effect. Additionally, standardized methods are needed for collection of the fire-injury data that are most useful in applying predictive models.

Our goal in the current study was to quantify the role of the Douglas-fir beetle in delayed Douglas-fir mortality following wildfire. Specifically we (*i*) developed a model for predicting the probability of Douglas-fir beetle attack as a function of individual-tree fire injury and stand characteristics and (*ii*) developed a model for predicting the probability of Douglas-fir mortality within 4 years following fire that includes fire-related injuries and the probability of attack by the Douglas-fir beetle.

Methods

Site description

Three late-summer wildfires were selected for the study. The lightning-caused Mussigbrod fire started on 31 July 2000 and burned approximately 23 876 ha on the Wisdom Ranger District of the Beaverhead–Deerlodge National Forest in southwestern Montana (N5069725, E284947, UTM Zone 12, NAD83). Elevation of the study area ranged from 1989 to 2006 m. Aspect was generally southwest, with an average slope of 38%. Douglas-fir and lodgepole pine were the dominate conifer species.

The Moose fire was started by lightning on 14 August 2001 on the Flathead National Forest in northwestern Montana (N5384955, E 695741, UTM Zone 11, NAD83). It burned approximately 28 733 ha on the Glacier View Ranger District of the Flathead National Forest, Coal Creek State Forest, and Glacier National Park. Most of the study area was located on the Flathead National Forest. Elevation of the study area ranged from 1402 to 1780 m, with slopes between 43% and 51% and south and southwest aspects. In addition to Douglas-fir, other dominant tree species in the area included subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), western larch (*Larix occidentalis* Nutt.), lodgepole pine, and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). The study area within Glacier National Park also contained ponderosa pine.

The Green Knoll fire was human-caused and started in late July 2001. It burned 1827 ha on the Jackson Ranger District of the Bridger–Teton National Forest in western Wyoming (N4807539, E0506333, UTM Zone 12, NAD83). Elevation of the study area ranged from 2073 to 2207 m. Aspect was generally southeast, with slopes between 0% and 14%. Douglas-fir was the dominant tree species, with alpine fir, lodgepole pine, and Engelmann spruce scattered throughout.

We established randomly located permanent plots within each fire boundary 1 year following fire by selecting areas that burned under mixed-severity conditions and were dominated by Douglas-fir larger than 30 cm diameter at breast height (DBH). Because our main objective was to examine the relationship between fire injury and bark beetle response, aerial detection surveys (ADS) (USDA Forest Service, Forest Health Protection, http://www.fs.fed.us/r1-r4/spf/fhp/aerial/gisdata) and ground reconnaissance surveys were used to ensure that plots were established in areas near active Douglas-fir beetle populations. Aerial detection surveys provide a measure of relative tree mortality, by species, determined manually (based on red tree crowns) by an observer from a fixed-wing aircraft. Based on ADS for the year prior to each fire, it was estimated that 157 trees were

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Table 1. Postfire characteristics of Douglas-fir (n = 789) sampled 1 year following the Mussigbrod, Moose, and Green Knoll wildfires in Montana and Wyoming.

	Mean	SE	Range
DBH (cm)	38.7	0.66	12.7–105.4
Percent crown volume scorched	37.4	1.28	0–100
Cambium-kill rating (CKR)	1.5	0.06	0–4
Bark char index (BCI)	1.78	0.02	0–3
Ground char index (GCI)	1.85	0.02	0–3
Stand density index (SDI)	779	6.50	212–1173
Stand density index for Douglas-fir only (SDI_{Df})	645	7.58	24–997

infested with Douglas-fir beetle within an 8 km wide buffer (25 537 ha) of the Green Knoll fire boundary, and fewer than 10 trees infested with Douglas-fir beetle were observed surrounding the Mussigbrod fire boundary. The area within Glacier National Park to the east of the Moose fire was not included in the ADS. Therefore, although our calculation of 555 trees infested with Douglas-fir beetle within an 8 km wide buffer (42 080 ha) to the west of the Moose fire is an underestimate, it does provide a relative measure of Douglas-fir beetle activity in the vicinity. Our sampled areas experienced primarily surface fire, resulting in variation in the percentage of crown volume scorched, with some green foliage remaining in the majority of the tree crowns. Also, no salvage activities in these areas were proposed, allowing us to monitor the trees over several years.

Field sampling

The summer following each fire, we installed 0.08 ha permanent plots within the Mussigbrod fire boundary and 0.04 ha permanent plots within the Moose and Green Knoll fire boundaries. Because Douglas-fir beetle emergence and flight occur from May through June, plots were installed and revisited no earlier than mid-July to ensure that flight and colonization had ended. The number of plots installed within each fire boundary was dependent on finding suitable areas. Four Douglas-fir plots were installed within the Mussigbrod fire boundary in September 2001, and 51 and 28 plots within the Moose and Green Knoll fire boundaries in July and August 2002, respectively. At each plot, all trees with DBH 12.7 cm or larger and believed to have been alive before the fire were tagged. Trees with no fine branches and little to no bark remaining were considered to have been dead before the fire and were not tagged. For each tagged tree we recorded tree species, status (live or dead), DBH, crown scorch, cambium-kill rating, bark char, ground char, and Douglas-fir beetle attacks (Table 1). Trees were considered dead when no green foliage remained in the crown, regardless of the time of beetle attack. Crown scorch was determined by visually assessing the volume of prefire crown that was killed by either direct flame contact or convective heating and therefore included both scorched and consumed portions of the crown. Prefire crown volume was estimated using the methods described in Ryan (1982) by visually reconstructing the crown to its prefire state based on crown scorch and fine branch structure. Bark char and ground char were visually assessed on four sides of each tree as unburned, light, moderate, or deep using the guidelines in Ryan (1982) and Ryan and Noste (1985). Cambium was sampled at groundline in the center of each bole quadrant, where bark and ground char were also assessed. Using an increment borer, we drilled to the bark–wood interface and visually determined whether the cambium was alive or dead using specifications described in Ryan (1982).

Trees attacked by Douglas-fir beetle were identified on the basis of external bole signs such as reddish orange boring dust on the lower portion of the bole (Thier and Weatherby 1991; Schmitz and Gibson 1996). A 15 cm × 30 cm section of the outer bark was removed from a random subsample of trees showing signs of attack. These bark sections were examined to develop a relationship between external signs of boring dust and Douglas-fir beetle gallery patterns within the phloem. Other insect species present were also noted. To correlate degree of fire injury with level of attack, each bole was visually examined round its whole circumference and as high as possible without the aid of climbing ladders, and an estimate of the percent circumference of each tree bole attacked by Douglas-fir beetle (e.g., with visible boring dust) was recorded. Because initial attacks by Douglas-fir beetle typically occur high (~3.6 m) on tree boles, with additional attacks above and below that height (Furniss 1962), our estimates taken from ground level may underestimate mass attacks. However, because plots were visited annually, we were able to more accurately correlate percent circumference attacked (estimated from ground level) with tree death. Mass-attacked Douglas-fir can take 12–15 months for foliage to completely fade, which is within the time frame of our annual remeasurements. Additionally, trees that died following fire and showed signs of attack were examined to confirm that Douglas-fir beetles had colonized the tree.

Stand density index (SDI) for all tree species and SDI for Douglas-fir only (SDI_{Df}) were calculated for each plot (Reineke 1933). We revisited all plots in late July and early August annually for 4 years following fire to monitor tree mortality and beetle attacks.

Data analyses and model development

General linear mixed models were used to examine differences in fire injury and tree size between live and dead and attacked and unattacked Douglas-fir (SAS Institute Inc. version 9.1; Littell et al. 1996). Yearly differences were analyzed by excluding dead trees from previous years. Statistical significance was set at $P \leq 0.05$.

To avoid direct sampling of the cambium, bole-char codes have often been used as a surrogate for cambium status (i.e., dead or alive) (Fowler and Sieg 2004). However, when bole-char codes were first described, Ryan (1982) stated that bole char alone is “not an adequate indicator of cambial injury”

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and should be used in conjunction with a direct assessment of cambium condition. To assess the accuracy of bole char as a predictor of cambium status, logistic regression was used to test for differences between direct measurements of cambium status and external ratings based on bole char. Because four samples were taken per tree, estimates from the generalized estimating equations were used to account for within-tree correlation.

Fire-injury variables collected by bole quadrant were summarized to the tree level for final analyses. The cambium-kill rating (CKR) was calculated by summing the dead cambium samples per tree (0–4). The four ground char ratings and four bark char ratings for each quadrant were coded as 0 (unburned), 1 (light), 2 (moderate), or 3 (deep). A ground-char index (GCI) and a bark-char index (BCI) were then calculated as the sum of the four quadrant codes divided by 4, creating an index ranging between 0 and 3.

Tree-mortality model

All Douglas-fir trees were coded as either 0 (live) or 1 (dead), based on their status at postfire year 4. The probability of tree death within 4 years following fire was modeled using general linear mixed models with a binomial error distribution, specified logit link function (Littell et al. 1996), and the model form

$$P_{\mathrm{m}} = 1/\{1 + \exp[-(B_0 + B_1X_1 + \ldots\ B_kX_k)]\}$$

where P_{m} is the probability of mortality, B_0, B_1, and B_k are regression coefficients, and X_1 and X_k are independent fixed variables. Fire and plot within fire were included as random effects. Because the tree-mortality model is intended for use in postfire-management applications and development of prescribed fire burn plans, we limited the variables tested for inclusion to those that were relatively easy and quick to measure and were repeatable. Candidate fixed-effect variables for the mortality model included DBH, crown scorch, CKR, GCI, and beetle-attack level. Based on plots of the logits, GCI and CKR were included as continuous rather than class variables (Hosmer and Lemeshow 2000).

Beetle-attack model

A beetle-attack model was developed to describe the probability of a tree being attacked (1) or not attacked (0) by Douglas-fir beetle as a function of fire injury to the host tree and stand characteristics. For the model, a tree was considered attacked if it was either partially or mass-attacked by Douglas-fir beetle. Only trees with DBH 23 cm or larger were included in attack-model development because Douglas-fir beetles prefer larger diameter trees (Furniss et al. 1979) and only trees with DBH greater than 23 cm were attacked on our plots. The probability of each tree being attacked within 4 years after fire was modeled using general linear mixed models with a binomial error distribution, specified logit link function (Littell et al. 1996), and the model form

$$P_{\mathrm{attack}} = 1/\{1 + \exp[-(B_0 + B_1X_1 + \ldots\ B_kX_k)]\}$$

where P_{attack} is the probability of attack, B_0, B_1, and B_k are regression coefficients, and X_1 and X_k are independent fixed variables. Fire and plot within fire were included as random effects. Candidate fixed-effect variables for the attack model were DBH, crown scorch, CKR, GCI, SDI, and $\mathrm{SDI_{Df}}$. SDI is known to influence Douglas-fir beetle attacks in unburned forests (Negron 1998), although the relative importance of stand characteristics and fire injury of individual trees in bark beetle attack preference is unknown.

Independent fixed-effect variables were screened for inclusion in the tree-mortality and beetle-attack models using univariate logistic regression. Only variables that differed between live and dead trees or attacked and unattacked trees ($P \le 0.1$) and were not strongly correlated were retained for model development. Once all candidate variables were screened, only variables with $P \le 0.05$ were considered statistically significant and retained in the multivariate models. Performance of all models was evaluated using the area under the receiver operator characteristic (ROC) curve and classification tables (Saveland and Neuenschwander 1990). The ROC value reflects the accuracy of the model in classifying live and dead or attacked and unattacked trees, a value of 0.5 being no better than chance and 1.0 indicating a perfect fit. A ROC value equal to 0.5 suggests no discrimination, values between 0.7 and 0.8 indicate acceptable discrimination, those between 0.8 and 0.9 indicate excellent discrimination, and those greater than 0.9 are considered to indicate outstanding discrimination (Hosmer and Lemeshow 2000).

Classification tables allow the user to select the most appropriate model probability level based on management objectives. Trees with predicted values above the selected cutoff probability are classified as dead (tree-mortality model) or attacked (beetle-attack model). Trees below the cutoff probability are classified as either live or unattacked. The classification tables presented for the models display the percentage of trees that were correctly classified, the percentage of trees that each model correctly predicted to die or be attacked, and the percentage of trees that each model correctly predicted to live or remain unattacked.

Validation of the tree-mortality and beetle-attack models

We validated the tree-mortality and beetle-attack models using fire-injury and beetle-attack data collected on 125 Douglas-fir that were monitored for 4 years following the wildfires in Yellowstone, Wyoming, in 1988 (Amman and Ryan 1991; Ryan and Amman 1994, 1996) and fire-injury data collected on 547 Douglas-fir monitored for 4 years following prescribed burns in 2002 on the University of Montana's Lubrecht Experimental Forest, Montana (S. Hood, unpublished data). Although data-collection methods were very similar across studies, in the Yellowstone data set, percent basal circumference girdled was recorded (Amman and Ryan 1991) rather than data from cambium samples taken from each bole quadrant (i.e., CKR) as in the current study. We developed a CKR value for each tree in the Yellowstone data set using the following rule set: CKR = 0 for trees with 0%–12% basal girdling; CKR = 1 for trees with 13%–37% basal girdling; CKR = 2 for trees with 38%–62% basal girdling; CKR = 3 for trees with 63%–87% basal girdling; and CKR = 4 for trees with 88%–100% basal girdling.

To evaluate the beetle-attack model, a predicted P_{attack} value was generated for each Douglas-fir in both validation data sets. Each tree was classified as attacked or unattacked using the attack-probability cutoff that best balanced correct

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Fig. 1. Average DBH, percent crown volume scorched, and cambium-kill rating for live and dead Douglas-fir 4 years after fire. Dead trees from previous years were excluded from analyses to show yearly survival and mortality attributes. Vertical bars indicate the standard error and an asterisk denotes a significant difference ($P < 0.05$) between live and dead trees each year.

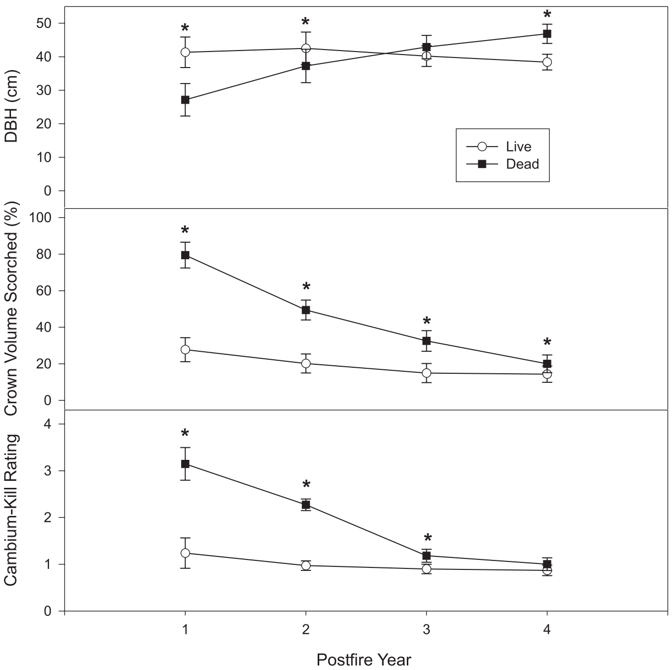
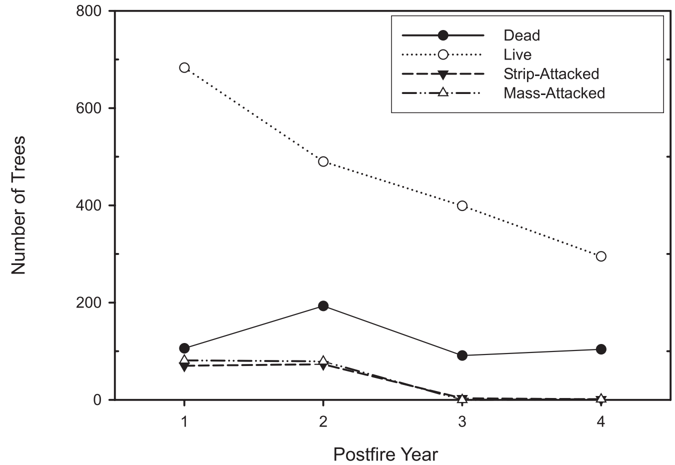


Fig. 2. Numbers of dead and live Douglas-fir at the beginning of each postfire year on the Mussigbrod, Moose, and Green Knoll wildfires, and numbers of Douglas-fir strip-attacked and mass-attacked by the Douglas-fir beetle during each postfire year. Dead trees from previous years were excluded to show yearly mortality and attack attributes.



predictions of attacked and unattacked trees. Trees were coded as attacked (1) if the predicted P_{attack} value was greater than or equal to the cutoff, and unattacked (0) if the predicted P_{attack} value was less than the cutoff or the tree was smaller than 23 cm DBH. We compared attack predictions for each tree with observed attack values in each data set.

Both predicted and observed beetle-attack values were used to evaluate the tree-mortality model. P_m was predicted for each tree in the validation data sets, and separate values were calculated on the basis of observed beetle attacks and values predicted by the beetle-attack model. Each tree was classified as live or dead using the probability cutoff that best balanced correct predictions of live and dead trees.

We also used the data collected in the current study to evaluate the postfire Douglas-fir mortality model originally developed by Ryan and Reinhardt (1988) and recently updated by Reinhardt and Crookston (2003). This model is widely used in the fire behavior and effects models BehavePlus, the Fire and Fuels Extension to the Forest Vegetation Simulator, and the First Order Fire Effects Model. Ryan and Reinhardt's (1988) model uses crown scorch and DBH to predict tree mortality that occurs within 3 years after fire.

Results

Of the 789 Douglas-fir on 83 plots monitored annually for 4 consecutive years (Mussigbrod (n = 118), Moose (n = 453), and Green Knoll (n = 218)), 90% of the trees had observable fire injuries. Four years following the fires, 62.6% of the sampled trees had died (n = 494). Overall, there was no significant difference in DBH between live (39.58 cm) and dead trees (39.65 cm). Dead trees had significantly greater crown scorch (48%) than live trees (19%) ($F_{[779]}$ = 154.09, $P < 0.001$), and dead trees also exhibited significantly greater cambium injury (CKR = 1.98) than live trees (CKR = 0.89) ($F_{[781]}$ = 94.17, $P \leq 0.001$).

Analysis of survival by year, with dead trees in previous years excluded, showed that trees with lower fire-injury levels survived longer (Fig. 1). The greatest number of trees died within 2 years after fire, although mortality remained relatively high throughout the study and similar numbers of trees died in postfire years 1 and 4 (Fig. 2). Trees dying 1 and 2 years after fire were significantly smaller in diameter than live trees (year 1: $F_{[781]}$ = 55.26, $P < 0.001$; year 2: $F_{[674]}$ = 10.86, P = 0.001). This trend then reversed, and by postfire year 4, DBH was significantly greater for dead trees than for live trees ($F_{[390]}$ = 17.53, $P < 0.001$) (Fig. 1).

Most Douglas-fir with visible boring dust contained Douglas-fir beetles. Woodborer larvae within two families (Coleoptera: Cerambycidae and Buprestidae) were also observed, although attacks were not quantified or identified to species. The majority of trees with signs of Douglas-fir beetle attack on less than 90% of the lower bole circumference had green foliage for more than a single year following the attack. We considered these trees strip-attacked. Trees with boring dust covering ≥90% of the lower bole circumference and no green foliage remaining the year following attack were considered mass-attacked. Douglas-fir beetle mass-attacked 27% (n = 161) and strip-attacked 23% (n = 142) of all Douglas-fir with DBH 23 cm or larger. Only 5% of trees attacked (n = 15) had no observable fire injuries. The majority of beetle attacks (98%) occurred within 2 years after fire (Fig. 2). Of strip-attacked trees, 63% were dead by postfire year 4. Of the trees that were suitable for attack (e.g., live and with DBH 23 cm or larger), 24% were attacked in the first year and 37% were attacked in the second year after fire. Of suitable trees within each fire boundary, 73%, 19.6%, and 43% were attacked within the

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Fig. 3. Average DBH, percent crown volume scorched, and cambium-kill rating for live Douglas-fir trees with DBH 23 cm or larger, according to Douglas-fir beetle attack status and postfire sampling year. Dead trees in year 1 were excluded from data shown for year 2. Different letters indicate significant differences ($P < 0.05$) among attack-status categories within each postfire year. Shaded bars show median values.

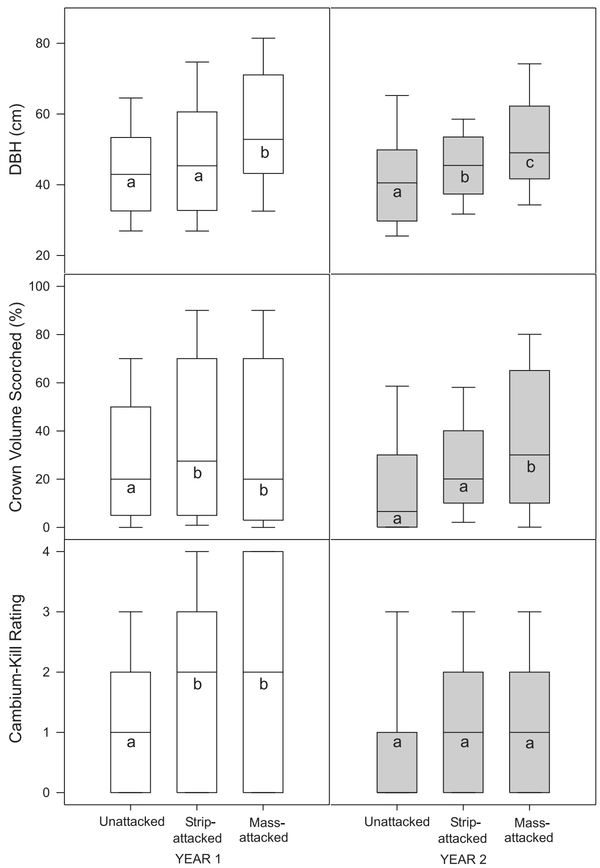

Table 2. Parameter estimates for the Douglas-fir postfire mortality model.

	Estimate	SE	P
Intercept	–0.8435	0.5262	0.154
Crown scorch	0.03719	0.004771	<0.001
Cambium-kill rating (CKR)	0.4786	0.09393	<0.001
DBH (cm)	–0.03015	0.01102	0.006
Douglas-fir beetle attack level*	–2.2999	0.7746	0.003
DBH × attack level	0.09395	0.01815	<0.001

*Attack level is equal to 1 if trees are beetle-attacked and 0 if they are not attacked.

Green Knoll, Mussigbrod, and Moose fire boundaries, respectively.

One and 2 years following fire, Douglas-fir beetles mass-attacked suitable trees with significantly greater crown scorch (year 1: $F_{[429]} = 7.71$, $P = 0.001$; year 2: $F_{[400]} = 7.39$, $P = 0.001$) and larger DBH (year 1: $F_{[429]} = 14.46$, $P < 0.001$; year 2: $F_{[384]} = 14.57$, $P < 0.001$) than unattacked trees (Fig. 3). Beetles attacked trees with a significantly higher CKR in year 1 ($F_{[521]} = 13.49$, $P < 0.001$), but differences in CKR between attacked and unattacked trees in year 2 were not significant (Fig. 3). The only significant difference in fire injury between strip- and mass-ttacked trees was in crown scorch in postfire year 2 (Fig. 3). Therefore, a binomial attack variable (e.g., attacked or unattacked) was used as the response variable in the beetle-attack model and as a predictor variable in the tree-mortality model.

Table 3. Classification table for the Douglas-fir postfire mortality model.

P_m	Total correct (%)	Correctly predicted mortality (%)	Correctly predicted survival (%)
0.1	66.7	65.3	97.1
0.2	74.4	72.4	83.9
0.3	77.1	76.8	77.9
0.4	77.7	79.1	74.5
0.5	77.4	81.3	70.5
0.6	77.9	85.1	68.2
0.7	76.9	89.2	64.5
0.8	73.5	92.3	59.5
0.9	65.9	95.2	52.4

Note: P_m is the predicted probability of mortality 4 years after fire (see Table 2). Also shown are the percentages of trees correctly predicted to die and survive by the model.

Cambium status (e.g., dead or alive) as determined by direct sampling was significantly correlated with bark-char codes based on ocular estimates ($\chi^2_{[3]} = 140.79$, $P < 0.001$), although individual bark-char codes were not clearly associated with either live or dead cambium. DBH was not significantly correlated with cambium status. Logistic regression model results suggest that unburned and light bark char were more often associated with live cambium, with the model predicting that 5.9% and 14.6%, respectively, of samples with these codes would have dead cambium. For moderate and deep bark-char, 34.3% and 63.6% were predicted to have dead cambium, respectively. The majority of the quadrants (73.4%) were rated as moderate bark char. The bark-char index was not considered a candidate in the tree-mortality model, based on these findings.

Tree-mortality model

The best model for predicting Douglas-fir mortality included crown scorch, DBH, CKR, beetle-attack level (i.e., attacked or unattacked), and the interaction of beetle-attack level and DBH (Table 2; ROC = 0.86). Model outcomes for a range of P_m values provide criteria for decision-making based on the percentages of Douglas-fir mortality and survival that were correctly predicted. A cutoff P_m value of 0.6 provided the best balance between correctly predicted survival and mortality and was chosen as the cutoff value to use in model validation (Table 3). The predicted P_m value increases with CKR and crown scorch for both unattacked and beetle-attacked trees, although the P_m value for a given fire-injury level is greatest for beetle-attacked trees (Fig. 4). Large Douglas-fir had the greatest chance of survival following fire in the absence of Douglas-fir beetle attacks (Fig. 5). However, because the P_{attack} value increases with tree size, predicted postfire Douglas-fir mortality increases with tree size after attack by the Douglas-fir beetle (Fig. 5).

At a P_m value of 0.6, 58% ($n = 348$) of trees with DBH 23 cm or larger were predicted to die. However, only 32% ($n = 194$) of trees with DBH 23 cm or larger were predicted

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Fig. 4. Predicted mortality curves for a 40 cm DBH Douglas-fir according to cambium-kill rating (CKR), percent crown volume scorch, and Douglas-fir beetle attack status (i.e., attacked or unattacked).

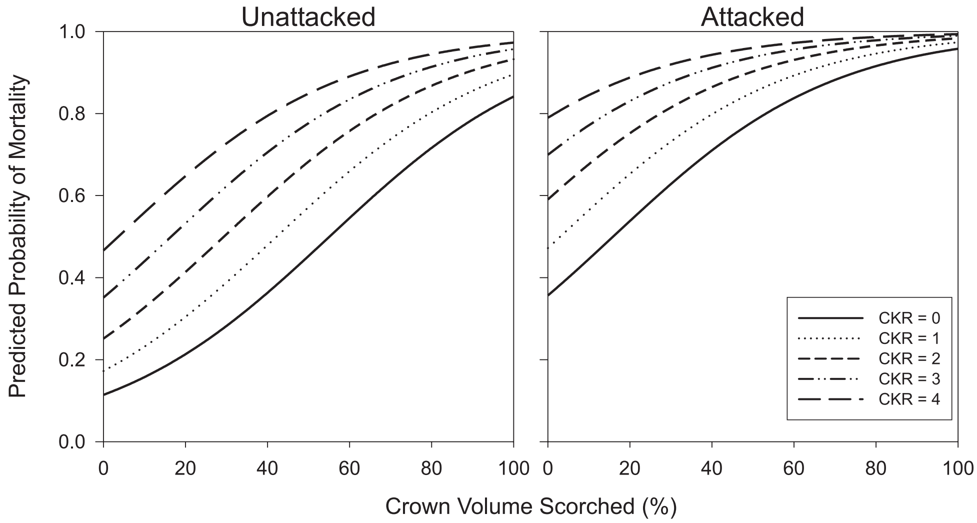
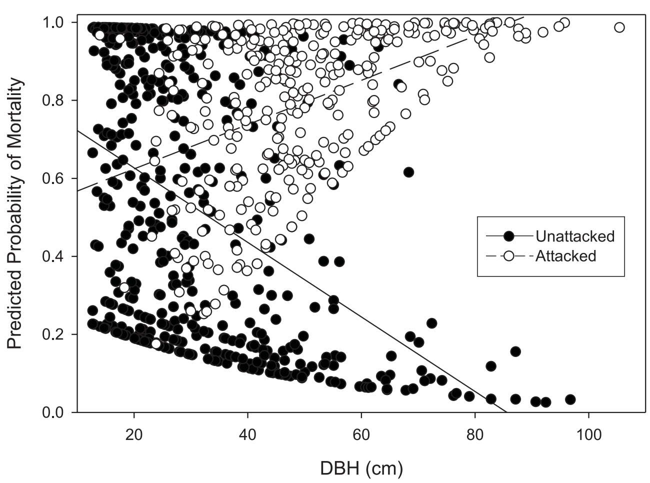


Fig. 5. Predicted probability of Douglas-fir mortality (P_m) as a function of Douglas-fir beetle attack status and DBH. P_m decreases with increasing DBH for unattacked trees and increases for attacked trees.



to die, based on fire injuries only. Therefore, at this probability level, the Douglas-fir beetle contributed an additional 25% mortality of trees with DBH 23 cm or larger.

Beetle-attack model

The best model for predicting the percentage of trees attacked by Douglas-fir beetle included crown scorch, CKR, DBH, SDI_{Df}, and the interaction between crown scorch, CKR, and SDI_{Df} (Table 4; ROC = 0.74). Model outcomes for a range of predicted P_{attack} values provide criteria for decision-making based on the percentage of Douglas-fir correctly predicted to be attacked and not attacked. A P_{attack} value of 0.3 maximized the number of correctly classified trees and was chosen as the cutoff probability to classify the trees as either attacked or unattacked for use in model validation (Table 5). Larger trees and trees in areas where Douglas-fir were denser had a higher P_{attack} value. As indicated by the significant interaction term in the model, the P_{attack} value differs according to crown scorch, CKR, and SDI_{Df}. P_{attack} increases with crown scorch at low CKR. However, P_{attack} decreases with increasing crown scorch at high CKR and increases in areas with higher SDI_{Df} (Fig. 6).

Validation of tree-mortality and beetle-attack models

The tree-mortality model performed well for both data sets when observed attack levels were used (Yellowstone: ROC = 0.90; Lubrecht: ROC = 0.94). Trees in the Yellowstone data set had characteristics similar to those of trees used in model development. Of the trees in the Yellowstone data set (n = 96), 77% died within 4 years after fire. Dead trees in the Yellowstone data set were larger in diameter (40.0 vs. 36.0 cm) and had greater crown scorch (52% versus 22%) and cambium injury (CKR = 2.9 versus 2.2) than live trees. Of the trees in the Yellowstone data set, 71% were attacked by Douglas-fir beetle. Using a P_m value of 0.6, the cutoff with the highest percentage of correctly classified trees (Table 3), 83% of the trees were correctly classified. The model correctly predicted 85% of the dead trees and 72% of the surviving trees. The majority of trees that the model misclassified as dead but were observed to be live, were strip-attacked, with moderate crown scorch and cambium-injury levels and DBH between 20 and 40 cm. The trees that the model misclassified as live but were observed to be dead had no fire injuries and were mass-attacked by Douglas-fir beetle.

Douglas-fir trees at the Lubrecht site were smaller, on average, than trees used for model development (23.8 versus 38.7 cm). Of trees in the Lubrecht data set (n = 121), 22% died within 4 years after fire. Live trees in the Lubrecht data set were larger than dead trees (24.9 versus 19.9 cm DBH). Dead trees had greater crown scorch (68% vs. 15%) and cambium injury (CKR = 2.9 versus 0.5) than live trees. Only 2% of the trees at Lubrecht were attacked by Douglas-fir beetles. Using P_m = 0.6, the model correctly predicted 64% of the dead trees and 96% of the live trees. Trees that were misclassified as dead but observed to be live largely had crown-scorch levels between 30% and 70%.

Using a cutoff probability of 0.3 (Table 5), the beetle-attack model correctly classified 70% of the Yellowstone

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Table 4. Parameter estimates for the postfire Douglas-fir beetle attack model.

	Estimate	SE	*P*
Intercept	–5.5625	1.1797	0.008
Crown scorch	0.01140	0.004956	0.022
Cambium-kill rating (CKR)	0.3031	0.1227	0.014
DBH (cm)	0.05371	0.007879	<0.001
Stand density index for Douglas-fir only (SDI_{Df})	0.003785	0.000796	<0.001
Scorch × CKR × SDI_{Df}	–0.00001	0.000003	0.001

Note: Only trees larger than 23 cm DBH were included in model development.

Table 5. Classification table for the postfire Douglas-fir beetle attack model.

P_{attack}	Total correct (%)	Correctly predicted to be attacked (%)	Correctly predicted to be unattacked (%)
0.1	53.4	51.5	100
0.2	61.8	57.4	76.8
0.3	68.1	64.2	74.6
0.4	67.1	66.8	67.4
0.5	64.8	69.9	61.9
0.6	64.5	78.5	59.9
0.7	62.3	86.0	57.6
0.8	55.9	88.4	53.4
0.9	52.1	85.7	51.3

Note: P_{attack} values, predicted P_{attack} values within 4 years after fire (see Table 4), and the percentages of trees the model correctly predicted to be attacked and unattacked are shown.

trees (ROC = 0.81). The model correctly predicted 85% of attacked trees in the Yellowstone data set, although only 48% of the unattacked trees were correctly predicted. Very few trees were predicted to be attacked at the Lubrecht site (2%), which is similar to the observed level of attacked trees. The beetle-ttack model correctly classified 96% of the Lubrecht trees (ROC = 0.85). The model correctly predicted 98% of the unattacked trees but only 8% of the attacked trees. When P_m was computed for each tree using the predicted P_{attack}, model accuracy decreased slightly from that of the model using observed attack levels (Yellowstone: ROC = 0.90 versus 0.87; Lubrecht: ROC = 0.94 versus 0.93), with concomitant slight decreases in model accuracy across a range of predicted probabilities.

Ryan and Reinhardt's (1988) model, which does not include a measure of cambium injury or bark beetle attack, underpredicted mortality of Douglas-fir monitored in the current study. Using a probability cutoff of 0.6, 34% of the trees predicted to survive to postfire year 3, the predictive limit of the model, died. However, mortality prediction was very accurate, with the model correctly classifying 88% of the trees predicted to die.

Discussion

Bark-char codes, or some measure of char height, have often been used as a surrogate for cambium injury in modeling postfire tree mortality, to avoid direct sampling of the cambium (Wyant et al. 1986; Peterson and Arbaugh 1989; McHugh and Kolb 2003; Thies et al. 2006). However, our comparison of ocular estimates of bark char with direct measurement of cambium condition suggests that a great deal of uncertainty would be introduced into a model that uses the extent of bark char rather than a direct measurement of cambium status. In our study, the majority of bark quadrants were assessed as having moderate bark char (73%), and dead cambium was only sampled beneath 35% of these quadrants. Because the majority of the quadrants were rated as having moderate bark char, which is the category with the most ambiguity, large errors could result if this rating was used to determine cambium status. This is likely due to Douglas-fir having thick bark, where a moderate bark char rating reveals little in terms of how much heating the cambium received. While unburned, light, and deep bark-char categories more accurately predicted cambium status, if ocular estimates are to be used, the moderate category should be more finely defined, possibly dividing it into two levels. This idea needs further research, as it could result in more efficient evaluations of tree cambium injury. Additionally, over a 12 year period no differences were found in mortality rates between cored and uncored California red fir (*Abies magnifica* A. Murr.) and white fir (*Abies concolor* (Gord. & Glend.) Lindl.) (van Mantgem and Stephenson 2004). Although the trees were unburned in this study, the results provide evidence that coring trees to assess cambium status does not contribute to tree mortality.

We found crown scorch, CKR, DBH, and Douglas-fir beetle attack to be the most important variables for predicting Douglas-fir mortality within 4 years after fire. GCI was not significant. Crown injury is widely considered the most influential factor in a tree's ability to survive a fire, and some measure of crown injury has been used in the majority of postfire mortality models (Fowler and Sieg 2004). It is important to distinguish among the measures of crown injury, and we emphasize that only crown scorch should be used with our tree-mortality model. We observed high rates of tree mortality with high levels of crown scorch, regardless of cambium injury, DBH, or beetle-attack level. Fewer than 9% of trees with more than 80% crown scorch were alive 4 years after fire. The additional measure of fire-induced cambium injury in our model provided greater predictive power than crown scorch alone. Given similar levels of crown scorch, mortality would be underpredicted for trees with high levels of cambium injury and overpredicted for those with low levels. Peterson and Arbaugh (1989) also found that the number of dead cambium quadrants was significant in predicting Douglas-fir postfire mortality, and Hood et al. (2007) reported that CKR was a significant variable in predicting postfire mortality of incense cedar (*Calocedrus decurrens* (Torr.) Florin), California red fir, white fir, ponderosa pine, and Jeffrey pine. While it has

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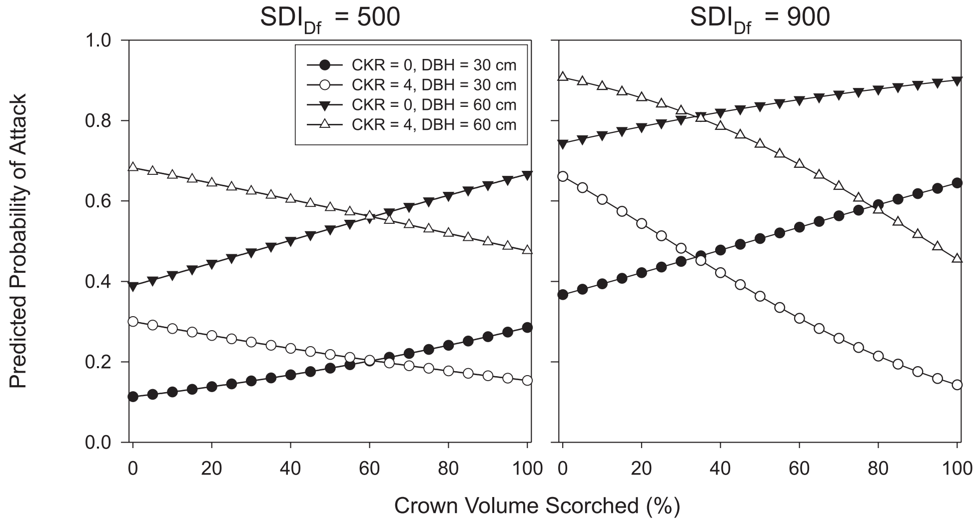
Fig. 6. Predicted probability of Douglas-fir beetle attack as a function of percent crown volume scorch, DBH, Douglas-fir stand density index (SDI_{Df}), and cambium-kill rating (CKR). For simplicity, results for two levels of SDI_{Df}, DBH, and CKR are shown; other CKR values fall between the two lines.



been suspected that larger trees, with potentially deeper duff mounds at the base, are more susceptible to cambium injury (McHugh and Kolb 2003), we observed no trend in cambium death with tree size.

The influence of tree size on postfire mortality is conflicting and varies with tree species. Many studies have shown that larger trees have a lower P_m than smaller trees, given the same level of fire injury (Bevins 1980; Wyant et al. 1986; Harrington 1993; Mutch and Parsons 1998; Stephens and Finney 2002; McHugh and Kolb 2003; Hood et al. 2007). However, the opposite has also been found (Ryan 1990; Ryan and Frandsen 1991; McHugh and Kolb 2003; Hood et al. 2007), and a few studies have reported that DBH was not a significant variable in explaining tree mortality (Stephens and Finney 2002; Thies et al. 2006; Hood et al. 2007). The inclusion of an interaction term for DBH and beetle-attack level in our Douglas-fir mortality model accounts for the relative importance of tree size, fire injury, and Douglas-fir beetle attacks (Weatherby et al. 2001). In the absence of beetle attacks, large trees are predicted to have a higher probability of survival than small trees, given the same level of fire injury. The reverse is predicted if a tree is attacked by Douglas-fir beetle, with large trees having a lower probability of survival. Douglas-fir beetles preferentially strip- and mass-attacked larger trees, and the majority of attacks occurred in postfire years 1 and 2. Mass-attacked trees were dead the year following attack (e.g., postfire years 2 and 3), while strip-attacked fire-injured trees sometimes retained green needles for up to 3 years (e.g., postfire years 3 and 4). Therefore, delayed mortality of large trees in postfire years 3 and 4 can be partially explained by the preference of the Douglas-fir beetle for large-diameter fire-injured trees in postfire years 1 and 2. Moreover, by postfire year 4, little difference was found in cambium injury and crown scorch between live and dead trees, further evidence that the Douglas-fir beetle was a significant factor in delayed tree mortality 4 years after fire. These results emphasize the importance of secondary effects, such as bark beetle attacks, in the relationship between fire-caused tree mortality and tree size.

These patterns highlight the possible of influence bark beetles on the timing of postfire delayed tree mortality. While some studies have shown little additional mortality beyond the second postfire year (Ryan et al. 1988), we observed considerable tree mortality 4 years after fire, with 30% of live trees in postfire year 3 dead by year 4. Of these trees (67%), 32% had been strip-attacked by Douglas-fir beetles in postfire years 1 and 2. Weatherby et al. (2001) also observed Douglas-fir beetle activity 5 years following a fire in southern Idaho. Therefore, differences in the influence of beetle attacks on fire-injured trees among studies (Peterson and Arbaugh 1986, 1989) may in part be a function of the length of time trees are monitored following fire. Unburned trees that are strip-attacked by Douglas-fir beetles typically survive. Similarly, Douglas-fir with only minimal fire injury typically survive. However, owing to the combination of stresses caused by fire injury and beetle attacks on only a portion of the tree bole, the majority of fire-injured, strip-attacked trees in the current study died by postfire year 4. It is therefore necessary to monitor mass and strip Douglas-fir beetle attacks because both can cause postfire delayed tree mortality, although the timing of death may vary.

Postfire weather can also be an important factor in the timing of delayed tree mortality. Drought and stress can influence a tree's capacity to recover from fire injury (Ryan 2000; van Mantgem et al. 2003), and warm, dry periods following fire may favor an increase in Douglas-fir beetle populations (Schmitz and Gibson 1996; Powers et al. 1999). The level of Douglas-fir beetle activity in the vicinity of the fire will also contribute significantly to the probability of beetle-caused postfire mortality.

Crown scorch, CKR, DBH, and SDI_{Df} were significant variables for determining P_{attack}. Cunningham et al. (2005) also found a significant relationship between crown scorch, DBH, bole char, and P_{attack}, and suggested that crown damage, rather than injury to the stem, was most important. The nonlinear relationship between crown scorch and CKR that we found suggests that beetles are not preferentially attacking trees with maximum fire injury (e.g., 100% scorch, CKR = 4). Instead, some intermediate level of fire-induced

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injury causes enough physiological stress for the tree to be both attractive to and overcome by Douglas-fir beetles. Our results suggest that this intermediate level could consist of four dead cambium samples or 100% crown scorch, but not both types of fire injury. While the level of crown scorch that was attractive to beetles was high in postfire years 1 and 2, beetles were no longer attracted to trees with high levels of cambium damage in postfire year 2, suggesting deterioration of the phloem quality necessary for brood colonization and (or) alterations in kinds and levels of host volatile compounds attractive to Douglas-fir beetle.

The Douglas-fir beetle is known to prefer large trees (Furniss et al. 1979) and stands with high host availability and density (Negron 1998). These beetles are also known to be highly attracted to fire-injured Douglas-fir (Furniss 1965; Peterson and Arbaugh 1986; Ryan and Amman 1994; Rasmussen et al. 1996; Weatherby et al. 2001; Cunningham et al. 2005). Our model results suggest that tree size, stand conditions, and host availability were slightly more important in determining the likelihood of beetle attacks than fire injuries sustained by trees. However, 95% of Douglas-fir beetle attacks in our plots were on fire-injured trees. Therefore, although tree size and stand conditions are important factors in Douglas-fir beetle attack and population success, the population appears to have been sustained because of the availability of fire-injured trees following these fires.

Using data from a wildfire (Yellowstone) and a prescribed fire (Lubrecht), predictions from the tree-mortality and beetle-attack models were relatively accurate. The tree-mortality model tended to overpredict mortality in the Yellowstone data for trees that were attacked but did not die. Because the Douglas-fir beetle attack variable in our model is binomial and a value of 1 comprises both strip and mass attacks, not all trees coded as attacked may die. Therefore, the number of observed mass- and strip-attacked trees will influence the accuracy of model mortality predictions. Mortality was overpredicted for the Lubrecht data. One reason for this may be that the data from the Lubrecht trees were generally outside the range of tree data used for model development, with the Lubrecht trees having smaller diameters and lower levels of fire injury. However, the beetle-attack model was very accurate in predicting unattacked trees for both the Yellowstone and the Lubrecht data. Similar to observations by Weatherby et al. (2001), a large proportion of the trees in our data set attacked by Douglas-fir beetles were misclassified by Ryan and Reinhardt's (1988) model, resulting in underprediction of tree mortality.

Prediction of tree death following fire is an important step in planning prescribed burns, managing stands, and developing salvage-marking guidelines following wildfire. Our results suggest that the Douglas-fir beetle can have a significant influence on postfire delayed Douglas-fir mortality, killing trees that otherwise would survive. Models that do not include this effect for Douglas-fir, such as Ryan and Reinhardt's (1988) model evaluated here, may significantly underestimate postfire delayed tree mortality when Douglas-fir beetle populations are active nearby. If surveys such as those conducted by Forest Health Protection (USDA Forest Service, http://www.fs.fed.us/r1-r4/spf/fhp/aerial/gisdata) indicate that Douglas-fir beetle populations are active in the vicinity of a recent wildfire or prescribed fire, the beetle-attack model can be used to estimate the number of fire-injured trees likely to be attacked. These values can then be directly input into the tree-mortality model to predict those trees most likely to die within 4 years after fire. The inclusion of beetle attacks in the delayed tree mortality model will provide managers with additional information for postfire planning in Douglas-fir forests of the northern Rocky Mountains. The field protocols we describe will also be useful for standardizing the field-collected fire-injury measurements that are most important for predicting postfire tree mortality and Douglas-fir beetle attack.

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