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# Predictive models of whitebark pine mortality from mountain pine beetle

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**Abstract**

Stand-level and tree-level data collected from whitebark pine (*Pinus albicaulis* Engelm.) stands in central Idaho were used to estimate the probability of attack and mortality of whitebark pine caused by mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera: Scolytidae). Logistic regression models were calibrated from reconstructed pre-epidemic stand conditions and post-epidemic mortality levels resulting from a widespread mountain pine beetle outbreak that occurred from 1909 to 1940. Basal area ($m^2$/ha) and stand density index (SDI) were stand-level variables that completely differentiated stands into attacked or non-attacked categories. Whitebark pine stands with basal areas above 10 $m^2$/ha (44 $ft^2$/acre) or with an SDI above 80 had a 100% probability of being attacked. Tree diameter, basal area per 0.04 ha, trees per 0.04 ha, and number of stems in a tree cluster were significant predictors of individual tree attack ($p \leq 0.001$) in logistic regression. The tree-level model may be used to estimate anticipated cumulative mortality in currently or potentially infested whitebark pine stands. Stand susceptibility to mountain pine beetle infestation may be identified from density (basal area) or relative density (SDI) thresholds. Predictor variables selected by the models corroborate the susceptible host characteristics identified in other mountain pine beetle–pine systems. This work presents evidence of the generality of host susceptibility characteristics across pine species and over elevation gradients.
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*Keywords:* Whitebark pine; Mountain pine beetle; Host susceptibility; Logistic regression; Generalized linear models

## 1. Introduction

Attention to whitebark pine (*Pinus albicaulis* Engelm.) population levels has been stimulated by reports that current environmental conditions have led to higher rates of mortality than establishment (Arno, 1986; Keane et al., 1990, 1994; Keane and Arno, 1993). Recognized factors causing whitebark pine decline in the northern Rocky Mountains include an exotic fungus, white pine blister rust (*Cronartium ribicola* Fisch.), infestation of whitebark pine by mountain pine beetle (*Dendroctonus ponderosae* Hopkins ) (Coleoptera: Scolytidae), and successional replacement by shade tolerant species as a result of fire suppression policies (Arno, 1986; Arno and Hoff, 1989; Keane et al., 1990; Morgan and Bunting, 1990; Keane and Arno, 1993; Kendall and Arno, 1990; Hoff and Hagle, 1990). Historically the principal natural mortality agent of whitebark pine was the mountain pine beetle (Ciesla and Furniss, 1975; Arno, 1986;

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Arno and Hoff, 1989; Bartos and Gibson, 1990; Perkins and Swetnam, 1996). As a phytophagous, cambial-feeding insect of western conifers, it is recognized as an aggressive forest insect responsible for tree mortality across large areas, and as an integral component of forest ecosystem dynamics for its role in stand thinning and redistribution of resources for regeneration (Amman, 1977; Peterman, 1978; Romme et al., 1986). While host susceptibility characteristics of economically valuable western pines have been described and used in risk and hazard rating systems (Cole and Amman, 1980; Stevens et al., 1980; McGregor et al., 1981; Schmid and Mata, 1992; Shore and Safranyik, 1992) and in models of mortality and attack for western pines (Cole et al., 1976; Schenk et al., 1980; Cole and McGregor, 1983; Anhold and Jenkins, 1987; Powell et al., 1996; Negron et al., 1999) and for southern pines (Reed et al., 1981, 1982), little quantitative information about the host susceptibility characteristics of whitebark pine has been documented.

Whitebark pine is valued for watershed protection (Farnes, 1990; Tomback et al., 2001). On the cold dry treeline sites of the northern Rocky Mountains it is generally the only long-lived species that provides shade to delay snow melt through early summer. It is a dendroclimatically sensitive tree (Perkins and Swetnam, 1996) and in the northern Rocky Mountains its tree-rings have been used for reconstructing over 1000 years of spring and summer temperature (Perkins, 2000; Biondi et al., 1999; Perkins and Grissino-Mayer, in preparation). Whitebark pine is also a keystone species (Paine, 1969; Krebs, 1994; Lanner, 1996) of critical importance to wildlife species dependent on its nutritious seeds, including Clark's nutcracker (*Nucifraga columbiana*), its seed dispersal agent (Lanner, 1980; Tomback, 1982; Hutchins and Lanner, 1982; Lanner, 1982), red squirrel (*Tamiasciurus hudsonicus*) (Reinhart and Mattson, 1990), black bear (*Ursus americanus*), and the endangered grizzly bear (*Ursus arctos horriblis*) (Kendall, 1983; Arno, 1986; Mattson and Jonkel, 1990; Kendall and Arno, 1990; Mattson et al., 1993). The decline of whitebark pine from exotic blister rust infestations, successional advance of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and infestations of mountain pine beetles, alters the hydrology and ecosystem processes of mountain environments, limits the usefulness of whitebark pine tree-ring chronologies as a proxy for long term climate variability, and has severe consequences to the wildlife species dependent on its nutritious seeds (Tomback et al., 2001).

Research on successional dynamics, white pine blister rust, restoration methods, genetics, and community and basic ecology of whitebark pine have recently been synthesized in a comprehensive volume edited by Tomback et al. (2001). Less research has focused on mountain pine beetle and whitebark pine interactions. This may be partly explained because determining the cause of mortality of whitebark pine has been confounded in regions of high blister rust incidence. Trees may be killed by either blister rust or mountain pine beetle, or they may be damaged by the combined effects of blister rust, fire, and other pathogens and subsequently killed by mountain pine beetle (Keane and Arno, 1993; Smith, 1997; Smith and Hoffman, 2000). However, up until the introduction of white pine blister rust, the most natural significant damaging agent of whitebark pine was mountain pine beetle. Host selection by mountain pine beetle and mortality levels sustained by whitebark pine populations are important for understanding natural disturbance related population dynamics. Therefore, we initiated this research to analyze the stand-level and tree-level host susceptibility characteristics of whitebark pine and to use this information to develop predictive models of probability of attack by mountain pine beetle. This is a hierarchical approach where we change the criterion from population (stand-level) to individual (tree-level) (Allen and Hoekstra, 1992). The potential predictor variables were chosen for ecological relevance to the stand or tree criterion. Another way to view the approach is as a conditional probability—given that the stand is attacked, what is the probability of individual trees in that stand being attacked?

Mountain pine beetles devastated whitebark pine forests in a widespread epidemic of the 1909–1940s from southern Canada to northern Wyoming (Arno, 1970; Ciesla and Furniss, 1975; Arno and Hoff, 1989). Throughout its northern Rocky Mountain distribution, a high percentage of whitebark pine dominants was killed (Arno, 1986). In the cold dry climate of central Idaho, the persistence of beetle-killed snags made it feasible to dendrochronologically determine the maxima of beetle-caused mortality at 1930 (Perkins and Swetnam, 1996). We found that large diameter trees were attacked more frequently than small trees and

that the duration of the outbreak in whitebark pine was 8–12 years. These characteristics are also typical of infestation in a common host, lodgepole pine (*Pinus contorta* Dougl.) (Roe and Amman, 1970; Cole and Amman, 1980).

In this work, we used the cross-dated peak mortality date (ca. 1930) as a reference point to reconstruct the stand structure before the epidemic. We recognized that reconstructions of stand structures in many forest types are biased towards the large trees. Small trees that die in the past decompose first so the likelihood of detecting their presence in reconstructions becomes problematic. However in the climax whitebark pine vegetation type there are several reasons stand reconstruction is not problematic: (1) first, whitebark pine sustains its highest mortality during the seedling stage, once established it then conforms to the life history patterns of other long-lived pines, investing heavily in roots and stems as juveniles, maturing later, and having a high probability of reaching several hundred years in age; (2) decomposition rates are slow in the cold, semi-arid region of our study area (Perkins and Swetnam, 1996) and evidence of dead trees in all but the smallest size class is readily apparent; (3) because mountain pine beetles generally select large diameter class pines (Craighead, 1925; Chamberlain, 1958; Roe and Amman, 1970; Sartwell and Stevens, 1975), a potential bias against small trees was not considered a problem.

We used a logistic regression model calibrated from reconstructed pre-epidemic stand conditions and post-epidemic mortality levels of ca. 70 years ago. Beetle-killed trees that were alive before the epidemic, and trees that survived the epidemic until our sampling in 1998 were used in the reconstruction. Trees that died in the interval between the ca. 1930 epidemic and 1998 were not used in the reconstruction because they comprised a small proportion of the dead trees inventoried.

The model's usefulness is to estimate anticipated cumulative mortality in currently or potentially infested whitebark pine stands. Predictor variables in the model also corroborate susceptible host characteristics identified in other mountain pine beetle–pine systems. Results from this research are expected to provide resource specialists with quantitative thresholds for evaluating whitebark pine stand susceptibility to mountain pine beetle infestations.

## 2. Methods

### 2.1. Study area

A central Idaho study area was chosen because field surveys from 1995 to 1997 showed that white pine blister rust was only present in low amounts (Smith, 1997; Smith and Hoffman, 2000; Perkins, personal observation). Accordingly, blister rust effects as a confounding factor in determining cause of tree mortality in this region are currently negligible. Fourteen treeline whitebark pine stands located within the Sawtooth National Recreation Area, the Sawtooth National Forest, and the Challis National Forest were sampled during the field season of 1998. Stands were located in six mountain ranges within the study area. Four sites were located near summits in the White Clouds Mountains (WC), three in the Headwater Mountains (HW), two in the Smoky Mountains (SM), three in the Salmon River Mountains (SR), one in the Boulder Mountains (BM), and one in the Sawtooth Mountains (SW) (Fig. 1). The Headwater Mountains are not identified in Fig. 1; they were considered either part of the Sawtooth or Smoky Mountains and form the divide between the Salmon and Big Wood rivers. Elevations ranged from 2700 to 3000 m (8800–9800 ft). Granitic bedrock of the Sawtooth and Idaho Batholiths forms the core of the study area, with Tertiary volcanic and sedimentary forms on southerly and easterly ranges (Williams, 1961). Stand names and physical site attributes are summarized in Table 1.

Long-term climatic information for treeline sites in central Idaho is lacking. The nearest and highest elevation meteorologic station is Stanley at 1920 m (6300 ft)—1000 m below the study sites. We report winter and summer temperature and precipitation averages from the Stanley station for general climatic description. However, adiabatic lapse rates, temperature inversions, and increased precipitation at high elevations cause departures from the valley floor data. The average minimum temperatures for December and January for the 1963–2000 period are approximately −18 °C (−1.0 °F) and average maximum temperatures for those months are approximately −3 °C (26 °F). Average maximum of 25 °C (78 °F) and average minimum of 1 °C (35 °F) are reported for July and August (Western Regional Climate Center,

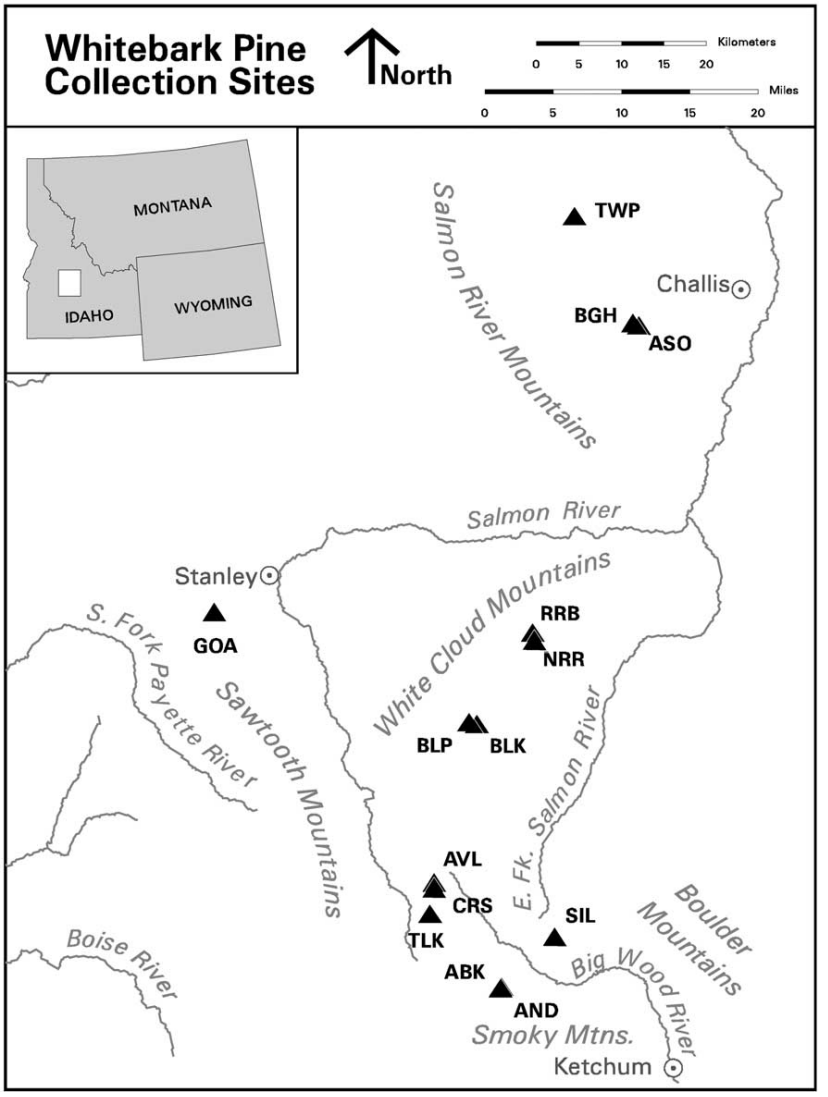


Fig. 1. Central Idaho study area and sampled whitebark pine sites.

Reno Nevada). Summers are cool with frequent early morning frosts and winters are cold. Extreme cold temperatures of −34 to −47 °C (−30 to −50 °F) are recorded from December to February (Steele et al., 1981). The study area is in a transition zone between maritime and continental climates with the maritime influence greater from fall through spring and drier continental influence greater during the summer months. At elevations above 2700 m most precipitation falls as snow and the greatest amounts occur between November and March. Winds redistribute snow around whitebark pine trees to form snowdrifts that may linger until July and occasionally August.

Across the study area, tree associates are lodgepole pine, subalpine fir (*A. lasiocarpa* (Hook.) Nutt.), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), and Engelmann spruce (*Picea engelmannii* Parry). The potential natural vegetation is classified in the

Table 1
Physical site attributes of sampled whitebark pine stands[a]

| Mountain range | Site | Elevation (m) | Aspect (°) | Slope (°) | Stand status | Longitude (UTM) | Latitude (UTM) | Number of plots |
|---|---|---|---|---|---|---|---|---|
| WC | NRR | 2800 | 23 | 10 | Non-attacked | 0695400 | 4891300 | 10 |
| WC | BLP | 2900 | 180 | 30 | Non-attacked | 0687900 | 4880700 | 10 |
| SR | ASO | 2900 | 75 | 30 | Non-attacked | 0707900 | 4927500 | 7 |
| HW | CRS | 2700 | 290 | 20 | Non-attacked | 0683800 | 4861100 | 10 |
| SM | AND | 2900 | 300 | 15 | Non-attacked | 0691700 | 4849500 | 7 |
| WC | BLK | 3000 | 200 | 30 | Attacked | 0688800 | 4880500 | 8 |
| SM | ABK | 2900 | 320 | 20 | Attacked | 0691600 | 4849300 | 7 |
| BL | SIL | 2800 | 260 | 30 | Attacked | 0698000 | 4855400 | 7 |
| HW | AVL | 2700 | 180 | 17 | Attacked | 0683800 | 4861800 | 10 |
| HW | TLK | 2900 | 290 | 20 | Attacked | 0683300 | 4858100 | 8 |
| SW | GOA | 2700 | 125 | 30 | Attacked | 0657900 | 4893700 | 8 |
| SR | TWP | 2900 | 180 | 20 | Attacked | 0700300 | 4940400 | 8 |
| SR | BGH | 2900 | 240 | 20 | Attacked | 0707200 | 4927800 | 8 |
| WC | RRB | 2900 | 135 | 25 | Attacked | 0695600 | 4890300 | 3 |

[a] Sites are: NRR: North Railroad Ridge, BLP: Blackman Peak, ASO: Assout Basin, CRS: The Cross, AND: Anderson Peak, BLK: Blackman Peak Beetle Kill, ABK: Anderson Peak Beetle Kill, SIL: Silver Peak, AVL: Avalanche Peak, TLK: Titus Lake Peak, GOA: Goat, TWP: Twin Peaks, BGH: Big Hill, RRB: Railroad Ridge Beetle Kill.

PIAL/ABLA or PIAL series, indicating that *P. albicaulis* is the climax dominant or co-dominant on these sites (Steele et al., 1981, 1983).

Sample stand selection criteria were: (1) whitebark pine was the dominant species with composition greater than or equal to 70% of total basal area; (2) stand elevations were between 2680 m (8800 ft) and an upper edaphic treeline bordering an unvegetated rock ridgetop; (3) stand extent was greater than 3 ha with homogeneous structure, constant aspect and slope; (4) tree form was upright (krummholz form trees were not sampled).

Aerial photographs were used to identify potential stands. Paired mountain pine beetle attacked and non-attacked stands within the same watershed were chosen whenever possible. By constraining the sampled stands to locations near to known attacks, we eliminated the uncertainty due to presence or absence of beetles. Thus stands had an equal probability of attack except for those aspects of stand structure and site variables that beetles might perceive. Attacked and non-attacked stands were differentiated by the presence of snags with J-shaped adult beetle galleries. Adult beetle galleries, had been used previously to determine beetle attack of trees killed in the 1909–1940 period (Perkins and Swetnam, 1996). Stands composed of ≥15% beetle-killed snags were considered attacked stands; stands composed primarily of living whitebark pines with few beetle-killed trees were considered non-attacked stands. Selected stands often extended below 2680 m (8800 ft) but were not sampled below this elevation because in this geographic region their character was distinctly seral, complicated by the successional advance of subalpine fir. Implicit in the near-treeline criterion is the idea that these stands represent the climax whitebark pine community and are self-replacing despite disturbance (Whittaker, 1975; Steele et al., 1981, 1983; Perkins, 2000).

### 2.2. Field sampling

Seven to ten circular 0.04 ha (1/10 acre) plots were established systematically on a grid on each of the attacked and non-attacked stands, except for one site, RRB, which only had three plots. We maintained a distance of 100 m between plots except for stands with spatial irregularities and constrictions where we had to drop the distance to 80–60 m. Spacing distance was determined before we entered and sampled stands to avoid sampling bias. For each plot, elevation, aspect, slope, and location coordinates were recorded. On each plot, diameter at breast height (DBH, 1.4 m (4.5 ft above ground surface)) and species of trees

≥10.2 cm (4.0 in.) were recorded. Additionally, the first trees north and south on a clockwise arc from plot center were cored with an increment borer for age determination. To maximize the precision of age estimates, trees were cored close to ground level, generally 30–35 cm (12–14 in.) from the ground surface. Individual trees were recorded as attacked and killed by mountain pine beetles (ca. 1930) versus not attacked; stands were recorded as attacked (≥15% mortality) versus not attacked. Trees that died from unknown causes, were older than ca. 1930 beetle-killed trees or were recently killed by beetles (within last 10 years) were recorded.

### 2.3. Analyses

To reconstruct the stand structure prior to the mountain pine beetle epidemic, the diameter of trees ca. 1930 (DBH30) was estimated from live cored trees as

$$\mathrm{DBH30} = \mathrm{DBH98} - 2\mathrm{RI}$$

where DBH98 was the diameter at breast height recorded in 1998 and RI was the radial increment measured to the nearest 0.25 cm (0.10 in.) along the increment core from the 1930 through the 1998 annual ring. To maximize precision of radial increment estimates and because tree-ring widths are small, all increment cores were measured under a microscope. Trees with reconstructed DBH30 less than 10 cm (4.0 in.) were not used in further analyses and reduced the sample size to 134 trees. From this subset we developed a regression model to calculate the DBH30 of all live trees sampled but not cored:

$$\mathrm{DBH30} = \left(a + b\sqrt{\mathrm{DBH98}}\right)^2$$

Because the width of a tree-ring in 1998 may be considered a function of linear increase in area of the ring added in 1998, modeling the DBH ca. 1930 was accomplished by fitting the model in the square root scale. The regression equation, standard diagnostics and plots of residuals versus predicted values were calculated using the software *Mathematica* version 3.0 (Wolfram, 1996). Diameters of beetle-killed trees that died in the epidemic and were recorded in 1998 were used for the ca. 1930 (preattack) diameter estimates. The reconstructed diameters were then used to compute basal area of the tree ca. 1930 (*batr30*), basal area per 0.04 ha ca. 1930 (*baplt30*), and trees per 0.04 ha ca. 1930 (*tplt30*). Additionally we recorded the number of stems in a tree cluster (clump) as a potential predictor variable. Multiple stem growth forms called tree clusters (Tomback et al., 1990) occur because multiple seeds are cached by Clark's nutcrackers (Lanner, 1980, 1982; Hutchins and Lanner, 1982; Tomback, 1982). They may be composed of single-trunk individuals, single genet multi-trunk forms, or multiple-genet tree clusters (Linhart and Tomback, 1985; Furnier et al., 1987). Our metrics on a 0.04 ha plot therefore characterize the local, tree-level environment of a tree (or tree cluster), and the number of stems ca. 1930 (*nstms*) characterizes the structure of a tree cluster. Stand-level attributes including stand density index, SDI, (*sdi*) (Reineke, 1933; Long and Daniel, 1990), quadratic mean diameter (*dq*), basal area (*ba*), and mean basal area (*mba*) were calculated ca. 1930 and 1998 for all 14 stands.

Stand-level and tree-level metrics and physical site attributes (elevation, aspect and slope) were used for two fundamental analyses: (1) stand-level metrics were used for a stand-level logistic regression model to explain the relative probability of attack as a function of stand-level variables; (2) tree-level metrics of attacked stands constituted the set of independent variables used in a 10-fold cross-validated logistic regression model for explaining the relative probability of individual tree attack given that the stand was attacked.

The utility of logistic regression to describe a discrete event as a function of independent site and stand variables is well established for forest tree mortality (Hamilton, 1974, 1986; Hamilton and Edwards, 1976; Reed et al., 1982; Berryman, 1986). In logistic regression the dependent or response variable, tree survivorship status is dichotomous taking the value of zero or one. The response distribution for logistic regression is the binomial distribution established through a logit link function that relates the log of the odds of attack with the linear predictor of independent variables (Hastie and Pregibon, 1992). The model can be expressed as

$$\ln\left(\frac{p}{1-p}\right) = b_0 + b_1x_1 + b_2x_2 + \cdots + b_nx_n$$

where $p$ is the probability of attack, $x_1, x_2, \ldots, x_n$ are the predictor variables and $b_0, b_1, \ldots, b_n$ are coefficients

determined in the logistic regression. The model is then back transformed to generate probabilities of attack as

$$p = \frac{1}{1 + e^{-(b_0 + b_1x_1 + b_2x_2 + \cdots + b_nx_n)}}$$

Logistic regression employing 10-fold cross-validation was accomplished with S-PLUS (S-PLUS 5, 1998). Analysis of deviance methods (Hastie and Pregibon, 1992) were used to search for a parsimonious model and to identify the significance of parameters. All permutations of the independent variables were analyzed and those that maximized the reduction of residual deviance (Hastie and Pregibon, 1992) were chosen for the logistic model. To approximate the general linear model goodness of fit statistic (the coefficient of determination, $R^2$) for the logistic regression model, a quasi $R^2$ was calculated as $1 - (\text{residual deviance}/\text{null deviance})$ (Yee and Mitchell, 1991).

To avoid the bias inherent in using the same data to develop and test the model, and to account for within-site dependencies, the analyses were 10-fold cross-validated as follows. Trees in each of the attacked stands were partitioned randomly into 10 segments. One segment was withheld and the remaining nine were used to calibrate the model. The 10th segment was then used to test the prediction against the known status to validate the model. This was repeated 10 times for each site leaving out each segment in turn. The predictions of the 10 independently verified models were compared to the actual survivorship status for each tree in a contingency (cross-tabulation) table. Percent correctly predicted, percent error of omission, and percent error of commission were calculated as well as bias of the models. Bias describes the model's errors in a directional sense with respect to actual and predicted attacks. A negative value indicates a tendency to underpredict and a positive value indicates a tendency to overpredict attacks. For a cross-tabulation of the form

| Predicted | | |
|---|---|---|
| Actual | False | True |
| False | *a* | *b* |
| True | *c* | *d* |

bias is calculated as

$$\frac{(c + d) - (b + d)}{b + d}$$

Differences in the significance of the independent variables across stands were explained by a qualitative interpretation of size-frequency distributions ca. 1930. Finally, trees in all stands were pooled and the 10-fold cross-validation assessment of the logistic model was repeated to see if the pooled model was different than the stand-specific models.

## 3. Results

The least squares regression for reconstructed diameter ca. 1930 was significant ($p < 0.001$) with 53% of the variability in DBH30 explained by DBH98 (Table 2). We considered this regression model adequate to reconstruct diameters of trees that survived the ca. 1930 epidemic. The moderate amount (53%) of variance explained may be partially based on the lack of circuit uniformity found in tree-ring patterns on individual stems within tree clusters in previous work (Perkins, 1995; Perkins and Swetnam, 1996). Intraspecific competition causes these stems to grow away from each other and from the tree centerline, resulting in stems that lack circuit uniformity in annual ring widths. Although trees were cored parallel to the contour of the slope to avoid tension and reaction wood, the irregularities of ring widths from individual stems in tree clusters is generally unavoidable, and therefore influences the distance measurements and reconstructed diameters. The model errors were randomly distributed when graphed but we present only the model fit in Fig. 2.

### 3.1. Stand-level conditions

Nine stands met the criteria for attacked stands and five stands met the criteria for non-attacked stands

Table 2
Regression statistics for reconstructed DBH ca. 1930, $n = 134$, $R^2 = 0.53$, M.S.E. = 1.06

| | Estimator | S.E. | *T*-stat | $p > T$ |
|---|---|---|---|---|
| Slope | 1.08337 | 0.08337 | 12.3005 | 0.0001 |
| Intercept | −2.2921 | 0.29047 | −4.95125 | 0.0001 |

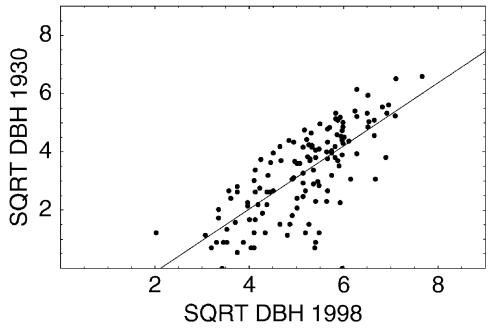


Fig. 2. Whitebark pine least square regression of diameter classes ca. 1930 against diameters in 1998.

(Table 1). Attacked and non-attacked paired stands were located adjacent to each other for stands ABK and AND, BLK and BLP, and AVL and CRS. Stands ASO and BGH and RRB and NRR were also paired but were separated by a ridge and not adjacent (Fig. 1).

For the 14 stands sampled, we found clear differences in structure between non-attacked versus attacked stands Table 3. Basal area (*ba30*), trees per hectare (*tph30*), mean basal area (*mba30*), quadratic mean diameter (*dq30*) and stand density index (*sdi30*) before the outbreak were lower on unattacked as compared to attacked stands (Table 3). Non-attacked stands were composed of smaller, younger trees at lower densities than attacked stands. On attacked stands, approximately 60–400 trees/ha were killed by mountain pine beetles. Site RRB was small (only three plots) and the mortality estimate of 734 trees/ha is possibly too high. No beetle-killed trees were recorded in sample plots on non-attacked stands. Whitebark pine identified as dead by unknown cause; recent beetle-kill (within 10 years); or older than ca 1930s epidemic; represented 0.12% of all whitebark pine sampled and 5.6% of dead whitebark pine sampled.

Table 3
Stand summary metrics ca. 1930[a]

| Site | ba30[b] | tph30[c] | mba30[d] | dq30[e] | sdi30[f] | babk[g] | tphbk[h] |
|---|---|---|---|---|---|---|---|
| NRR | 3.4 | 178 | 0.02 | 15 | 33 | 0 | 0 |
| BLP | 3.9 | 195 | 0.02 | 16 | 38 | 0 | 0 |
| ASO | 4.6 | 27 | 0.17 | 46 | 30 | 0 | 0 |
| CRS | 5.1 | 210 | 0.02 | 18 | 47 | 0 | 0 |
| AND | 6.7 | 289 | 0.02 | 17 | 63 | 0 | 0 |
| ABK | 13.1 | 403 | 0.03 | 20 | 114 | 12.2 | 338 |
| SIL | 14.0 | 272 | 0.05 | 26 | 111 | 11.5 | 188 |
| AVL | 16.3 | 356 | 0.05 | 24 | 132 | 10.6 | 143 |
| TLK | 16.5 | 195 | 0.21 | 33 | 119 | 14.7 | 101 |
| GOA | 18.4 | 124 | 0.15 | 44 | 119 | 16.8 | 59 |
| TWP | 21.6 | 257 | 0.08 | 33 | 156 | 20.4 | 183 |
| BLK | 26.4 | 316 | 0.08 | 33 | 190 | 25.3 | 249 |
| BGH | 32.1 | 479 | 0.07 | 29 | 242 | 30.3 | 380 |
| RRB | 50.3 | 889 | 0.05 | 27 | 393 | 46.8 | 734 |

[a] The first five rows are stands that were not attacked by mountain pine beetle and the last nine rows were attacked stands.
[b] Basal area ($m^2$/ha).
[c] Trees per hectare.
[d] Mean basal area.
[e] Quadratic mean diameter (cm).
[f] Stand density index.
[g] Basal area of trees killed by mountain pine beetles.
[h] Trees killed by mountain pine beetles per hectare.

The implication of having paired stands is that they generally experienced the same beetle pressure and that structural rather than environmental site variables would differentiate susceptibility. This was shown with basal area (*ba30*) and stand density index (*sdi30*) as the only significant predictors in logistic regression models. None of the site variables contributed to predicting attack. However because the outcome of a stand being attacked or not attacked was split perfectly by basal area or SDI, the odds ratio was undefined and we do not present a logistic regression model. Whitebark pine stands with basal areas above 10 $m^2$/ha (44 $ft^2$/acre) and SDI above 80 (Fig. 3) had a 100% probability of being attacked in either model. The probability of correctly predicting 14 out of 14 stands, with 9 out of 14 attacked is 0.002 calculated using the probability mass function of a binomial random variable (Ross, 1976).

### 3.2. Tree-level model

Analyses of the pooled tree-level data set identified four significant ($p < 0.001$) independent variables: diameter ca. 1930 (*dbh30*), basal area per 0.04 ha ca. 1930 (*baplt30*), trees per 0.04 ha ca. 1930 (*tplt30*), and number of stems in a tree cluster (nstms). As in the stand-level model, none of the recorded environmental site variables (aspect, elevation, and slope) was significant. Analyses of deviance of the model predictors with the $\chi^2$ test statistic (Venables and Ripley, 1999) demonstrated statistical significance ($p < 0.001$) for all four variables in the 10-fold cross-validation models. Results from cross-validation models were cross-

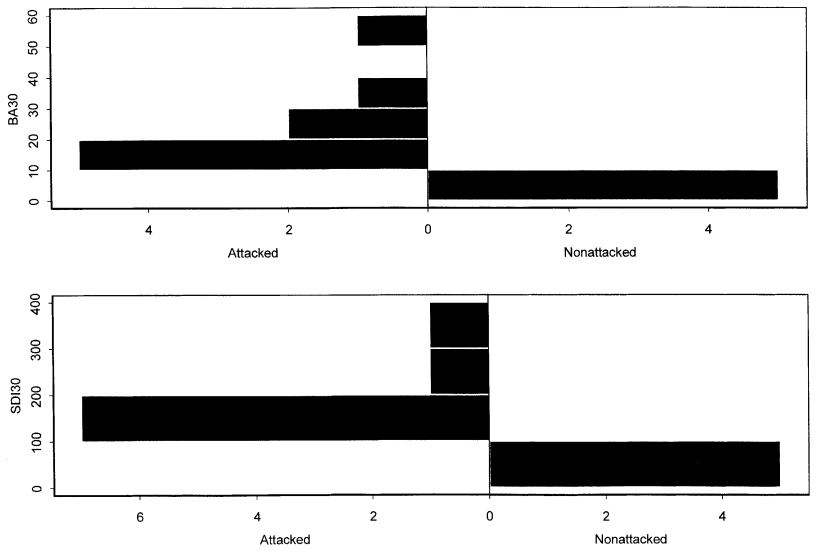


Fig. 3. Number of whitebark pine stands that were and were not attacked by mountain pine beetle for reconstructed basal area ca. 1930 (BA30) and SDI ca. 1930 (SDI30).

tabulated with observed tree attacks on each stand in contingency tables (Perkins, 2000). The mean of the percent of trees correctly predicted was 90%. Number correctly predicted, errors of omission and commission, and bias are given in Table 4. Models from two stands tended to slightly underpredict tree mortality but generally all bias metrics were close to zero.

Analyses of the coefficients of the independent variables revealed that *dbh30* was the most consistently significant ($p < 0.001$) on all nine sites, followed by nstms on seven sites, *baplt30* on five sites, and *tplt30* on two sites (Table 5). The difference in the significance of the predictors may be explained in part by size-frequency distributions (Fig. 4) and stand summary metrics (Table 3). For instance, on the goat site (GOA) the quadratic mean diameter was large at 43.7 cm (17.2 in.) with a low density of 124 trees per hectare (50 trees/acre). With few large diameter trees, nearly all of which were selected by beetles, the contribution of *baplt30* and *tplt30* as predictors was negligible (Fig. 4). On Anderson Peak (ABK), beetles selected small diameter trees (there were no large

Table 4
Number of trees correctly predicted (attacked or not attacked) in 10-fold cross-validation models, errors of omission and commission, and bias[a]

| Site | Correct | Errors of omission | Errors of commission | Bias |
|---|---|---|---|---|
| ABK | 114 (91) | 4 (3) | 7 (6) | 0.028 |
| AVL | 130 (90) | 7 (5) | 7 (5) | 0.000 |
| BGH | 148 (93) | 5 (3) | 7 (4) | 0.008 |
| BLK | 86 (83) | 6 (6) | 11 (11) | 0.061 |
| GOA | 39 (95) | 1 (2.5) | 1 (2.5) | 0.000 |
| RRB | 99 (87) | 4 (3) | 11 (10) | 0.071 |
| SIL | 61 (80) | 7 (9) | 8 (11) | 0.018 |
| TLK | 64 (98) | 1 (2) | 0 (0) | −0.030 |
| TWP | 77 (95) | 3 (4) | 1 (1) | −0.036 |

[a] The values inside the parentheses are in percentage.

Table 5
Significance table of the four independent variables used in the tree-level logistic regression model by site[a]

| Site | dbh30 | nstms | baplt30 | tplt30 |
|---|---|---|---|---|
| ABK | ** | ** | * | |
| AVL | ** | ** | ** | * |
| BGH | ** | ** | ** | ** |
| BLK | ** | * | ** | * |
| GOA | ** | * | * | * |
| RRB | ** | ** | * | |
| SIL | ** | ** | * | |
| TLK | ** | ** | ** | ** |
| TWP | ** | ** | ** | * |

[a] Blank spaces are non-significant variables.
[*] Moderately significant ($0.001 < p < 0.1$).
[**] Highly significant ($p < 0.001$).

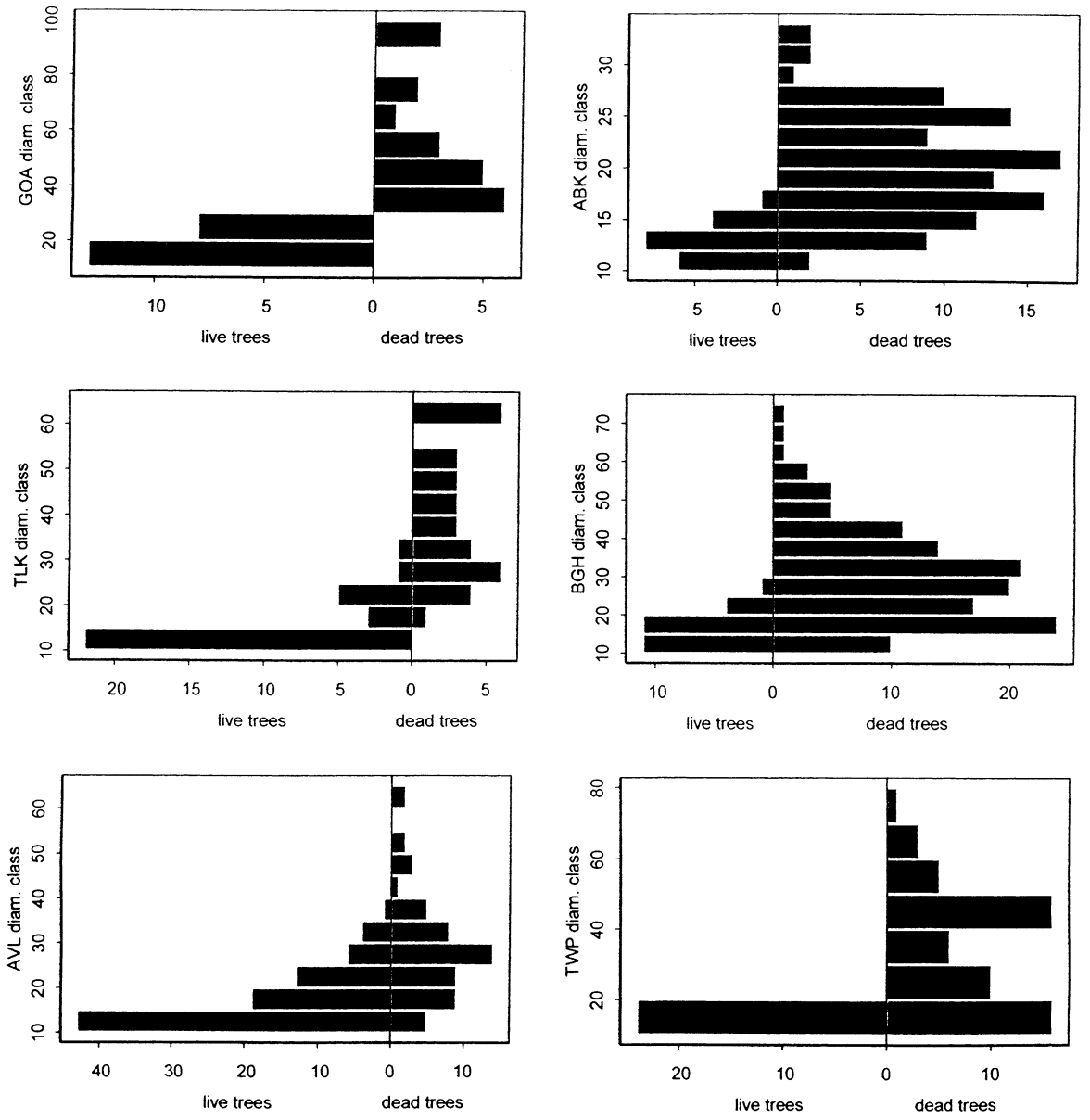


Fig. 4. Size-frequency histograms of attacked and non-attacked whitebark pines ca. 1930. Bars on left are live trees, and bars on right are trees killed by mountain pine beetles.

ones) and *nstms* was significant ($p < 0.001$) with intermediate significance ($0.001 < p < 0.1$) for balt30. On two stands, Titus Lake Peak (TLK) and Big Hill (BGH), all four predictors were significant ($p < 0.001$); both stands were dominated by an abundance of large diameter trees at high to moderate densities (Fig. 4). Local basal area was significant on AVL, BGH, BLK, TLK, and TWP stands that lost small as well as large diameter trees (Fig. 4). The cross tabulation for the pooled data set of all trees across all

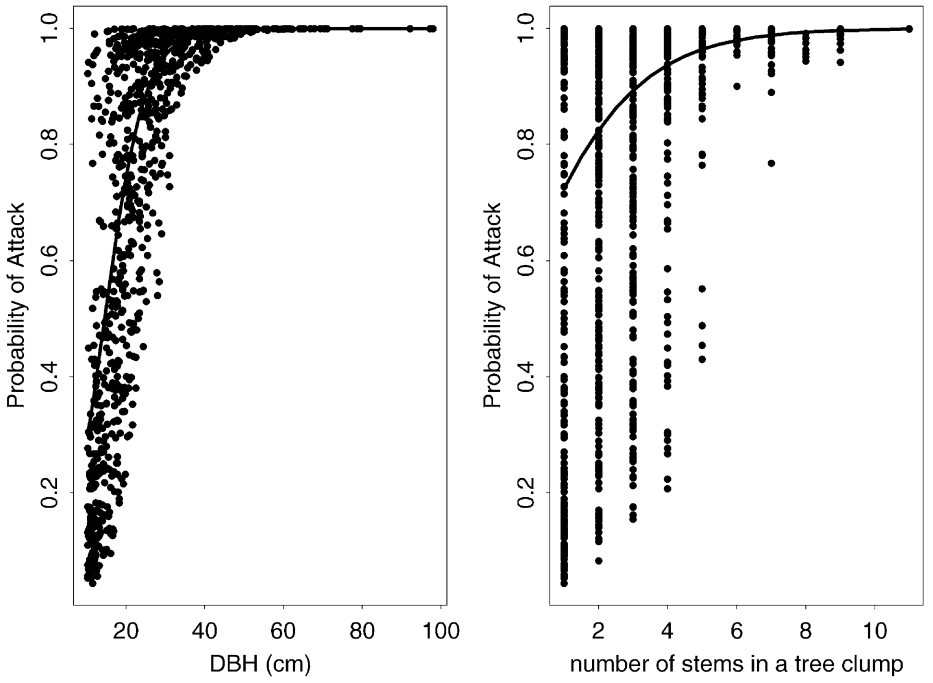


Fig. 5. Tree-level fitted logistic regression model plotted showing contribution of dbh30 and nstms to the probability of tree attack while holding other independent variables constant at their mean. The equation for the probability of tree attack ($p$) from the pooled data set is $p = 1/(1 + \exp(-6.0167 + 0.1954\,\text{dbh30} + 0.0944\,\text{baplt30} + 0.0668\,\text{tplt30} + 0.5792\,\text{nstms}))$.

Table 6
Pooled data cross-tabulations of logistic model prediction versus actual tree survivorship status[a]

| Predicted | | | |
|---|---|---|---|
| Actual | False | True | Row total |
| False | 194 | 75 | 269 |
| True | 68 | 573 | 641 |
| Column total | 262 | 648 | 910 |

[a] $\chi^2 = 349.70$, d.f. $= 1$, $p \leq 0.0001$. Correctly predicted $= 84\%$, errors of omission $= 8\%$, errors of commission $= 8\%$, bias $= 0.011$.

sites dropped to 84% correct in predicting tree fate (Table 6). The logistic equation for the pooled data set was

$$\ln\left(\frac{p}{1-p}\right) = -6.0167 + 0.1954\,\text{dbh30} + 0.0944\,\text{baplt30} + 0.0668\,\text{tplt30} + 0.5792\,\text{nstms}$$

The quasi $R^2$ was 0.44. The contributions of diameter ca. 1930 (*dbh30*) and number of stems (*nstms*) to the probability that a tree is attacked and killed are shown in Fig. 5. The bias was 0.011, indicating a potential to slightly overpredict tree mortality.

## 4. Discussion

It has been well established that tree size, age, and stand density are factors correlated with tree mortality (Yoda et al., 1963; Lee, 1971; Hamilton and Edwards, 1976; Hamilton, 1986). For the whitebark pine–mountain pine beetle system, that diameter and basal area were positive significant predictors in the logistic models is not surprising and is consistent with mountain pine beetle–host susceptibility characteristics identified by others (Amman et al., 1977; Cole and Amman, 1980; Stevens et al., 1980; Berryman, 1982; Shore and Safranyik, 1992; Schmid and Mata, 1992;

Olsen et al., 1996). Susceptibility refers to stand or tree characteristics independent of beetle population levels (Shore and Safranyik, 1992; Bentz et al., 1993). Tree and stand-level characteristics associated with attack are qualitatively similar to other mountain pine beetle–pine host systems, although the attack thresholds are quantitatively different. For instance, whitebark pine stands with basal areas below 10 $m^2$/ha (44 $ft^2$/acre) and trees with average diameters below 18 cm (7 in.) were not attacked in the early 20th century epidemic in central Idaho. These are the same variables identified for susceptible lodgepole pine stands where basal areas below 18 $m^2$/ha (80 $ft^2$/acre) and average diameters less than 20 cm (8 in.) are seldom attacked (Cole and Amman, 1969; Amman et al., 1977) and in ponderosa pine (*Pinus ponderosa* (Doug.) stands where high probabilities of attack are associated with 27–34 $m^2$/ha (120–150 $ft^2$/acre) basal area (Sartwell and Stevens, 1975; Schmid and Mata, 1992) and average mean diameters of greater than 20 cm (8 in.) (Stevens et al., 1980; Sartwell and Stevens, 1975). Our work presents evidence of the generality of host susceptibility characteristics across pine species and over elevation gradients.

Quantifying 'risk' as opposed to 'susceptibility' of stands and trees to mountain pine beetle infestation requires evaluation of population levels of beetles (Shore and Safranyik, 1992; Bentz et al., 1993). An epidemic by definition, requires high levels of mountain pine beetles. The epidemic of the 1909–1940 period in central Idaho was documented in lodgepole pine, limber pine (*Pinus exilis* James) and whitebark pine forests (Renner, 1929) and mortality levels of whitebark pine were high (Perkins and Swetnam, 1996). Beetles were reported to have dispersed from lower elevation lodgepole forest into high elevation whitebark pine stands (Arno, 1970; Ciesla and Furniss, 1975; Arno, 1986; Arno and Hoff, 1989; Schmitt and Scott, 1998). Although conclusive empirical evidence has not been presented to support dispersal of beetles from one host type to another, these stands were not only susceptible as described by tree and stand structural characteristics, but were also at high risk of infestation because of high levels of mountain pine beetles in nearby lodgepole pine stands.

Whitebark pine trees with multiple stems in tree clusters are more likely to be attacked than single stems. This indicates that distance between stems is a factor in the probability of mountain pine beetle attack. Donnegan and Rebertus (1999) also found that mortality of mid-successional stage limber pine was correlated with its clumped or clustered pattern. The nstms variable indirectly incorporates a spatial component identified by Bentz et al. (1993) to improve risk rating systems and by Powell et al. (1996) to incorporate dispersal effects. This is a simple metric useful for bird dispersed pines whose growth forms are the result of the seed caching behavior of birds. Mitchell and Preisler (1991) used a logistic regression spatial analysis of lodgepole pine attack by mountain pine beetles and found that among small diameter classes spatial relationships among trees and tree size were the most important covariates. That small diameter whitebark pine trees were attacked may be related more to their proximity to larger stems in tree clusters than to their size alone.

High elevations are generally associated with decreasing beetle-caused mortality levels because of unfavorable heat balance for beetle development (Amman, 1973; Logan and Bentz, 1999). However, elevation is not correlated with beetle attack of trees or stands during the epidemic conditions of the ca. 1930 outbreak. This may be explained in part by the narrow elevation band ≈300 m (1000 ft) of the study area and the fact that differences in elevation among sites were imperceptible. Additionally, aspect and slope, site variables frequently used as surrogates for radiation loads, were not significantly correlated $(p > 0.01)$ with beetle attack. However, climatic conditions during the ca. 1930 epidemic were characterized by above average departures in summer temperatures (Finklin, 1988; Perkins and Swetnam, 1996; Biondi et al., 1999). This likely contributed to the outbreak's extent and magnitude by improving conditions for the mountain pine beetle by resulting in an adaptive seasonality (Logan and Bentz, 1999; Logan and Powell, 2001). Beetle development is under direct temperature control (Logan and Bentz, 1999) and warm temperatures would likely have favored successful brood development, beetle survivorship, and successful attacks (Reid and Gates, 1970; Amman, 1972, 1973; Bentz et al., 1991; Logan and Bentz, 1999).

Another noteworthy observation is that infestation occurred at the start of the longest sustained low growth period for the last 200 years as revealed in whitebark tree-ring width chronologies (Perkins,

1995; Perkins and Swetnam, 1996). This growth suppression likely reflects poor growing conditions for trees, and may support the plant-drought stress hypothesis (Mattson and Haack, 1987), which suggests that water-stressed individuals are more susceptible to damaging agents than non-water-stressed individuals. The combined interactions of suceptible stand and tree characteristics, regionally high beetle populations, above average temperatures, and reduced vigor of trees provided optimum conditions for mountain pine beetles to attack and kill a high proportion of whitebark pines ca. 1930. With projected global warming, growth of trees and increasing stand densities in the 70 years since the beetle epidemic, conditions in Idaho are again becoming favorable for whitebark pine's susceptibility to beetle infestations.

Our study provides an unusual, retrospective approach to predictive modeling of tree mortality. The logistic regression model presented here explains the probability of whitebark pine tree attack by mountain pine beetle based on tree characteristics calibrated in the pre-epidemic phase of a historic outbreak. Not surprisingly, diameter and density were positively associated with tree attack even on relatively open-canopy, single species conditions of upper treeline. Stands that were attacked were also composed of densely spaced large diameter trees. Because the reconstructed DBH at 1930 was the foundation for calculating pre-epidemic stand structure and the assessment of mortality was post-epidemic, the model is suited for estimates of cumulative mortality anticipated in sustained (outbreak phase) epidemics. The tree-level predictive model, and the density thresholds presented here to differentiate stand suceptibility to mountain pine beetle attack are limited to whitebark pine in the geographic area of central Idaho, and require verification with independent data outside the region.

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