Stand Conditions Associated with Roundheaded Pine Beetle (Coleoptera: Scolytidae) Infestations in Arizona and Utah

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ABSTRACT Stand conditions associated with outbreak populations of the roundheaded pine beetle, *Dendroctonus adjunctus* Blandford, in ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., forests were studied in the Pinaleno Mountains, AZ, and the Pine Valley Mountains, UT. Classification tree models to estimate the probability of infestation based on stand attributes were built for both study areas using growth rate and ponderosa pine basal area information. Cross-validation estimates of correct classification were 0.60 for the Pinaleno Mountains and 0.58 and 0.78 for the Pine Valley Mountains. Regression tree and linear regression models to estimate amount of mortality caused by the beetles were also built for both sites using growth rate, ponderosa pine basal area, and trees per hectare information. The occurrence and mortality levels caused by the roundheaded pine beetle are positively related at both the stand and tree scale with reduced growth rates caused by high stocking densities.

KEY WORDS *Dendroctonus adjunctus*, roundheaded pine beetle, risk, hazard, bark beetles, disturbance

THE ROUNDHEADED PINE beetle, *Dendroctonus adjunctus* Blandford, is an important bark beetle associated with ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., in the southwestern United States. Periodic outbreaks of this disturbance agent have caused considerable mortality across the Southwest (Lucht et al. 1974, Massey et al. 1977). Stevens and Flake (1974) indicated that basal area and numbers of ponderosa pines were reduced up to 50% in some stands during an outbreak in the early 1970s. That study also indicated that southwestern dwarf mistletoe, *Arceuthobium vaginatum* subsp. *cryptopodum* (Engelmann) Hawksworth & Wiens, infestations were common in bark beetle infested stands. Negrón (1997) developed models to predict probabilities of infestation and extent of mortality in terms of basal area killed for different habitat type series in the Sacramento Mountains, NM. That study indicated that poor growth before the onset of an outbreak was an important factor in determining the probability of attack. Average diameter at breast height (dbh) was smaller in infested areas than in uninfested areas. Ponderosa pine basal area at the onset of the outbreak was found to be a good predictor of amount of basal area killed during the outbreak.

The roundheaded pine beetle has been active in the Pinaleno Mountains, AZ, and the Pine Valley Mountains, UT, for a number of years. The outbreaks in both of these areas have been in forest stands with very different stand conditions when compared with the Sacramento Mountains. Stocking levels are higher and diameter classes larger in the Pine Valley and the Pinaleno Mountains.

In this study we examined stand conditions associated with roundheaded pine beetle infestations in the Pinaleno and Pine Valley Mountains and developed probability of infestation and extent of mortality models.

Materials and Methods

Study Sites and Sampling. *Pinaleno Mountains.* Sampling was conducted at the Safford Ranger District of the Coronado National Forest. Roundheaded pine beetle populations began increasing in 1988 and were at outbreak levels by 1991 (Wilson 1993). Seven stands, ranging in size from 42 to 79 ha, were selected for sampling. Sampled stands included trees killed at the initiation of the outbreak (initial mortality). This initial mortality is of particular interest because it represents stand conditions susceptible to roundheaded pine beetle infestations in the early stages of the outbreak. Sampling was conducted during the summers of 1995 and 1996. In each selected stand a network of 10–14 variable radius plots that included infested and uninfested plots was established. First, infested plots were established at random in areas of the stand that contained initial mortality; subsequent infested and uninfested plots were established at random by taking a random azimuth and distance from a previously established plot. Infested plots had to include at least 1 ponderosa pine ≥12.7 cm dbh that had been killed by roundheaded pine beetle. Uninfested plots had to include at least 1 ponderosa pine ≥12.7 cm in dbh and no trees killed or infested by roundheaded

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pine beetle. No plots were established within 40 m of another plot. In total, 46 infested and 39 uninfested plots were established.

Pine Valley Mountains. The study area was located at the Browse area of the Pine Valley Ranger District of the Dixie National Forest, UT. Roundheaded pine beetle populations in the area began increasing in 1992 and were at epidemic levels by 1995. Sampling was conducted in an aggregate of stands that included initial mortality. Sampling was conducted during the summer of 1996. Plot establishment protocols were the same as described above for the Pinaleno Mountains study area. A total of 36 plots was established; 18 infested and 18 uninfested plots.

Stand and Tree Data. For all plot trees, tree species was recorded and measurements were taken for dbh, total height, phloem thickness of live conifers, and radial growth measurements for the last two 5-yr growth periods from cores extracted from the south side of all conifers at breast height. Trees were classified as live, killed, or infested by roundheaded pine beetle, or dead from other causes. Dead or infested trees were always inspected for presence of roundheaded pine beetle galleries. At the Pinaleno Mountains study site, dwarf mistletoe ratings were obtained for all live ponderosa pines using the 6-class system described by Hawksworth (1977). Site index was determined from tree heights and ages of 1–2 healthy dominant or codominant trees in the vicinity of the plot using relationships developed by Minor (1964).

Data Analysis. Metrics were computed for total and ponderosa pine basal area, percent ponderosa pine, quadratic mean diameter for all species, ponderosa pine quadratic mean diameter, average tree dbh for all species, average ponderosa pine dbh, and trees per hectare (based on trees $\geq$12.7 cm dbh). Periodic growth ratio was also calculated as a measure of vigor by obtaining the ratio of the most recent 5-yr radial increment growth to the earlier 5-yr growth radial increment (Mahoney 1978).

To compare similar rate growth periods between infested and uninfested plots in each study area, a variable called ponderosa pine matched growth was created (Negrón 1997). Tree mortality sampled in the Pinaleno Mountains was primarily $\approx$4 yr old. Sampling was conducted during the summers of 1995 and 1996. Therefore, for dead trees, the last 5-yr growth rate measured the interval 1987–1991 and the 2nd-to-last 5-yr growth rate measured the time frame of 1982–1986. For live trees, the last 5-yr growth rate measured the approximate time frame 1991–1995 and the 2nd-to-last 5-yr growth rate measured the approximate interval 1986–1990. Ponderosa pine matched growth for infested plots is calculated as the average growth rate for roundheaded pine beetle-killed trees during the last 5 yr (1987–1991) and 2nd-to-last 5 yr (1986–1990) growth rate for live ponderosa pines. For uninfested plots, the 2nd-to-last 5 yr (1986–1990) growth rates for the live ponderosa pines are averaged. Some wood shrinkage may have occurred in roundheaded pine beetle-killed trees but it was not considered an important factor because only a few years set apart tree mortality and growth rate measurements. The variable is not always a year-to-year match because not all mortality sampled occurred in the same year; but it closely approximates similar periods for growth measurements. The variable represents growth rates 5 yr **before** attack by roundheaded pine beetle.

The same approach was used to calculate ponderosa pine matched growth for the Pine Valley Mountains study site. Sampling in this site was conducted during the summer of 1996 and sampled trees had also been dead for $\approx$4 yr as determined by their condition and stage of deterioration. Therefore, growth rate measurements represent the same time frames as those described above for the Pinaleno Mountains.

To compare forest conditions associated with infested plots with those associated with uninfested plots at each study site, normality tests using the Shapiro–Wilks test were conducted on the differences of the plot-level means for the variables measured between infested and uninfested plots. Because most variables were not normally distributed, Mann–Whitney tests were used to detect differences between infested and uninfested plots.

To determine the type of trees being attacked by the roundheaded pine beetle at each study site, the characteristics of roundheaded pine beetle-attacked (killed and infested) and live trees within infested plots were compared. Analysis of variance examined differences in average dbh, total height, phloem thickness, last 5-yr growth rate, 2nd-to-last 5-yr growth rate, 10-yr growth rate, periodic growth ratio, ponderosa pine matched growth, and dwarf mistletoe rating for the Pinaleno Mountains. Response variables examined for the Pine Valley Mountains were average dbh, last 5-yr growth rate, 2nd-to-last 5-yr growth rate, 10-yr growth rate, periodic growth ratio, and ponderosa pine matched growth. For this particular analysis the ponderosa pine matched growth represents the last 5-yr growth rate for roundheaded pine beetle-killed trees, and 2nd-to-last 5-yr growth rate for live trees.

Classification and regression trees (CART), a statistical technique developed by Breiman et al. (1984), was used to construct probability of infestation and extent of mortality models in terms of basal area killed by roundheaded pine beetle for each study site. A module produced for use with Systat was used for the CART analysis (Steinberg and Colla 1992). For classification trees, CART performs a binary recursive partitioning of the data set based on predictor variables into the most pure class memberships possible (Verbyla 1987). When the response variable is continuous, homogenous clusters with reduced variances are produced. The result are easy to use binary tree models with predictor variables as splitting rules and class memberships at the end nodes for probability models or average response variable for regression trees (Breiman et al. 1984). The approach is nonparametric, can use nominal, interval, ordinal, or ratio-scaled predictor variables, and is adequate for evaluating data sets with multiple structures. Potential classification trees are cross-validated during the model construction phase by dividing the data set into

10 subsets. Nine subsets are then used for model construction and the 10th subset is used for validation. This procedure is repeated until all subsets have been used for model construction and for model validation. The cross-validation estimates of classification accuracy or, percent of cases correctly classified, obtained from each validation run are averaged, which results in an overall cross-validation estimate. The highest cross-validation estimate of classification accuracy is used to select the best model. The cross-validation estimate is a nearly unbiased estimate of how well the model will perform with a new sample of cases from the same population.

Tree classification approaches have been used in forest pathology applications by Byler et al. (1990) for estimating probability of root disease on the Lolo National Forest, MT, and by Baker et al. (1993) for annosus root disease, *Heterobasidion annosum* (Fr.:Fr) Bref., in southern pines. Reynolds and Holsten (1994; 1996) also used a tree classification approach to predict mortality in Lutz spruce, *Picea* X *lutzii* Little, stands and in Lutz and Sitka spruce, *Picea sitchensis* (Bong.) Carr., stands to spruce beetle, *Dendroctonus rufipennis* Kirby, in terms of basal area killed in Alaska. Negrón (1997, 1998) applied CART methodology to estimate probabilities of infestation and extent of mortality to roundheaded pine beetle infestations in New Mexico and Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in Colorado. Verbyla (1987) indicated that CART was a robust approach when outliers are present in the data and that it is less likely to include nonsignificant predictor variables. Additional information about CART and classification trees can be obtained from the above mentioned references and citations therein. Linear regression analysis was also used to model extent of mortality in terms of basal area killed.

Results

Pinaleno Mountains. Infested plots exhibited significantly higher ponderosa pine basal area ($P < 0.05$) suggesting that trees in infested plots were growing under conditions of increased host-type stocking (Table 1). Within infested plots, roundheaded pine beetle-attacked trees were smaller in dbh and total height than live trees ($P < 0.05$) (Table 2).

Periodic growth ratio was identified in the CART analysis as a predictor of the probability of infestation by roundheaded pine beetles (Fig. 1). A periodic growth ratio ≤1.14 resulted in a probability of infestation of 0.60, whereas periodic growth ratio >1.14 resulted in a reduced probability of infestation. An alternate model kept the reduced periodic growth ratio condition node as an intermediate node and made another split using ponderosa pine basal area (Fig. 1). Increased host-type basal area resulted in a higher probability of infestation. Cross-validation estimate of correct classification (percentatge of cases correctly classified) was 0.60 for both models.

A model was built with regression tree analysis to estimate potential basal area killed by roundheaded pine beetle based on initial ponderosa pine basal area (Fig. 2). A significant linear regression equation was also built (Table 3). Both models indicate that ponderosa pine basal area can be used to estimate potential roundheaded pine beetle-killed basal area. Increased ponderosa pine basal area was associated with increased beetle-caused mortality in both analyses. The regression tree model had a larger r^2 and a reduced mean square error compared with the linear regression model. This suggests increased precision in estimates of potential mortality obtained with the regression tree model.

Pine Valley Mountains. Significant differences were detected for all variables measured between infested and uninfested plots with the exception of ponderosa pine phloem thickness, periodic growth ratio, or percent ponderosa pine basal area. Infested plots had increased total and ponderosa pine basal areas, greater number of trees per hectare, reduced growth rate, and reduced diameter and quadratic mean diameter compared with uninfested plots (Table 1). This suggests that trees in infested plots were growing under more crowded conditions that fostered reduced growth rates than trees in uninfested plots. Roundheaded pine beetle-attacked trees in infested plots exhibited reduced growth compared with live trees in infested plots (Table 2).

Ponderosa pine matched growth, which represents growth rate during the last 5 yr before beetle attack, was identified as an important variable to predict the probability of infestation by roundheaded pine beetles (Fig. 3A). With average growth ≤6.6 mm, the probability of infestation was 0.93. Increased growth rate resulted in a reduced probability of infestation. Cross-validation estimate of correct classification was 0.78. An alternate classification tree was constructed which used ponderosa pine basal area as the splitting variable with higher stocking densities resulting in a higher probability of infestation (Fig. 3B). Cross-validation estimate of correct classification was 0.58.

Two regression tree models were constructed to estimate the extent of mortality associated with roundheaded pine beetles in infested plots. The 1st model used ponderosa pine matched growth as splitting variable with reduced growth associated with increased basal area killed (Fig. 4A). The 2nd model used ponderosa pine basal area and trees per hectare as splitting variables (Fig. 4B). In both nodes, increased stocking densities were associated with increased basal area killed. A significant relationship was modeled between initial ponderosa pine basal area and beetle-caused mortality using linear regression (Table 3). Both regression tree models, particularly the growth rate-based model, had a higher r^2 and reduced root mean square error when compared with the linear regression model (Table 3). This implies that the regression tree models for the Pine Valley Mountains can provide better estimates of potential mortality than the linear regression model.

Mortality Categories. Relative mortality categories representing low, medium, and high potential mortality were derived from the tree regression analyses for

Table 1. Means ± SE of variables for all plots combined, infested, and uninfested plots, Pinaleno Mountains, Coronado National Forest, AZ, 1995–1996 and Pine Valley Mountains, Dixie National Forest, UT, 1996

Variable	Overall	Infested	Uninfested	$\mid Z \mid^a$	$P > Z^a$
	Pinaleno Mountains, AZ, 1995-1996				
	n = 84	n = 45	n = 39		
Quadratic mean dbh (cm) – all species	45.3 ± 1.1	44.4 ± 1.4	46.4 ± 1.7	1.02	0.309
Mean dbh (cm) – all species	42.5 ± 1.0	41.7 ± 1.2	43.5 ± 1.5	0.1	0.351
Ponderosa pine quadratic dbh, cm	47.1 ± 1.2	46.8 ± 1.8	47.4 ± 1.6	0.57	0.569
Ponderosa pine mean dbh, cm	45.4 ± 1.2	45.0 ± 1.7	45.9 ± 1.6	0.50	0.619
Ponderosa pine total ht, m	15.5 ± 0.4	15.5 ± 0.5	15.6 ± 0.6	0.22	0.828
Last 5 yr growth, mm	4.3 ± 0.2	4.1 ± 0.2	4.4 ± 0.3	0.54	0.590
Second-to-last 5 yr growth, mm	5.2 ± 0.9	6.0 ± 1.7	4.3 ± 0.3	1.36	0.176
Last 10 yr growth, mm	9.5 ± 0.9	10.1 ± 1.7	8.7 ± 0.5	0.63	0.531
Ponderosa pine matched growth, mm	4.1 ± 0.1	3.9 ± 0.1	4.3 ± 0.3	0.29	0.773
Periodic growth ratio	1.0 ± 0.02	1.0 ± 0.03	1.1 ± 0.03	1.79	0.074
Live ponderosa pine phloem thickness, mm	2.2 ± 0.1	2.2 ± 0.1	2.2 ± 0.1	0.60	0.547
Dwarf mistletoe rating	0.35 ± 0.1	0.42 ± 0.2	0.28 ± 0.1	0.18	0.854
Total basal area, m^2/ha	58.1 ± 2.7	60.2 ± 3.7	55.5 ± 3.9	1.00	0.317
Ponderosa pine basal area, m^2/ha	34.4 ± 2.0	38.5 ± 3.0	29.6 ± 2.2	2.12	0.034
Percent ponderosa pine	62.1 ± 2.6	65.9 ± 3.3	57.6 ± 3.9	1.70	0.089
Trees per hectare	684.1 ± 46.6	710.6 ± 60.5	653.5 ± 72.7	1.06	0.288
Site index	60.6 ± 1.5	60.9 ± 1.8	60.2 ± 2.5	0.14	0.889
	Pine Valley Mountains, UT, 1996				
	n = 36	n = 18	n = 18		
Quadratic mean dbh (cm) – all species	56.5 ± 1.6	53.5 ± 2.5	59.6 ± 1.9	2.41	0.016
Mean dbh (cm) – all species	55.1 ± 1.7	52.2 ± 2.4	58.1 ± 2.1	2.12	0.034
Ponderosa pine quadratic dbh, cm	57.0 ± 1.7	53.5 ± 2.5	60.5 ± 1.9	2.66	0.008
Ponderosa pine mean dbh, cm	55.7 ± 1.7	52.3 ± 2.4	59.1 ± 2.1	2.47	0.014
Last 5 yr growth, mm	7.0 ± 0.3	6.3 ± 0.4	7.8 ± 0.4	2.61	0.009
Second-to-last 5 yr growth, mm	7.6 ± 0.4	6.6 ± 0.4	8.5 ± 0.5	2.72	0.006
Last 10 yr growth, mm	14.6 ± 0.7	12.9 ± 0.9	16.3 ± 0.9	2.79	0.005
Ponderosa pine matched growth, mm	7.4 ± 0.4	6.2 ± 0.5	8.5 ± 0.5	3.30	0.001
Periodic growth ratio	0.95 ± 0.01	0.96 ± 0.02	0.94 ± 0.01	0.22	0.825
Live ponderosa pine phloem thickness, mm	2.8 ± 0.1	2.7 ± 0.1	2.8 ± 0.1	0.53	0.594
Total basal area, m^2/ha	52.4 ± 4.4	64.9 ± 6.7	40.0 ± 4.1	2.67	0.008
Ponderosa pine basal area, m^2/ha	51.5 ± 4.5	64.7 ± 6.7	38.4 ± 4.0	2.84	0.004
Percent ponderosa pine	97.7 ± 0.9	99.5 ± 0.5	95.8 ± 1.7	1.85	0.064
Trees per hectare	331.1 ± 39.0	415.7 ± 57.3	246.5 ± 46.3	2.12	0.034

n, Number of plots sampled.
[a] Results from Mann–Whitney tests comparing differences between infested and uninfested plots.

both study sites. The categories are associated with average ponderosa pine basal area killed and are based on the predictor variables identified in the regression trees (Table 4). It can be seen that on average, the percent of basal area killed at each site and across all mortality categories are substantial. The low mortality category for the Pinaleno Mountains exhibited 66% of the ponderosa pine basal area killed (Table 4) and just under 50% for the 2 models from the Pine Valley Mountains (Tables 4).

Discussion

Results from this study suggest that the roundheaded pine beetle prefers stands and trees exhibiting poor growth. This agrees with results from the study conducted in the Sacramento Mountains, NM (Negrón 1997). Stand conditions in terms of diameter classes and stocking levels were quite different because they are larger and higher in the Pine Valley and the Pinaleno Mountains compared with the Sacramento Mountains, but susceptibility patterns associated with poor tree growth where quite similar.

Comparison of infested and uninfested plots at each study site revealed more distinct differences from the Pine Valley mountains data set (Table 1). The Pine Valley mountains study area was an aggregate of adjacent stands, whereas the Pinalenos mountains study area included stands from a number of different areas. This resulted in increased variability in the forest conditions sampled in the Pinaleno mountains. As a result, differences in stand conditions between infested and uninfested plots were not readily detected in the Mann–Whitney tests for the Pinaleno Mountains (Table 1). However, through the CART analysis, we were still able to identify stand conditions that are suitable for the development of roundheaded pine beetle infestations at both study areas, that is stands exhibiting poor growth resulting from high stocking densities.

Probability of infestation models for the Pinaleno Mountains were based on periodic growth ratio and ponderosa pine basal area; with reduced growth rates and higher stocking densities resulting in increased probabilities of infestation (Fig. 1). Both models require the use of growth rate data. Although cross-validation estimates for both models are the same, the 2nd model adds ponderosa pine basal area to the decision tree. This model provides a better perspective about forest conditions where roundheaded pine beetle infestations are more likely to occur, that is,

Table 2. Means ± SE for live and roundheaded pine beetle-attacked trees in infested plots, Pinaleno Mountains, Coronado National Forest, AZ, 1995–1996 and Pine Valley Mountains, Dixie National Forest, UT, 1996

Variable	Live	Beetle-attacked	F^a	P^a
Pinaleno Mountains, AZ, 1995–1996	n = 65	n = 158		
Ponderosa pine dbh, cm	52.2 ± 2.9	43.3 ± 1.4	7.2	0.011
Ponderosa pine total ht, m	16.4 ± 0.7	15.8 ± 0.4	8.6	0.006
Last 5 yr growth, mm	4.3 ± 0.3	4.2 ± 0.1	1.0	0.325
Second-to-last 5 yr growth, mm	4.1 ± 0.2	6.7 ± 2.1	1.2	0.290
Last 10 yr growth, mm	8.4 ± 0.5	10.9 ± 2.1	0.9	0.358
Ponderosa pine matched growth, mm	4.1 ± 0.2	4.2 ± 0.1	1.4	0.244
Periodic growth ratio	1.1 ± 0.06	0.9 ± 0.03	2.6	0.115
Ponderosa pine phloem thickness, mm	2.1 ± 0.1	2.4 ± 0.1	0.5	0.509
Dwarf mistletoe rating	0.1 ± 0.1	0.8 ± 0.3	1.2	0.304
Pine Valley Mountains, UT, 1996	n = 76	n = 192		
Ponderosa pine dbh, cm	56.6 ± 1.7	47.7 ± 0.9	2.0	0.178
Last 5 yr growth, mm	7.5 ± 0.4	4.9 ± 0.2	27.0	0.001
Second-to-last 5 yr growth, mm	7.4 ± 0.3	5.6 ± 0.2	5.7	0.033
Last 10 yr growth, mm	14.9 ± 0.7	10.5 ± 0.3	20.3	0.001
Ponderosa pine matched growth, mm	7.4 ± 0.3	4.8 ± 0.2	23.3	0.001
Periodic growth ratio	1.03 ± 0.03	0.90 ± 0.02	1.6	0.224

n, Number of trees sampled.
[a] Results from ANOVA comparing differences between beetle-attacked and live trees within the infested plots.

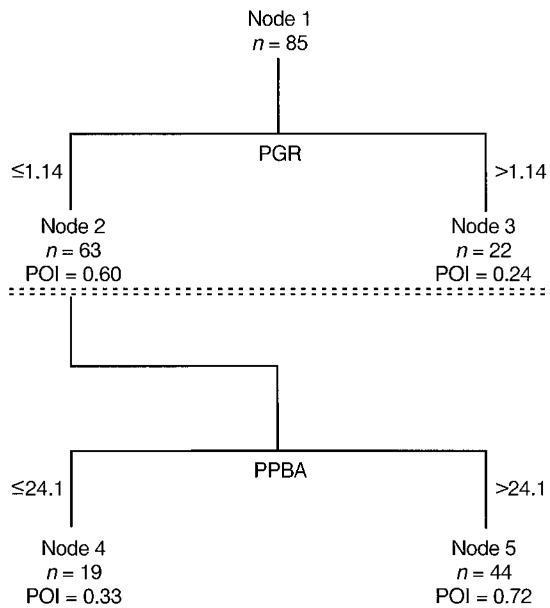

Fig. 1. Classification trees for estimating the probability of infestation by the roundheaded pine beetle in the Pinaleno Mountains, Coronado National Forest, AZ, 1995–1996. *n*, Number of plots; PGR, periodic growth rate; PPBA, ponderosa pine basal area (m^2/ha); POI, probability of infestation. The periodic growth rate-based model is presented above the dashed line. An alternate model includes the split above the dashed line and adds another split based on PPBA presented under the dashed line. Cross-validation estimate of correct classification = 0.60 for each model.

stands exhibiting poor growth and higher stocking levels.

Probability of infestation models for the Pine Valley Mountains were based on ponderosa pine matched growth, that is, growth rates before the onset of the outbreak and ponderosa pine basal area (Fig. 3). Again, reduced growth rates and greater basal area predicted higher probabilities of infestation. The 1st model requires growth rate data whereas the 2nd model requires ponderosa pine basal area data. Basal area data are easier to collect and is usually more readily available to managers; consequently, the 2nd model may be more practical for use. The growth rate model, however, has a higher cross-validation estimate of correct classification than the basal area model.

The probability model based on periodic growth ratio obtained for the Pinaleno Mountains may have broader applicability across many stand conditions within that mountain range (Fig. 1). Being a ratio instead of a specific amount of growth in 5 yr may make this metric less sensitive to site-specific conditions and therefore easier to apply to other stands within that geographic area. Stands with average periodic growth ratio for ponderosa pine ≤1.14, though exhibiting improved growth over the last 5 yr, were still more susceptible because they were still the slowest growing groups of trees.

For the purpose of estimating potential mortality caused by roundheaded pine beetle in high value stands, information obtained from the regression tree approaches is likely to be more relevant than the linear regression models. Regression tree models aggregate data points into clusters of reduced variance (Breiman et al. 1984). This results in statistically meaningful groups. This was evident in the mortality categories derived from the 2 regression tree models for the Pine

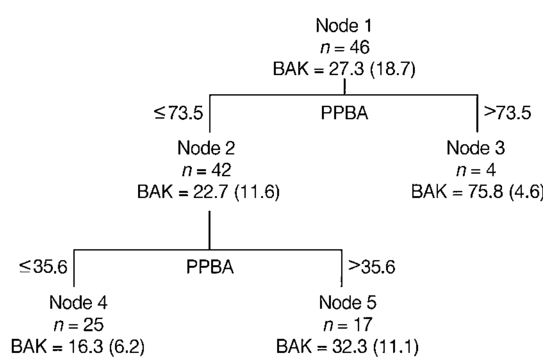

Fig. 2. Regression tree estimating average amount of mortality caused by the roundheaded pine beetle based on initial ponderosa pine basal area, Pinaleno Mountains, Coronado National Forest, AZ, 1995–96 (r^2 = 0.81, root mean square error = 8.1). *n*, Number of plots; BAK, average basal area killed (SD) (m^2/ha); PPBA, ponderosa pine basal area (m^2/ha).

Table 3. Results from linear regression and regression trees (CART) analyses used to model ponderosa pine basal area killed based on initial ponderosa pine basal area for the Pinaleno Mountains, AZ, and the Pine Valley Mountains, UT

Model	y-intercept (SE) (β_0)	Slope (SE) (β_1)	Coefficient of determination (r^2)	Mean square error	P
		Pinalenos Mountains, AZ			
Linear regression[a]	-4.0 ± 3.2	0.81 ± 0.07	0.76	9.7	0.001
Regression tree[b]	—	—	0.81	8.1	—
		Pine Valley Mountains, UT			
Linear regression[a]	−16.6	0.96	0.70	17.6	0.001
Regression tree–PMG[b]	—	—	0.96	6.0	—
Regression tree–PPBA and TPH[b]	—	—	0.79	15.3	—

PMG, ponderosa matched growth; PPBA, ponderosa pine basal area; TPH, trees per hectare.
[a] $y = \beta_0 + \beta_1 x$, where y is ponderosa pine basal area killed in m^2/ha, and x is initial ponderosa pine basal area in m^2/ha.
[b] Only the coefficient of determination and mean square errors are given for the regression trees (CART) analyses.

Valley Mountains (Fig. 4). Although the 2 models used different predictor variables, the resulting clusters of mortality in the terminal nodes were quite similar in the percent of basal area killed, particularly in the low and medium categories (Table 4). Because the terminal nodes represent an average for a group of data points, it is also more meaningful to use the standard deviation as a measure of dispersion around the mean. The regression tree estimates of mortality and the mortality categories derived can be an effective methodology to assess the relative potential mortality that may occur in a stand.

Prior studies have demonstrated the relationship between susceptibility to bark beetle attacks and poor growth. Slow growth was reported for nearly all measured mountain pine beetle-killed ponderosa pines in the Northwest (Sartwell 1971, Sartwell and Stevens 1975). Inception of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, outbreaks occurred simultaneously with reduced tree growth in lodgepole pine, *Pinus contorta* Dougl. ex Loud., in British Columbia (Shrimpton and Thompson 1983). Preference for slower growing trees has also been shown by spruce beetle in white spruce, *Picea glauca* (Moench) Voss (Watson 1928, Hard et al. 1983, Hard 1985). Slow

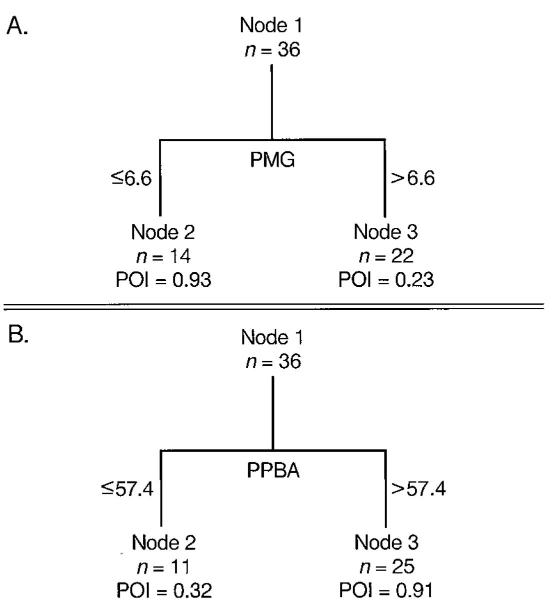

Fig. 3. Classification trees for estimating the probability of infestation by the roundheaded pine beetle in the Pine Valley Mountains, Dixie National Forest, UT, 1996. *n*, Number of plots; PMG, ponderosa pine matched growth; PPBA, ponderosa pine basal area (m^2/ha); POI, probability of infestation. (A) ponderosa pine matched growth-based model, cross-validation estimate of correct classification = 0.78. (B) Ponderosa pine basal area-based model, cross-validation estimate of correct classification = 0.58.

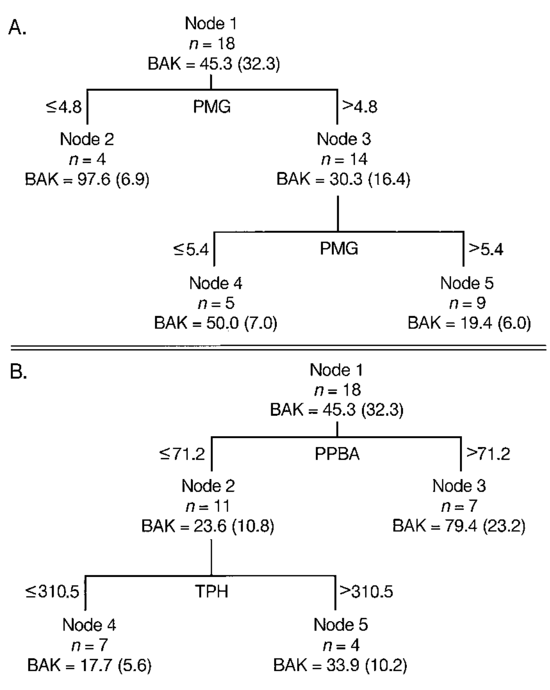

Fig. 4. Regression trees for estimating average amount of mortality caused by the roundheaded pine beetle, Pine Valley Mountains, Dixie National Forest, UT, 1996. *N*, Number of plots; BAK, average basal area killed (SD) (m^2/ha); PMG, ponderosa pine matched growth rate (mm); PPBA, ponderosa pine basal area (m^2/ha); TPH, trees per hectare. (A) Ponderosa pine matched growth model (r^2 = 0.96, root mean square error = 6.0). (B) Ponderosa pine basal area - trees per hectare model (r^2 = 0.79, root mean square error = 15.3).

Table 4. Mortality categories with corresponding average ponderosa pine basal area killed (SD) and percent ponderosa pine basal area killed (SD) derived from regression tree models for study sites in the Pinaleno Mountains, AZ, and Pine Valley Mountains, UT, 1995–1996

Mortality category	Splitting criteria	Ponderosa pine basal area killed (m^2/ha)	% ponderosa pine basal area killed
Pinaleno Mountains–Ponderosa pine basal area (PPBA) model			
Low	PPBA ≤ 35.6	16.3 ± 6.2	66.3 ± 23.0
Medium	35.6 < PPBA ≤ 73.5	32.3 ± 11.1	71.2 ± 23.8
High	PPBA > 73.5	75.8 ± 4.6	85.4 ± 11.8
Pine Valley Mountains–Ponderosa pine matched growth (PMG) model			
Low	PMG > 5.4	19.4 ± 6.0	49.1 ± 18.3
Medium	4.8 < PMG ≤ 5.4	50.0 ± 7.0	66.9 ± 12.5
High	PMG ≤ 4.8	97.6 ± 6.9	100 ± 0.0
Pine Valley Mountains–Ponderosa pine basal area (PPBA) and trees per hectare (TPH) model			
Low	PPBA ≤ 71.2 and TPH ≤ 310.4	17.7 ± 5.6	48.8 ± 18.8
Medium	PPBA ≤ 71.2 and TPH > 310.4	33.9 ± 10.2	62.4 ± 20.6
High	PPBA > 71.2	79.4 ± 23.2	83.6 ± 21.7

growth has also been implicated with high probability of infestation by the roundheaded pine beetle in the Sacramento Mountains, NM (Negrón 1997), and with the Douglas-fir beetle in Douglas-fir, *Pseudotsuga menziesii* (Mirb) Franco, in Colorado (Negrón 1998). Christiansen et al. (1987) hypothetized that the ability of the tree to withstand bark beetle attacks is linked to the availability of carbohydrates for defensive mechanisms. Poor growth efficiency caused by overstocking may negatively impact the ability of the tree to mobilize carbohydrates for defensive strategies such as the production of resin for withstanding bark beetle attacks.

Models estimating extent of mortality caused by roundheaded pine beetle indicate that increased mortality was observed with increasing host-type basal area (Figs. 2 and 4B; Table 3). This agrees with earlier studies. McCambridge et al. (1982) indicated that there was a positive relationship between original basal area of ponderosa pine and the number of pines killed by mountain pine beetle in north-central Colorado. Total stand basal area, percent of total basal area comprised by spruce, and percent of spruce basal area represented by trees larger than 25 cm were connected to spruce basal area killed by spruce beetle in Alaska (Reynolds and Holsten 1994, 1996). A positive relationship between initial basal area and beetle-caused mortality has also been described with the roundheaded pine beetle in the Sacramento Mountains, NM (Negrón 1997), and with the Douglas-fir beetle in Colorado (Negrón 1998).

This study confirms that susceptibility to roundheaded pine beetle infestations is increased by the availability of slow growing trees under high stocking conditions. Roundheaded pine beetle has long been active in ponderosa pine ecosystems in parts of the Southwest; but in the past, its occurrence was sporadic and outbreaks short-lived. The 2 most recent outbreaks in the Sacramento Mountains of New Mexico and the Pinaleno Mountains of Arizona have been more intense and widespread (Wilson and Tkacz 1996). Because there are still many ponderosa pine stands across the southwest with high stocking levels and slow growing trees, this trend is likely to continue. Fire suppression efforts across the southwestern United States since the turn of the century have resulted in overstocked ponderosa pine forests, which are more susceptible to insect and disease outbreaks (Covington and Moore 1994, Johnson 1994). Although the fire history of our specific study sites has not been examined, it is possible that fire suppression may be contributing to overstocking, reduced growth rates, and increased susceptibility to roundheaded pine beetles.

Probability of infestation models presented can assist in identifying susceptible stands in the Pinalenos (Fig. 1) and the Pine Valley Mountains (Fig 3). In stands where roundheaded pine beetle infestations are more likely to occur, potential mortality can be estimated using stand density or growth rate data (Figs. 2 and 4). These models are simple tools that forest managers can use to manage ponderosa pine stands where mortality to roundheaded pine beetles may not be acceptable.

The empirical nature of the models developed in this study dictate that their application to other areas be made with discretion (Hedden 1981). However, the study agrees with data collected from the Sacramento Mountains in that forest conditions fostering poor growth are important factors in determining susceptibility to roundheaded pine beetle (Negrón 1997). Additional work needs to be conducted to develop biological models to rate stands for probabilities of infestation or extent of mortality, or both, that would be applicable to the diversity of forest conditions that occur within the range of the roundheaded pine beetle.

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