

Estimating probabilities of infestation and extent of damage by the roundheaded pine beetle in ponderosa pine in the Sacramento Mountains, New Mexico

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Abstract: Classification trees and linear regression analysis were used to build models to predict probabilities of infestation and amount of tree mortality in terms of basal area resulting from roundheaded pine beetle, *Dendroctonus adjunctus* Blandford, activity in ponderosa pine, *Pinus ponderosa* Laws., in the Sacramento Mountains, New Mexico. Classification trees were built for combined habitat types sampled and for each habitat type series or type sampled. Cross-validation estimates of classification accuracy ranged from 0.64 to 0.79. The data suggest that stands attacked by the roundheaded pine beetle exhibit poor growth during the last 5 years prior to attack, abundant host type, and smaller diameter than uninfested stands. Trees prone to attack by the roundheaded pine beetle within infested points also exhibited reduced growth rates and smaller diameters than uninfested trees. Linear regression analysis indicates that initial amount of ponderosa pine basal area is a good predictor variable for the amount of basal area affected.

Résumé : Des analyses d'arborescence et de régression linéaire ont été utilisées pour construire des modèles capables de prédire les probabilités d'infestation et la quantité de mortalité des arbres en terme de surface terrière en se basant sur l'activité du dendroctone à tête ronde du pin, *Dendroctonus adjunctus* Blandford, sur le pin ponderosa, *Pinus ponderosa* Laws., dans les montagnes de Sacramento, au Nouveau-Mexique. Les arborescences ont été construites pour les types combinés d'habitats échantillonnés, et pour chaque groupe ou chaque type d'habitats échantillonnés. Les estimés de la validation croisée pour la justesse de la classification variaient de 0,64 à 0,79. Les données suggèrent que les peuplements attaqués par le dendroctone à tête ronde ont eu une faible croissance au cours des derniers 5 ans qui ont précédé l'attaque, contenaient un type d'hôtes en abondance et avaient un diamètre plus petit que les peuplements non infestés. Les arbres sujets à l'attaque par le dendroctone à tête ronde à l'intérieur d'une zone d'infestation avaient également un taux de croissance et un diamètre plus faibles que les arbres non infestés. La régression linéaire montre que la surface terrière initiale du pin ponderosa est une bonne variable pour prédire la surface terrière qui est affectée.

[Traduit par la Rédaction]

Introduction

Periodic epidemics of the roundheaded pine beetle, *Dendroctonus adjunctus* Blandford, have killed large numbers of ponderosa pine trees, *Pinus ponderosa* Laws., in the southwestern United States, particularly in New Mexico. Lucht et al. (1974) reported an infestation of ca. 16 000 pole- and saw-timber sized ponderosa pine trees in 1012 ha near Cloudcroft, N. Mex., in 1950. Another outbreak in the early 1960s killed several hundred trees near Ruidoso, N. Mex. (Massey et al. 1977), and in 1971 an estimated 400 000 trees were killed in ca. 60 700 ha from Mayhill to Ruidoso, N. Mex. (Massey et al. 1977). Historically, outbreaks of the roundheaded pine beetle were short-lived; therefore the insect was not considered an important pest for many years (Chansler 1967).

Little research has been conducted on the roundheaded pine beetle or its impacts. The insect's biology and life history in the Sacramento Mountains, N. Mex., were studied by Chansler (1967). Lucht et al. (1974) studied emergence and attack behavior in the same area. Stevens and Flake (1974) studied associated stand conditions and impacts during an outbreak of

roundheaded pine beetle also in the Sacramento Mountains. Basal area and numbers of ponderosa pines were reduced up to 50% in some stands; reductions in ponderosa pine basal area averaged 25% in infested stands. Most affected trees were co-dominants, and dwarf mistletoe, *Arceuthobium vaginatum* (Willdenow), infection was common.

The roundheaded pine beetle is currently causing increased mortality to ponderosa pine in the southwest. Roundheaded pine beetle populations have been at outbreak levels in the Sacramento Mountains since the late 1980s (Forest Pest Management Staff 1995) and in the Pinalenos Mountains in southern Arizona since the early 1990s (Wilson 1993).

The purpose of this project was to study stand and tree characteristics associated with roundheaded pine beetle infestations in ponderosa pine in the Sacramento Mountains and develop models to predict the probabilities of infestation and extent of damage in affected stands. Based on this kind of information, management activities could be planned to reduce the probability of infestation and the likelihood of catastrophic losses in stands where there may be a low tolerance for losses.

Materials and methods

Study site

Sampling was conducted southeast of Cloudcroft, N. Mex., at the Sacramento Ranger District, Lincoln National Forest. Since the onset

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Table 1. Number of stands sampled, infested points, and uninfested points established in each habitat type, Lincoln National Forest, N. Mex., 1994–1995.

Habitat type ^a	Stands sampled	Infested points	Uninfested points
PIPO–QUGA ^b	4	28	28
PIPO–QUUN	2	14	14
PSME–QUGA ^c	4	28	28
PSME–QUUN	1	7	7
ABCO–QUGA ^d	4	21	25

^aPIPO–QUGA, *Pinus ponderosa* – *Quercus gambelii*; PIPO–QUUN, *Pinus ponderosa* – *Quercus undulata*; PSME–QUGA, *Pseudotsuga menziesii* – *Quercus gambelii*; PSME–QUUN, *Pseudotsuga menziesii* – *Quercus undulata*; ABCO–QUGA, *Abies concolor* – *Quercus gambelii*. Total number of points across all habitat types = 200 (100 infested and 100 uninfested).

^bTotal number of points for PIPO habitat types = 84 (42 infested and 42 uninfested).

^cTotal number of points for PSME habitat types = 70 (35 infested and 35 uninfested).

^dTotal number of points for ABCO–QUGA habitat type = 46 (21 infested and 25 uninfested).

of the current roundheaded pine beetle outbreak, USDA Forest Service personnel have conducted annual aerial detection flights over the Lincoln National Forest. The aerial detection map generated for the Sacramento Ranger District from the 1988 flight was used to select sampling sites because roundheaded pine beetle populations began expanding to outbreak proportions at this time.

In the past, timber management programs at the Lincoln National Forest were very active. Therefore, the forest database contains extensive vegetation data, particularly as it pertains to ponderosa pine. With the use of the habitat type classification for the Lincoln National Forest developed by Alexander et al. (1984) five habitat types that compose the majority of the ponderosa pine component in the forest were selected for sampling. Sampling was then stratified by these habitat types with the purpose of developing probability models that would apply to the combined and individual habitat types sampled.

Sampling

A map of the Sacramento Ranger District with its management units delineated was overlaid on the 1988 aerial survey map. The study area was then delineated to include the core of the affected forest in the early stages of the outbreak. The forest database was then queried, and a listing of the stands in each management unit in the study area was generated and sorted by habitat type.

Stands that contained infested and uninfested host type were then randomly selected for sampling. Under this design the probability that uninfested points were exposed to beetles but not attacked is likely to be higher than if infested and uninfested points are placed in different stands and separated by considerable distances. This design is more likely to detect true low probability of infestation conditions in uninfested points than uninfested host type in isolation with no beetle pressure.

Although little is known about tree and stand factors associated with roundheaded pine beetle infestations, Stevens and Flake (1974) indicated an average diameter at breast height (DBH) of 16.5 cm for infested trees and 18.8 cm for uninfested trees. Chansler (1967) and Massey (1977) reported large-diameter trees being attacked; however, Stevens and Flake (1974) acknowledge that it is possible that large trees are attacked under epidemic conditions. Because other species of bark beetles have shown preference to larger diameter size classes (such as mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Amman et al. 1977; Mitchell and Preisler 1991), and spruce

beetle, *Dendroctonus rufipennis* Kirky (Schmid and Frye 1977; Werner et al. 1977)), it is possible that a diameter relationship exists in the roundheaded pine beetle interaction with its host. Therefore, ponderosa pine DBH data were used as a surrogate variable to determine adequate sampling intensity for the stands. Inventory data were obtained for six stands from Forest Service's files. Diameter at breast height data for all the points in those stands were tallied. Power calculations were made using the Power Analysis and Sample Size program described by Hintze (1991). The number of points needed per stand in order to detect differences between two diameter size classes (5.1 cm difference) at a 80% power ($\alpha = 0.1$), for a stand of ca. 14.5 ha, was 13. Therefore, a total of 14 variable radius plots were established in each stand, divided equally between the infested and the uninfested condition, thus maintaining a balanced design. Stands representing each of the following habitat types were sampled: *Pinus ponderosa* – *Quercus gambelii* (PIPO–QUGA), *Pinus ponderosa* – *Quercus undulata* (PIPO–QUUN) (hereafter ponderosa pine habitat types), *Pseudotsuga menziesii* – *Quercus gambelii* (PSME–QUGA), *Pseudotsuga menziesii* – *Quercus undulata* (PSME–QUUN) (hereafter Douglas-fir habitat types), and *Abies concolor* – *Quercus gambelii* (ABCO–QUGA) (hereafter white fir habitat type). Although habitat type data were obtained from Forest Service's database and because habitat type can vary within a stand, habitat type was verified at every sampling point. A total of 200 points (100 infested and 100 uninfested) were established across all habitat types. The number of stands sampled, infested points, and uninfested points established for each habitat type are presented in Table 1.

Stand and tree data

Sampling for this study was conducted in 1994 and 1995. Individual tree measurements taken from all point trees included species, DBH, total height, crown position, phloem thickness of live conifers, and growth measurements for the last two 5-year periods from cores collected on the south side of all conifers at breast height. In addition, dwarf mistletoe rating was obtained from all live ponderosa pines using the six-class rating system described by Hawksworth (1977). Data were also collected on tree status as follows: live, killed by roundheaded pine beetle, dead due to other causes, or infested by roundheaded pine beetle.

Infested points had to include at least one ponderosa pine at least 12.7 cm in DBH that had been killed by roundheaded pine beetle because this is about the smallest tree that the roundheaded pine beetle would normally attack. Infested points were established at random from the available mortality in the stand, which was at least 3–4 years old as indicated by the loss of foliage, fine twigs, and loose bark. Dead trees were always examined for presence of roundheaded pine beetle galleries. The intent was to sample tree mortality that occurred in the time frame from the initiation of the outbreak to its peak in terms of tree mortality. Only 43 infested trees were identified in the points out of a total of 711 sample trees, indicating that most of the mortality in the stands sampled had already occurred. Uninfested points had to include at least one ponderosa pine at least 12.7 cm in DBH. Uninfested points were established at random in the stand by taking random azimuths and distances from previously established points. No points were established within 40 m of another point. Site index was determined from tree age and heights of two healthy dominant or codominant trees in the vicinity of the point using equations presented by Minor (1964).

Data analysis

Data collected were used to generate metrics for basal area, percent ponderosa pine type, quadratic mean diameter, stand density index (Avery and Burkhardt 1994), and trees per hectare (calculated on the basis of all trees ≥ 12.7 cm in DBH). Periodic growth ratio, which is a ratio of the most recent 5-year growth radial increment divided by the preceding 5-year growth radial increment, and used by Mahoney

Table 2. Cross-validation estimates, costs of misclassification for infested and uninfested conditions, overall misclassification cost, number of terminal nodes, and number of variables for probability of infestation classification trees built, Lincoln National Forest, N. Mex., 1994–1995.

Habitat type model	Cross-validation accuracy of classification ^a	Cost of misclassification of infested condition	Cost of misclassification of uninfested condition	Overall misclassification cost (± SE) ^b	No. of terminal nodes	No. of variables
Comprehensive	0.67	0.45	0.22	0.66(0.06)	5	4
Ponderosa pine	0.79	0.24	0.19	0.43(0.09)	3	2
Douglas-fir	0.64	0.06	0.68	0.71(0.09)	2	1
White fir	0.76	0.29	0.20	0.49(0.13)	4	3

^aCross-validation accuracy of classification = 1 – (overall misclassification cost/2).

^bOverall misclassification cost = cost of misclassification of infested condition + cost of misclassification of uninfested condition.

(1978) as a measure of lodgepole pine, *Pinus contorta* Dougl., vigor, was also calculated.

Mortality data indicate that the current outbreak reached its peak in terms of number of trees killed in 1991 (Rogers et al. 1993); this represents trees attacked primarily in 1990. Since sampling for this study was conducted in 1994 and 1995, it follows that average radial growth measurements of the last 5 years of growth for ponderosa pine killed by roundheaded pine beetle in infested points measured in 1995 correspond to the time frame between 1985 and 1989; the second to last 5 years correspond to the time frame between 1980 and 1984. For live trees in infested and uninfested points, the last 5 years' growth rate measurements compose the 1990–1994 time frame and the second to last 5 years' growth rate, the 1985–1989 time frame. To represent similar growth periods a variable called ponderosa pine matched growth (PMG) was created. This variable represents average last 5 years' growth rate for ponderosa pine killed by roundheaded pine beetle, second to last 5 years' growth rate for live ponderosa pine in infested points, and average second to last 5 years' growth rate of ponderosa pine in uninfested points. Because few infested trees were included in the points sampled, and because they represent trees attacked towards the latter part of the outbreak, they were not included in this variable. Admittedly this variable does not represent a year to year match in all cases because not all mortality sampled occurred in the same year, as is indicated by the presence of some infested trees in the points sampled, but it more closely approximates similar time periods where growth rates were measured. Although some wood shrinkage may have occurred and therefore affected this comparison, it was not considered to be an important factor. The PMG variable then represents average growth rate of ponderosa pine for the last 5 years prior to roundheaded pine beetle attack in infested points and about the same years for live trees in uninfested and infested points.

To develop probability of infestation models, a statistical technique developed by Breiman et al. (1984) called Classification and Regression Trees (CART) was used. A module developed for use with Systat[®] was used to run the CART analysis (Steinberg and Colla 1992). This technique sequentially partitions the data set based on predictor variables into the most pure class memberships possible (Verbyla 1987). The result is a binary tree, which uses the best predictor variables as splitting rules and class memberships as the end nodes. During the model construction phase the potential classification trees are cross-validated by dividing the data set into 10 subsets. The model is built with 9 subsets and validated with the tenth subset. The process is repeated until all subsets have been used for model construction and for model validation. The cross-validation estimate of classification accuracy (% of cases correctly classified) resulting from each validation run are averaged, resulting in an overall cross-validation estimate. The best model is that which has the highest cross-validation estimate of classification accuracy. This 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. Costs of misclassification for the different class memberships are calculated by applying the selected model to the data and determining the number of correct and incorrect classifications. Classification trees

have been used in forest pathology applications to estimate the probability of root disease on the Lolo National Forest (Byler et al. 1990) and for annosus root disease in southern pines (Baker et al. 1993). Reynolds and Holsten (1994, 1996) also used a tree classification approach to predict spruce beetle hazard (extent of damage in terms of basal area killed) in Alaska.

Because splitting and predictor variables identified with classification and regression trees do not necessarily represent average conditions in the class groups, descriptive statistics of the variables measured were generated to better describe the conditions associated with the study area, the infested, and the uninfested condition. Normality tests were conducted on the differences of the means between the infested and the uninfested condition using the Shapiro–Wilk test. Since most variables were not normally distributed, Wilcoxon rank-sum tests were conducted to detect significant differences between the infested and the uninfested condition for all points combined, by habitat type series, and for the white fir habitat type.

I was also interested in determining the kinds of trees attacked by the roundheaded pine beetle. The focus of this particular analysis was comparing dead, infested, and live trees within the infested points. Analysis of variance was used to determine whether there were differences in average ponderosa pine diameter, height, last 5 years' radial growth, second to last 5 years' radial growth, last 10 years' radial growth, and matched growth. For matched growth, the value for this variable is equal to the last 5 years' growth rate for trees killed by roundheaded pine beetle and infested trees and to the second to last 5 years' growth rate for live trees. The variable represents growth rate for the last 5 years prior to roundheaded pine beetle attack in infested trees and approximately the same years for live trees. Orthogonal comparisons were used to compare means between live and dead trees and the average of combined infested and dead trees with live trees. Cross tabulations and a χ^2 test were used to determine whether there were any relationships between (1) trees killed by roundheaded pine beetle, live trees, and infested trees and (2) crown position.

Linear regression analysis was used for constructing models to predict extent of damage in terms of basal area of ponderosa pine killed by roundheaded pine beetles. Variables measured as described above were examined using a stepwise regression approach (SAS Institute Inc. 1990).

Results and discussion

Probabilities of infestation

Classification trees to determine probabilities of infestation by the roundheaded pine beetle were successfully built for all habitat types combined (hereafter comprehensive model) and separately for each habitat type strata sampled. Cross-validation estimates of classification accuracy ranged from 0.64 for the Douglas-fir habitat types model to 0.79 for the ponderosa pine habitat types. Costs of misclassification for the infested condition were higher than for the uninfested condition in the

Fig. 1. Classification tree for estimating probability of infestation by the roundheaded pine beetle across all habitat types sampled. Abbreviations are as follows: PMG, ponderosa pine mean matched growth (mm); PCPP, percent basal area in ponderosa pine; PDBH, ponderosa pine mean DBH (cm); PPBA, ponderosa pine basal area (m²/ha); POI, probability of infestation. Lincoln National Forest, N. Mex., 1994–1995.

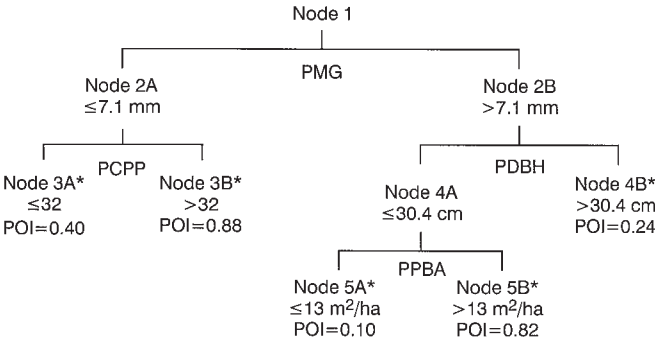


Table 3. Node, splitting criteria, number of cases, class membership, and class proportion for the probability of infestation comprehensive model, Lincoln National Forest, N. Mex., 1994–1995.

Node ^a	Split ^b	N	Class ^c	Class proportion	
				Infested	Uninfested
1	—	200	—	0.49	0.51
2A	PMG ≤ 7.1	82	I	0.69	0.31
3A*	PCPP ≤ 32.0	33	U	0.40	0.60
3B*	PCPP > 32.0	49	I	0.88	0.12
2B	PMG > 7.1	118	U	0.36	0.64
4A	PDBH ≤ 30.4	37	I	0.63	0.37
4B*	PDBH > 30.4	81	U	0.24	0.76
5A*	PPBA ≤ 13	10	U	0.10	0.90
5B*	PPBA > 13	27	I	0.82	0.18

^aAn asterisk indicates a terminal node. No asterisk indicates intermediate node. Node numbers correspond to nodes in Fig. 1.

^bPMG, ponderosa pine mean matched growth (mm); PCPP, percent basal area in ponderosa pine; PDBH, ponderosa pine mean DBH (cm); PPBA, ponderosa pine basal area (m²/ha).

^cI, infested; U, uninfested.

comprehensive model, slightly higher for the infested condition for the ponderosa pine habitat types model and the white fir habitat type model, and much lower for the infested condition than the uninfested condition in the Douglas-fir habitat types model (Table 2).

The comprehensive model indicates that high probabilities of infestation are associated with poor growth during the last 5 years prior to infestation (PMG) and higher percent basal area represented by ponderosa pine (PCPP). With increased growth during the last 5 years prior to infestation, high probabilities of infestation are associated with average ponderosa pine diameter (PDBH) of less than 30.4 cm and ponderosa pine basal area (PPBA) over 13 m²/ha (Table 3, Fig. 1).

The model for the ponderosa pine habitat type series also suggests a high probability of infestation under poor PMG. With better growth conditions during the same period, PDBH of less than 30.4 cm results in a high probability of infestation (Table 4, Fig. 2).

Fig. 2. Classification tree for estimating probability of infestation by the roundheaded pine beetle in *Pinus ponderosa* habitat types sampled. Abbreviations are as follows: PMG, ponderosa pine mean matched growth (mm); PDBH, ponderosa pine mean DBH (cm); POI, probability of infestation. Lincoln National Forest, N. Mex., 1994–1995.

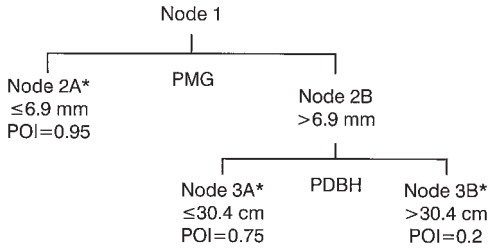


Table 4. Node, splitting criteria, number of cases, class membership, and class proportion for the probability of infestation model built for ponderosa pine habitat types sampled, Lincoln National Forest, N. Mex., 1994–1995.

Node ^a	Split ^b	N	Class ^c	Class proportion	
				Infested	Uninfested
1	—	84	—	0.50	0.50
2A*	PMG ≤ 6.9	19	I	0.95	0.05
2B	PMG > 6.9	65	U	0.37	0.63
3A*	PDBH ≤ 30.4	20	I	0.75	0.25
3B*	PDBH > 30.4	45	U	0.20	0.80

^aAn asterisk indicates a terminal node. No asterisk indicates intermediate node. Node numbers correspond to nodes in Fig. 2.

^bPMG, ponderosa pine mean matched growth (mm); PDBH, ponderosa pine mean DBH (cm).

^cI, infested; U, uninfested.

The model for the Douglas-fir habitat type series indicates that a PMG of less than 8.3 mm results in a higher probability of infestation (Table 5, Fig. 3). This was the simplest probability of infestation model built.

The model developed for the white fir habitat type indicates that a higher average ponderosa pine phloem thickness (PPHLT) results in a higher probability of infestation (Table 6, Fig. 4). In the next split, PCPP once again becomes a splitting variable with a higher percent of basal area represented by ponderosa pine, resulting in a high probability of infestation. The last split is made on PMG with reduced growth during the last 5 years prior to infestation, resulting in a higher probability of infestation. Amman (1972) indicated that increased phloem thickness is an important factor contributing to increased brood production by mountain pine beetle in lodgepole pine. Perhaps a similar relationship occurs in the roundheaded pine beetle – ponderosa pine interaction. It should be noted that phloem thickness data were collected only from live ponderosa pines in the points. Still, the variable exhibited strong discriminatory power at the point level.

The ponderosa pine and Douglas-fir habitat types models and the white fir habitat type model were simpler than the comprehensive model in terms of number of nodes and number of predictor variables (Table 2). Although sample sizes used to develop the habitat type-specific models were small, classification trees with good cross-validation estimates were built. The ponderosa pine habitat types model has the higher cross-validation of

Fig. 3. Classification tree for estimating probability of infestation by the roundheaded pine beetle in *Pseudotsuga menziesii* habitat types sampled. Abbreviations are as follows: PMG, ponderosa pine mean matched growth (mm); POI, probability of infestation. Lincoln National Forest, N. Mex., 1994–1995.

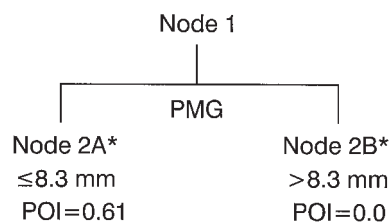


Table 5. Node, splitting criteria, number of cases, class membership, and class proportion for the probability of infestation model built for the Douglas-fir habitat types sampled, Lincoln National Forest, N. Mex., 1994–1995.

Node ^a	Split ^b	N	Class ^c	Class proportion	
				Infested	Uninfested
1	—	70	—	0.50	0.50
2A*	PMG ≤ 8.3	57	I	0.61	0.39
2B*	PMG > 8.3	13	U	0.0	1.00

^aAn asterisk indicates a terminal node. No asterisk indicates intermediate node. Node numbers correspond to nodes in Fig. 3.

^bPMG, ponderosa pine mean matched growth (mm).

^cI, infested; U, uninfested.

classification accuracy, the lowest misclassification cost for the uninfested condition, and the lowest overall misclassification cost. Therefore, its use would provide increased reliability over the comprehensive model in ponderosa pine habitat types. For the Douglas-fir types, the cross-validation accuracy of classification was lower than in the comprehensive model. The Douglas-fir habitat types model had the highest overall cost of misclassification. This was a function of a high cost of misclassification of the uninfested condition. Therefore, use of the Douglas-fir habitat types model would be justifiable if there is an interest in minimizing the cost of misclassification of the infested condition. The white fir habitat type model compares well in terms of cross-validation accuracy and misclassification costs with the ponderosa pine habitat types model. Its use in white fir habitat types should provide increased reliability over the comprehensive model.

Point and tree characteristics

Of all variables examined only PDBH, average ponderosa pine growth over the last 5 years (PLFYG), and total basal area (TOTBA) were normally distributed. Wilcoxon tests results for all habitat types combined indicated significant differences in PDBH, average ponderosa pine growth over the last 5 years (PLFYG), average ponderosa pine growth over the second to last 5 years (PPFYG), average ponderosa pine growth over the last 10 years (PTENYRG), PMG, ponderosa pine quadratic mean diameter (PQMD), PPBA, and trees per hectare (TPH). Significant differences were detected for PDBH, PLFYG, PPFYG, PTENYRG, PMG, PQMD, and TPH for the ponderosa pine habitat type series; PLFYG, PPFYG, PTENYRG, PMG, and average ponderosa pine periodic growth rate

Fig. 4. Classification tree for estimating probability of infestation by the roundheaded pine beetle in the *Abies concolor* – *Quercus gambelii* habitat type. Abbreviations are as follows: PPHLT, live ponderosa pine mean phloem thickness (mm); PCPP, percent basal area in ponderosa pine; PMG, ponderosa pine mean matched growth (mm). Lincoln National Forest, N. Mex., 1994–1995.

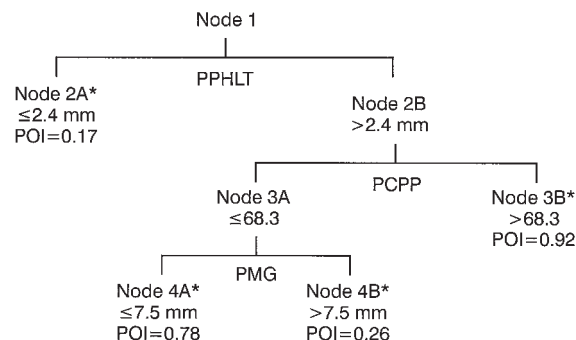


Table 6. Node, splitting criteria, number of cases, class membership, and class proportion for the probability of infestation model built for the *Abies concolor* – *Quercus gambelii* habitat type, Lincoln National Forest, N. Mex., 1994–1995.

Node ^a	Split ^b	N	Class ^c	Class proportion	
				Infested	Uninfested
1	—	46	—	0.54	0.46
2A*	PPHLT ≤ 2.4	14	U	0.17	0.83
2B	PPHLT > 2.4	32	I	0.64	0.36
3A	PCPP ≤ 68.3	21	U	0.45	0.53
3B*	PCPP > 68.3	11	I	0.92	0.08
4A*	PMG ≤ 7.5	8	I	0.78	0.22
4B*	PMG > 7.5	13	U	0.26	0.74

^aAn asterisk indicates a terminal node. No asterisk indicates intermediate node. Node numbers correspond to nodes in Fig. 4.

^bPPHLT, live ponderosa pine mean phloem thickness (mm); PCPP, percent basal area in ponderosa pine; PMG, ponderosa pine mean matched growth (mm).

^cI, infested; U, uninfested.

(PPGR) for the Douglas-fir habitat type series; and PPHLT, PPBA, PCPP, and SI (site index) for the white fir habitat types (Table 7).

Many of the variables that exhibit differences between the infested and uninfested points for all habitat types combined, the ponderosa pine and Douglas-fir habitat types, and the white fir habitat type were identified by the tree classification approach as splitting variables. For example, PMG was a splitting variable in all tree classification models, and significant differences between the infested and uninfested points were detected for all habitat types combined, the ponderosa pine habitat type series, and the Douglas-fir habitat type series. In the comprehensive model and in the ponderosa pine habitat type series model, PDBH was a splitting variable and significant differences were detected between infested and uninfested points for all points combined and for ponderosa pine habitat type series. In the comprehensive model and in the white fir habitat type model, PCPP was a splitting variable; however, it was only significantly different between the infested and the uninfested points for the white fir habitat type.

Table 7. Mean ($\pm$ SEM) for variables measured for all points combined (All), ponderosa pine (Pp) and Douglas-fir (Df) habitat types, and white fir (Wf) habitat type points, infested (-I) and uninfested (-U) points, Lincoln National Forest, N. Mex., 1994–1995.^a

Habitat type	N	PDBH	PTOTHT	PLFYG	PPFYG	PTENYRG	PMG	PPGR	PPHLT	PQMD	TOTBA	PPBA	PCPP	TPH	SI	SDI
All	200	34(0.5)	58.2(0.9)	6.9(0.2)	8.5(0.2)	15.4(0.4)	8.2(0.2)	0.85(0.01)	2.7(0.1)	35.1(0.6)	28.8(0.7)	17.7(0.7)	64.7(2.1)	465(17.7)	100(1.6)	218(5.5)
All-I	98	32.9(0.8)	56.7(1.3)	6.4(0.2)	7.8(0.3)	14.2(0.5)	7.3(0.2)	0.85(0.01)	2.7(0.1)	34(0.8)	29.6(1.0)	19.8(1.1)	68.4(2.8)	485(24.6)	101(2.5)	225(8.1)
All-U	102	35(0.8)	59.7(1.3)	7.4(0.2)	9.1(0.3)	16.5(0.6)	9.1(0.3)	0.84(0.01)	2.7(0.1)	36.1(0.8)	28(0.9)	15.8(0.9)	61.2(3.2)	428(25.1)	100(2.1)	210(7.4)
Z		2.2	1.6	3.3	2.9	3.2	4.2	0.5	0.6	2.1	0.8	2.7	1.5	2.1	0.3	1.3
p > Z		0.0249	0.0956	0.0009	0.0028	0.0014	0.0001	0.6285	0.5481	0.0323	0.4133	0.0068	0.1382	0.0300	0.7984	0.1865
Pp	84	34.1(0.8)	57.8(1.3)	7.8(0.3)	9.8(0.3)	17.7(0.6)	9.5(0.3)	0.82(0.01)	2.7(0.1)	35(0.7)	28.6(0.9)	23.1(1.2)	80.1(2.9)	418(22)	101(2.4)	213(7)
Pp-I	42	31.9(1.0)	55.3(1.9)	7(0.3)	8.9(0.4)	15.9(0.7)	8.3(0.4)	0.82(0.01)	2.6(0.1)	32.8(1.0)	29.8(1.5)	25(1.9)	81.7(3.8)	485(36)	101(3.2)	227(12)
Pp-U	42	36.4(1.0)	60.3(1.8)	8.7(0.4)	10.8(0.5)	19.4(0.8)	10.7(0.5)	0.83(0.02)	2.8(0.1)	37.3(1.0)	27.4(1.0)	21.3(1.4)	78.6(4.3)	352(21)	101(3.5)	199(7)
Z		3.1	1.9	3.4	2.8	3.2	3.5	0.5	1.1	3.1	0.9	1.3	0.2	2.5	0.4	1.6
p > Z		0.0018	0.0561	0.0007	0.0049	0.0015	0.0004	0.6227	0.2579	0.0016	0.3602	0.1893	0.8296	0.0134	0.6709	0.1143
Df	70	32.1(1.0)	53.7(1.6)	5.8(0.2)	7(0.3)	12.8(0.4)	6.8(0.3)	0.85(0.01)	2.6(0.1)	33.3(8.7)	26.4(10.7)	13.7(5.5)	58.4(25.6)	467(297)	93(20)	204(88)
Df-I	35	32(1.5)	53.1(2.4)	5.3(0.2)	6.2(0.2)	11.5(0.4)	5.9(0.2)	0.88(0.02)	2.6(0.1)	33.2(9)	27.3(10.1)	14.8(5.7)	58.8(24)	493(279)	89(19)	213(84)
Df-U	35	32.2(1.3)	54.3(2.3)	6.3(0.3)	7.8(0.4)	14.1(0.7)	7.8(0.4)	0.83(0.02)	2.6(0.1)	33.4(8.4)	25.5(11.3)	12.7(5.3)	58(28)	441(315)	96(21)	196(93)
Z		0.2	0.4	2.1	2.9	2.6	3.7	2.1	0.4	0.2	0.9	1.8	0.05	1.5	1.6	1.1
p > Z		0.8509	0.6983	0.0398	0.0031	0.0094	0.0002	0.0376	0.7116	0.9188	0.3553	0.0745	0.9578	0.1327	0.1128	0.2595
WF	46	36.7(1.1)	65.8(1.6)	6.9(0.3)	8.3(0.5)	15.2(0.7)	7.9(0.4)	0.89(0.03)	2.9(0.1)	38(1.2)	32.6(1.4)	13.9(1.3)	46.3(4.4)	508(36)	113(3.5)	246(11)
Wf-I	21	36.4(1.3)	65.3(1.9)	6.9(0.3)	8.4(0.6)	15.3(0.9)	7.7(0.5)	0.87(0.03)	3.2(0.1)	38(1.5)	32.8(2.4)	17.9(2.0)	57.7(6.4)	472(45)	124(5.3)	245(18)
Wf-U	25	36.9(1.7)	66.3(2.4)	7(0.5)	8.1(0.7)	15.2(1.2)	8.1(0.7)	0.9(0.04)	2.7(0.2)	38(1.8)	32.5(1.8)	10.7(1.5)	36.6(5.4)	539(55)	105(3.9)	248(15)
Z		0.5	0.2	0.06	0.6	0.4	0.08	0.6	2.2	0.4	0.4	2.8	2.6	0.8	2.6	0.3
p > Z		0.5966	0.8513	0.9472	0.5216	0.6669	0.9295	0.5224	0.0261	0.6995	0.7143	0.0048	0.0101	0.4273	0.0087	0.7575

^aPDBH, ponderosa pine mean DBH (cm); PTOTHT, ponderosa pine mean total height (m); PLFYG, ponderosa pine mean growth during last 5-year period (mm); PPFYG, ponderosa pine mean growth during second to last 5-year period (mm); PTENYRG, ponderosa pine mean growth rate in last 10 years (mm); PMG, ponderosa pine mean matched growth (mm); PPGR, ponderosa pine mean periodic growth rate; PPHLT, live ponderosa pine mean phloem thickness (mm); PQMD, ponderosa pine quadratic mean diameter (cm); TOTBA, total basal area (m²/ha); PPBA, ponderosa pine basal area (m²/ha); PCPP, percent basal area in ponderosa pine; TPH, trees per hectare; SI, site index; SDI, stand density index.

Table 8. Means ($\pm$ SEM) for roundheaded pine beetle-killed, infested, and live ponderosa pines within infested points, Lincoln National Forest, N. Mex., 1994–1995.^a

Tree status	N	PDBH	PTOTHT	PLFYG	PPFYG	PPGR	PTENYRG	PMG
RPB-killed	311	29.3(0.6)	50.3(1.1)	5.6(0.1)	6.6(0.1)	0.88(0.01)	12.2(0.2)	5.6(0.1)
Infested	43	32.5(1.9)	56.2(2.8)	7.1(0.4)	8.8(0.4)	0.82(0.03)	15.9(0.8)	8.8(0.5)
Live	357	34.8(0.6)	60.1(0.9)	7.5(0.2)	9.6(0.2)	0.81(0.01)	17.1(0.3)	9.6(0.2)

^aPDBH, ponderosa pine mean DBH (cm); PTOTHT, ponderosa pine mean total height (m); PLFYG, ponderosa pine mean growth during last 5-year period (mm); PPFYG, ponderosa pine mean growth during second to last 5-year period (mm); PPGR, ponderosa pine mean periodic growth rate; PTENYRG, ponderosa pine mean growth rate in last 10 years (mm); PMG, ponderosa pine mean matched growth (mm).

Table 9. Number of roundheaded pine beetle-killed, infested, and live ponderosa pines by crown position, expected numbers, deviation, and cell χ^2 in points infested by the roundheaded pine beetle, Lincoln National Forest, N. Mex., 1994–1995.^a

Tree status	Value	Co-dominant	Crown position		Totals
			Intermediate	Suppressed	
RPB-killed	Frequency	71	136	104	311
	Expected	103.6	103.6	103.6	
	Deviation	-32.6	32.4	0.4	
	Cell χ^2	10.26	10.13	0.0015	
Infested	Frequency	19	19	5	43
	Expected	14.3	14.3	14.3	
	Deviation	4.7	4.7	-9.3	
	Cell χ^2	1.54	1.55	6.05	
Live	Frequency	166	139	52	357
	Expected	119	119	119	
	Deviation	47	20	-67	
	Cell χ^2	18.56	3.36	37.7	
Totals		256	294	161	711

^aOverall $\chi^2 = 89.15$, $p > 0.001$.

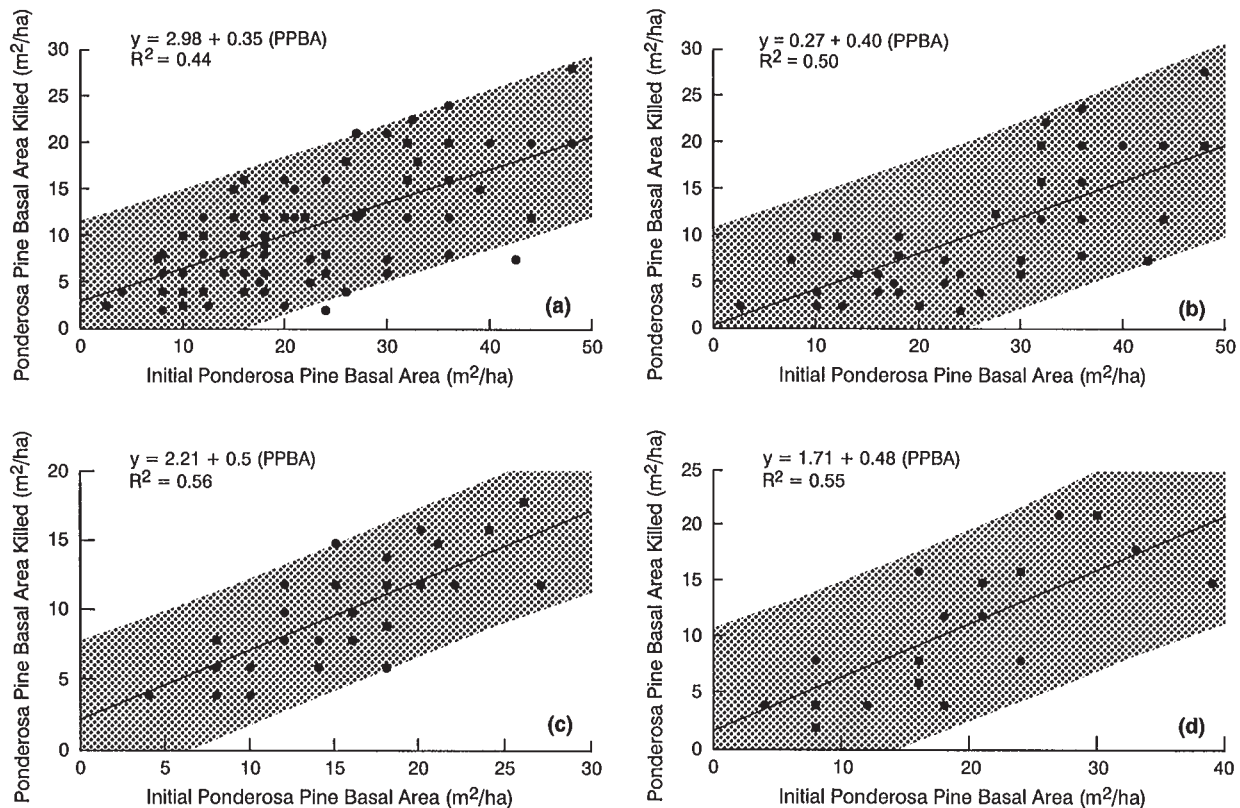
Also in the comprehensive model, PPBA was a splitting variable and there were significant differences between the infested and uninfested points for the combined habitat types, and also in the white fir habitat type. In the white fir model, PPHLT was a splitting variable and there was a statistical difference detected between the infested and the uninfested condition. Both analyses suggest that the roundheaded pine beetle is infesting areas where tree growth is poor; PDBH is less than in uninfested points; and host type is plentiful in terms of percent of basal area represented.

Table 8 presents PDBH, average ponderosa pine total height (PTOTHT), PLFYG, PPFYG, PPGR, PTENYRG, and PMG for trees killed by roundheaded pine beetle, infested trees, and live trees within the infested points. Live trees were larger in diameter, taller, and had increased growth rates when compared with infested trees and those killed by roundheaded pine beetle. For all variables, infested trees had intermediate measurements, and dead trees were the smallest in diameter and height, and had reduced growth rates. Dead trees had slightly higher PGR than infested and live trees, but this difference may not have biological significance. Orthogonal comparisons between live and dead trees indicated significant differences for PDBH ($F = 43.03$, $P > 0.0001$), PTOTHT ($F = 51.2$, $P > 0.0001$), PLFYG ($F = 88.5$, $P > 0.0001$), PPFYG ($F = 140.9$, $P > 0.0001$), PPGR ($F = 19.1$, $P > 0.0001$), PTENYRG ($F = 129.3$, $P > 0.0001$), and PMG ($F = 263.2$, $P > 0.0001$), and significant differences between the mean of infested and killed trees when compared with live trees for PDBH ($F = 13.9$, $P > 0.0002$), PTOTHT ($F =$

16.1, $P > 0.0001$), PLFYG ($F = 20.8$, $P > 0.0001$), PPFYG ($F = 36.9$, $P > 0.0001$), PPGR ($F = 4.1$, $P > 0.04$), PTENYRG ($F = 32.6$, $P > 0.0001$), and PMG ($F = 111.8$, $P > 0.0001$). When these differences between live, dead, and infested trees within the infested points are examined, it again suggests that the roundheaded pine beetle attacked trees with significantly smaller DBH, poor growth rate, and somewhat reduced height compared with the live trees. Therefore the trend towards selecting poor growing trees and smaller diameter trees holds true at the point level and at the individual tree level.

Cross tabulation and χ^2 analysis of crown position of live, killed, and infested trees within all infested points were conducted with the assumption that trees in all crown positions are equally likely to be attacked by the roundheaded pine beetle. Results indicated that a higher than expected number of the trees killed by the roundheaded pine beetle were in the intermediate position with fewer than expected in the co-dominant position. These cells had important contribution to the overall χ^2 (Table 9). For live trees, more were classified as co-dominants than expected. Overall χ^2 was significant ($\chi^2 = 89.15$, $P > 0.001$). These data agree with data presented by Chansler (1967), also from the Sacramento Mountains, in which the majority of attacks, both successful and unsuccessful, were on intermediate trees. Stevens and Flake (1974), however, indicated that most of the trees attacked in the 1970s outbreak were co-dominants but also suggested that larger trees can be attacked during an outbreak. It is possible that crown position interpretations varied somewhat among the different field crews in the different

Fig. 5. Relationship between initial basal area of ponderosa pine and basal area killed by roundheaded pine beetle. Shading represents 95% confidence intervals for individual observation prediction. (a) Across all habitat types (28 hidden observations). (b) *Pinus ponderosa* habitat types (4 hidden observations). (c) *Pseudotsuga menziesii* habitat types (9 hidden observations). (d) The *Abies concolor* – *Quercus gambelii* habitat type (3 hidden observations). Lincoln National Forest, N. Mex., 1994–1995.



studies. Data from this study suggest that the roundheaded pine beetle seems to prefer trees in the intermediate crown position, and attacks suppressed and to a lesser extent co-dominant trees.

Extent of damage

Simple linear equations using PPBA as a predictor variable resulted in positive correlations with amount of basal area affected, with R^2 values ranging from 0.44 to 0.56 (Table 10, Fig. 5). Positive slopes indicate that increases ranging from 0.35 to 0.5 m^2/ha of PPBA result in mortality increases of a unit of ponderosa pine m^2/ha . Use of these models will allow estimation of potential mortality of ponderosa pine with initial ponderosa pine basal area with a precision of about 5–10 m^2/ha of basal area.

This finding is consistent with other studies. McCambridge et al. (1982) showed a correlation between original basal area of ponderosa pine with number of pines killed by the mountain pine beetle in north central Colorado. Reynolds and Holsten (1994, 1996) indicated that total stand basal area, percent of total basal area composed of spruce, and percent of spruce basal area composed of trees larger than 25 cm were related to spruce basal area killed by spruce beetle in Alaska.

Prior studies have indicated the relationship between poor growth and bark beetle attacks. Sartwell (1971) and Sartwell and Stevens (1975) indicated that slow growth was characteristic of nearly all ponderosa pines killed by mountain pine beetle measured in the Northwest. Shrimpton and Thompson

Table 10. Y-intercept, slope, coefficient of determination, root mean square error, and significance level for loss prediction linear regression equations, $y = b_0 + b_1x$, where y is ponderosa pine mortality in terms of m^2/ha of basal area and x is initial ponderosa pine basal area in terms of m^2/ha , Lincoln National Forest, N. Mex., 1994–1995.

Habitat type ^a	y-intercept (b_0)	Slope (b_1)	R^2	Root MSE	p
Comp	2.98	0.35	0.44	4.2	0.0001
Pp	0.27	0.40	0.50	4.9	0.0001
Df	2.21	0.50	0.56	2.5	0.0001
Wf	1.71	0.48	0.55	3.9	0.0001

^aComp, comprehensive; Pp, ponderosa pine; Df, Douglas-fir; Wf, white fir.

(1983) reported that the beginning of outbreaks of mountain pine beetle were coincidental with periods of reduced tree growth in lodgepole pine in British Columbia. In this study, sampling was specifically conducted at sites that were affected by the roundheaded pine beetle in the early stages of the outbreak. Mitchell et al. (1983) measured lodgepole vigor using the amount of stem growth per square metre of crown leaf area in thinned and unthinned stands and indicated that thinning from below improved the vigor of the residual stand and reduced mountain pine beetle attack. Preference for slower growing trees has also been shown by spruce beetle in white spruce by Watson (1928), Hard et al. (1983), and Hard (1985).

Sutherland (1983, 1989) suggested that increases in tree densities in the southwest can result in reductions in tree growth. It is likely that the strong influence that growth rate seems to be having in determining probabilities of infestation by the roundheaded pine beetle is a reflection of the increase in basal areas and tree densities that are evident in the Southwest as a result of fire suppression since the turn of the century, as suggested by Covington and Moore (1994) and Johnson (1994). Both studies suggested that decades of aggressive fire control have resulted in overstocked, stagnant stands in the southwest. There has been a marked increase in the area of mixed conifer forests, especially white fir, and a corresponding decrease in early successional species such as ponderosa pine and aspen. Current stands have also increased in density, growing stock, and number of trees in the larger diameter classes. These stand conditions are likely to be more prone to insect and disease outbreaks. This may be the reason why the last two roundheaded pine beetle outbreaks have been more destructive than previous outbreaks (Wilson and Tkacz 1996).

Average dwarf mistletoe rating of live ponderosa pine in infested points (1.4 ± 0.16 , mean $\pm$ SE) was slightly higher than in uninfested points (0.7 ± 0.2). The rating system used is designed to rate live trees. No attempt was made to detect statistical differences in mistletoe infection rates. Determining ratings for trees killed by roundheaded pine beetle would have been difficult, particularly since sampling was conducted 3–4 years after tree mortality. Therefore, from these data, it can only be stated that dwarf mistletoe was present in the study area. Hawksworth (1961) showed reductions in growth rates in dominant ponderosa pines in New Mexico with various levels of mistletoe infection. However, reductions were significant only in trees in infection classes 4, 5, and 6. Stevens and Flake (1974) indicated that mistletoe infection was common in stands infested with roundheaded pine beetle. It is possible that reductions in growth due to mistletoe infestations may be another contributing factor that may be operating on its own or synergistically with high tree densities, leading to reduced growth conditions and increased roundheaded pine beetle infestations.

During the current outbreak at the Sacramento Mountains, mortality of ponderosa pine is widespread and most stands that contain ponderosa pine have some mortality. Ponderosa pine mortality may be tolerable and even beneficial in some stands and not in others depending on land manager objectives. Most of the trees being killed are in the intermediate and suppressed crown classes. Such mortality may result in growth releases for the residual trees in the stand. The resulting increases in growth rates and reductions in host type basal area should lower the probability of infestation in the stands and also reduce the amount of mortality likely to occur if an infestation does develop. In stands where losses to roundheaded pine beetle are not tolerable, this study suggests that active forest management, perhaps through silvicultural thinnings that reduce stand density and increase growth rates and vigor in residual trees, would also result in lower probabilities of infestations and reduced damage potential.

Sustainability of ponderosa pine in outbreak areas in the Sacramento Mountains could be affected. This is particularly true in mixed conifer stands where shade-tolerant species growing in the understory such as Douglas-fir or white fir may be released and become the dominant species, thereby exclud-

ing ponderosa pine. In addition, tree mortality caused by the roundheaded pine beetle will result in increased fuel loads and higher fire hazard in outbreak areas. In the future excessive mortality, however, may be preventable by maintaining vigorously growing stands that may be less suitable to the development of large roundheaded pine beetle epidemics. Probability of infestation models developed in this study are tools that silviculturists can use to identify stands where conditions are suitable for the buildup of outbreaks. Extent of damage models are tools that can be used to predict the amount of ponderosa pine mortality likely to occur in a stand where roundheaded pine beetle is active. These tools will assist in the management of stands where losses to roundheaded pine beetle may be unacceptable or where the resulting stand conditions caused by roundheaded pine beetle activity may be undesirable.

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