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Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range

Jose F. Negron *

USDA Forest Service, Rocky Mountain Research Station, 240 W. Prospect, Ft Collins, CO 80526, USA

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Abstract

Infested and uninfested areas within Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, stands affected by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. were sampled in the Colorado Front Range, CO. Classification tree models were built to predict probabilities of infestation. Regression trees and linear regression analysis were used to model amount of tree mortality in terms of basal area killed in infested stands. Classification trees had cross-validation estimates of classification accuracy ranging from 0.55 to 0.63. The data suggests that Douglas-fir beetle-attacked stands contain a high percentage of the basal area represented by Douglas-fir, high tree densities, and poor growth during the last 5 years prior to attack. Trees prone to attack by the Douglas-fir beetle within infested points also exhibited reduced growth rates. Tree and linear regression analysis indicate that initial amount of Douglas-fir basal area can be used as a predictor variable for the amount of basal area affected. © 1998 Elsevier Science B.V.

Keywords: *Dendroctonus pseudotsugae*; Bark beetles; Scolytidae; Risk; Hazard

1. Introduction

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk., occurs throughout much of the range of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in the western United States and is the most important bark beetle affecting its host (Furniss and Carolin, 1977). Endemic populations are usually restricted to injured or felled trees (McMullen and Atkins, 1962; Furniss, 1965; Rudinsky, 1966; Wright et al., 1984) but periodic epidemic populations are able to kill apparently healthy trees in large numbers (Furniss et al., 1979; Johnson and Belluschi, 1969).

Numerous studies have been conducted in the Pacific Northwest relating biological and ecological aspects of this insect. Furniss (1979) compiled much of the earlier literature including information relating to host susceptibility. (Furniss et al., 1979, 1981) proposed that host type proportion, tree density, and age were key factors in Douglas-fir stand susceptibility to Douglas-fir beetle, with most trees attacked being over 120 years of age. Furniss et al. (1981) also indicated that vegetational species diversity in the stand also affected stand susceptibility and spread of infestations. Various disturbance agents such as root disease (Wright and Lauterbach, 1958), defoliation (Berryman and Wright, 1978; Wright et al., 1984), windthrow (Rudinsky, 1966), snow breakage (McGregor et al., 1974), fire (Furniss, 1965), and

* Corresponding author. Tel.: +1-970-498-1252; fax: +1-970-498-1010; e-mail: jnegron@lamar.colostate.edu.

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logging (Lejeune et al., 1961; McGregor et al., 1974) have also been implicated in increasing the susceptibility to attack by Douglas-fir beetle. Furniss et al. (1981) explained how some of these factors may affect susceptibility of host trees. Weatherby and Thier (1993) presented a system developed on the basis of published biological relationships for rating stands for susceptibility to losses to Douglas-fir beetle. The system uses stand basal area, proportion of stand basal area in Douglas-fir, average stand age, and average diameter at breast height (dbh) of all Douglas-firs larger than 22.9 cm.

Information is generally lacking on the habits and ecological relationships of the Douglas-fir beetle in Colorado. Hadley and Veblen (1993) studied responses in stands affected by western spruce budworm, *Choristoneura occidentalis* Freeman, and Douglas-fir beetle in the Colorado Front Range and suggested that stand response is a function of stand structure and age prior to the insect outbreaks. Schmid and Mata (1996) indicate that past Douglas-fir beetle epidemics in Colorado and Wyoming have been triggered by western spruce budworm epidemics. Douglas-fir beetle-infested trees in northern Colorado exhibited a decline in growth prior to Douglas-fir beetle attack, which was apparently caused by a western spruce budworm outbreak preceding the Douglas-fir beetle activity (Lessard and Schmid, 1990). Since western spruce budworm outbreaks are becoming more widespread and more intense in the Southern Rocky Mountains due to anthropogenic induced changes (Swetnam and Lynch, 1989, 1993), Douglas-fir beetle outbreaks are also more likely to become more significant in the Southern Rockies.

Studies from the northwestern United States suggest that approaches to managing forest stands to reduce losses to Douglas-fir beetle include thinning (Williamson and Price, 1971) and sanitation logging (Furniss and Orr, 1978; Lejeune et al., 1961; Furniss et al., 1979). Recently, there has been renewed interest in the development of semiochemical-based management strategies for Douglas-fir beetle (Ross and Daterman, 1994, 1995a,b, 1997; Ross and Niwa, 1997).

Although data have been collected to develop a better understanding of site and stand factors that are conducive to Douglas-fir beetle activity (Furniss et al., 1981; Weatherby and Thier, 1993), no attempts have been made to develop empirically-based models which quantify these relationships and provide predictive ability. The purpose of this study was to quantify stand and tree characteristics associated with Douglas-fir beetle infestations and to develop models to predict the probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range.

The use of models that predict infestation probabilities or extent of mortality provide managers with tools to assist in proactive land management, particularly where reducing resource impact from epidemic insect populations is needed. These models can be particularly valuable for identifying stands or forest conditions which may be particularly susceptible to Douglas-fir beetle infestation, or where conditions for sustained mortality exist, or both. Stands identified as susceptible may benefit from management activities, such as silvicultural management or perhaps the use of semiochemical-based strategies, if compatible with management objectives.

2. Methods

2.1. Study location

The study area was located in the Salida Ranger District of the Pikes-San Isabel National Forest, just east from the town of Salida and north to Trout Creek Pass. Douglas-fir beetle populations had been active in the district since the early 1990s. Western spruce budworm had been active in the area prior to Douglas-fir beetle activity. District personnel and Forest Health specialists had information on the extent of the area affected by the Douglas-fir beetle. To better define Douglas-fir beetle activity in the project area, Forest Health specialists conducted an aerial survey in May 1994. The resulting map was used as a guide for this study. Of particular interest where those areas affected early in the outbreak. They are more likely to represent conditions which support the development of epidemics and thus were selected for sampling.

2.2. Sampling

Sampling was conducted from 1994 to 1996. Stands which contained infested and uninfested host type were sampled. A network of variable radius plots was established in each stand. Infested points were established at random in areas of mortality in the stand. Uninfested points were established at random in unaffected areas of the stand. No points were established within 61 m of another point. This methodology resulted in infested and uninfested points being intermingled. This layout assumes that the likelihood of sampling uninfested points which may have been exposed to Douglas-fir beetle but not attacked during the outbreak is greater than if infested and uninfested points are established on separate isolated stands. This scenario is more likely to represent a true low probability of infestation condition in uninfested points than uninfested host type in isolation with no beetle pressure. Because Douglas-fir beetle rarely attacks trees ≤ 15.2 cm in dbh, infested points included at least one Douglas-fir beetle-killed tree ≥ 15.2 cm in dbh and uninfested points included no trees attacked or killed by Douglas-fir beetle and included at least one Douglas-fir ≥ 15.2 cm in dbh.

Studies in the Pacific Northwest indicate that the Douglas-fir beetle prefers larger diameter trees for attack (Furniss et al., 1979). This concept was used to determine an adequate sampling intensity. From the first series of points established in the first stand, dbh data was used for sample size estimation. Power calculations were made using a 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 an 80% power, alpha = 0.1, for a stand of ca. 68 ha was 12. Therefore, in most of the stands sampled, a total of 12 variable radius plots were established. Due to variability in stand size and availability of infested host type, there was some variation in the number of points per stand. A balanced design, however, was maintained by establishing an equal number of infested and uninfested points in every stand. A total of 200 points (100 infested and 100 uninfested) distributed among 17 stands was established in 1994 and 1995.

Sampled stands ranged in elevation from 2650 to 2865 m. Using the descriptions presented by Johnston (1987), 11 different plant associations were identified in the established points, however, the majority of the points (60%) were in the *P. menziesii / Arctostaphylos adenotricha–Juniperus communis*, *P. menziesii / Juniperus communis*, and *Pinus ponderosa–P. menziesii / Muhlenbergia montana* plant associations. Plant associations were generally uniform within stands. As a result, plant associations were not distributed evenly across the study area but were clustered and their inclusion in the analysis would have been biased. Therefore, plant association was not tested as a discriminatory variable.

Another aerial survey of the study area conducted in June 1996 detected very little new mortality. Additionally, infested points established in 1994 were re-surveyed in 1995 to determine if additional mortality was occurring and none was detected. This suggests that the outbreak had subsided by the time sampling was conducted.

2.3. Data collected

Data collected for all trees in the points included species, condition (live, Douglas-fir beetle-killed or infested, or other dead), dbh, total height, crown position, phloem thickness of live conifers, last 5 years', second-to-last 5 years', and last 10 years' radial growth of conifers obtained from cores extracted at dbh from the south side of the trees. Periodic growth ratio, which is a ratio of the current 5-year growth radial increment divided by the previous adjacent 5-year growth radial increment (Mahoney, 1978), was also calculated for Douglas-fir.

Data collected was used to generate metrics of basal area, percent host type, stand density index (Avery and Burkhart, 1994), and trees per hectare (of trees ≥ 12.7 cm in dbh). Site index was determined from tree age and heights of two healthy dominant or co-dominant trees in the vicinity of the point using equations developed by Edminster et al. (1991).

2.4. Douglas-fir beetle population trend

Tree mortality data were collected in August, 1996 to compare Douglas-fir beetle population trends between infested and uninfested points during the course of the outbreak. Data was collected from 21 infested and 21 uninfested points in three of the stands where points had been previously established. Twelve trees ≥ 15.2 cm in dbh were randomly selected in each cardinal location from each point center and classified as (1) live; (2) Douglas-fir beetle infested/killed in 1996, 1995, 1994, 1993, 1992, 1991 or older; or (3) dead to other causes. The classification used was developed after intensive inspection of numerous Douglas-fir beetle-attacked trees in the study area. The categories used were as follows: live, green tree with no symptoms of Douglas-fir beetle attack; 1996 attack, green tree under attack, resin flow and fresh boring dust evident; 1995 attack, fader, foliage orange but some green may still be present, bark still hard and tight, galleries evident, exit holes present; 1994 attack, most foliage (if not all) missing, remaining foliage (if any) is orange, galleries still identifiable, small twigs present, secondary wood borers may be present but not abundant, exit holes present; 1993 attack, all foliage gone but small twigs still present, bark loose and galleries hard to find, lots of secondary wood borer burrowing, exit holes present; 1992 attack, smaller twigs gone, exit holes present; 1991 or older, larger branches beginning to break off, exit holes present. Cross-tabulation and a likelihood-ratio Chi-square test were conducted to detect associations between infested and uninfested points and attacked tree categories in all three stands combined (SPSS, 1997).

2.5. Data analysis

2.5.1. Probability of infestation

Most of the trees killed during this outbreak were attacked in 1992 and died in 1993. Therefore, measurements of the last 5 years' growth for Douglas-fir beetle-killed trees in infested points measured in 1995 correspond mostly to the time frame 1987–1991; the second-to-last 5 years' correspond best to the time frame 1982–1986. For live trees in infested points, the last 5 years' growth measurements correspond to the time frame 1990–1994 and the second-to- last 5 years' growth correspond to the time frame 1985 and 1989. For uninfested points, Douglas-fir last 5 years' growth measurements correspond to the 1990–1994 time frame, and Douglas-fir second-to-last 5 years' growth rate correspond to the 1985–1989 time frame. In order to represent similar growth periods, a variable called 'Douglas-fir matched growth' (DFMG) was created. The value for this variable for infested points is calculated as the average growth rate for Douglas-fir beetle-killed trees during the last 5 years and second-to-last 5 years' growth rate for live Douglas-firs. For uninfested points, the second-to-last 5 years' growth rates for live Douglas-firs in the point are averaged. Few newly infested trees were detected in the infested points, probably because the epidemic had subsided by the time sampling was conducted, and thus were excluded when this variable was created. Some wood shrinkage may also have occurred in the Douglas-fir beetle-killed trees but it was not considered to be an important factor because only 2–3 years separated tree mortality and growth rate estimation and the study area was rather mesic. Although this variable may not be a year-to-year match in all cases because not all mortality sampled occurred in the same year, it more closely approximates similar time periods where growth was measured. The variable then represents growth rate for the last 5 years prior to Douglas-fir beetle attack in infested points and about the same years for uninfested 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). A binary tree is produced with splits made by predictor variables. Potential classification trees are cross-validated during the model construction phase by dividing the data set in 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. Misclassification costs for the different class memberships are also calculated and provide another measure of model performance. Other variables which could also serve

Table 1
Number of Douglas-fir beetle attacked trees by year in infested and uninfested points, expected numbers, and adjusted residuals, Pikes-San Isabel National Forest, CO, 1996[ab]

Plot Status	Value	1991 or older	1992	1993	1994	1995	1996	Total
Infested	Frequency	2	31	217	37	17	33	339
	Expected	3.8	31.7	202.5	45.3	19.6	34	
	Adj. Res.	−1.9	−0.3	3.3	−2.7	−1.2	−0.4	
Uninfested	Frequency	3	11	51	23	9	12	109
	Expected	1.2	10.3	65.5	14.7	6.4	11	
	Adj. Res.	1.9	0.3	−3.3	2.7	1.2	0.4	
Totals		5	42	268	60	26	45	

[a]Set of Chi-square tables	*df*	χ^2	$P < \chi^2$
All years	5	14.539	0.013
Excluding 1993 data	4	4.057	0.398
All data except 1993 vs. 1993	1	10.482	0.001

[b]Live, unattacked trees in the vicinity of infested points = 510; live, unattacked trees in the vicinity of uninfested points = 849.

as splitting variables in the absence of the selected variable and are termed competitor variables are identified in the analysis. During the model construction phase, variables can be removed or reentered in the model. This process allows identification of variables that may be masking other variables and the development of alternate models. Tree classification approaches have been used 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* Kirky, in terms of basal area killed in Alaska.

2.5.2. Differences between infested and uninfested points

Splitting and predictor variables used in classification trees do not represent average conditions in the class groups. Therefore, descriptive statistics of the measured variables were generated to describe the conditions associated with the study area, the infested, and the uninfested conditions. Variables measured were tested for normality using the Shapiro–Wilk test. Since most variables were not normally distributed, Wilcoxon Signed-Rank tests were con-

Table 2
Cross validation accuracy of classification, cost of misclassification for infested and uninfested conditions, overall misclassification cost (±SE), number of terminal nodes, and number of variables used in tree classification models built to predict probability of infestation by the Douglas-fir beetle, Pikes-San Isabel National Forest, CO, 1994–1995

Model	Cross validation accuracy of classification[a]	Cost of misclassification for infested condition	Cost of misclassification for uninfested condition	Overall misclassification cost (±SE)[b]	No. of terminal nodes	No. of variables
Model 1	0.63	0.37	0.38	0.75(0.07)	4	2
Model 2	0.62	0.36	0.41	0.77(0.07)	2	1
Model 3	0.55	0.40	0.50	0.90(0.07)	2	1

[a] Cross-validation accuracy of classification = 1 − (Overall Misclassification Cost/2).
[b] Overall Misclassification Cost = Cost of misclassification of infested condition + Cost of misclassification of uninfested condition.

ducted to detect significant differences between the infested and the uninfested condition for all points combined. This analysis was conducted using the NPAR1WAY procedure in SAS software (SAS Institute, 1990).

2.5.3. Characteristics of attacked and unattacked trees in infested points

To determine the kinds of trees attacked by the Douglas-fir beetle, characteristics of Douglas-fir beetle-killed, infested, and live trees within the infested points were compared. Analysis of variance was used to determine if there were differences in average Douglas-fir diameter, total height, last 5 years', second-to-last 5 years', 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 dead trees and to the second-to-last 5 years' growth rate for live and infested trees. The variable represents growth rate for the last 5 years prior to Douglas-fir beetle attack in attacked trees and ca. the same years for live trees. Contrasts were used to compare means between live and dead trees, and the average of combined infested and dead trees with live trees. Cross tabulation and a Chi-square test were used to determine if there were any relationships between Douglas-fir beetle-killed trees and crown position.

2.5.4. Extent of mortality

Two approaches were used to build models to predict extent of mortality in terms of basal area killed by the Douglas-fir beetle in the infested points. First, linear regression was used to examine measured variables as potential predictors of basal area killed by the Douglas-fir beetle using a stepwise approach. Since the primary use of the resulting regression model would be for predictive purposes, a prediction R^2 was calculated using prediction sums of squares (Allen and Cady, 1982). Second, the regression tree option available with CART was used. The regression tree approach in CART is similar to the classification approach described above. However, in this case, since the response variable is continuous, an average value of the response is calculated for each node. Cross-validation is performed as described above and an estimate of cross-validation relative error is provided. A predictive R^2 value is then calculated as 1 − cross-validation relative error.

3. Results

3.1. Douglas-fir beetle population trend

By definition it was known that infested points included attacked trees. In addition, results indicated

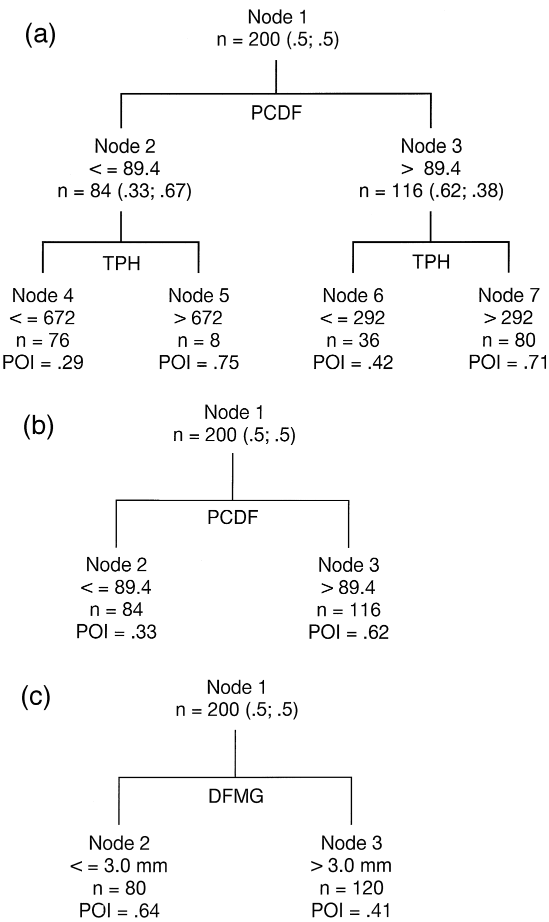

Fig. 1. Classification trees for estimating probability of infestation by the Douglas-fir beetle, (a) Model 1; (b) Model 2; (c) Model 3. Numbers in parenthesis represent class frequencies for infested and uninfested classes, respectively. Abbreviations are as follows: PCDF = percent basal area in Douglas-fir; TPH = trees per hectare; POI = probability of infestation; DFMG = Douglas-fir matched growth. Pikes-San Isabel National Forest, CO, 1994–1995.

Table 3
Means (±SEM) for variables measured for all points combined, infested, and uninfested points, Pikes-San Isabel National Forest, CO, 1994–1995

Variable	All points	Infested points	Uninfested points	$\|Z\|$-value	$p > Z$
Number of points	200	100	100	–	–
Douglas-fir dbh (cm)	28.5 (0.4)	27.8 (0.6)	29.3 (0.5)	2.4	0.0166
Douglas-fir total height (m)	10.8 (0.2)	10.7 (0.2)	10.9 (0.2)	0.8	0.4346
Douglas-fir last 5 years radial growth (mm)	2.9 (0.05)	2.9 (0.07)	2.9 (0.08)	0.3	0.7507
Douglas-fir second-to-last 5 years radial growth rate (mm)	3.6 (0.09)	3.4 (0.11)	3.8 (0.14)	1.8	0.0644
Douglas-fir last 10 years radial growth (mm)	6.4 (0.13)	6.2 (0.17)	6.6 (0.2)	1.1	0.2868
Douglas-fir periodic growth rate	0.8 (0.01)	0.9 (0.01)	0.8 (0.02)	4.0	0.0001
Live Douglas-fir phloem thickness (mm)	4.6 (.08)	4.4 (0.14)	4.7 (0.1)	1.4	0.1482
Douglas-fir matched growth (mm)	3.4(0.08)	3.1(0.1)	3.7(0.14)	3.5	0.0005
Trees per hectare	424 (15)	460 (22)	387 (19)	2.6	0.0099
Total basal area (m^2/ha)	32.3 (0.7)	33.1 (1.7)	31.4 (1.0)	1.2	0.2370
Douglas-fir basal area (m^2/ha)	28.8(0.7)	30.8 (1.0)	26.9 (1.0)	2.5	0.0131
Percent basal area represented by Douglas-fir	88.5 (1.1)	92.4 (1.3)	85 (1.8)	3.5	0.0005
Site index	38(0.5)	37(0.7)	38(0.9)	0.3	0.7996
Stand density index	233(4.6)	242(6.3)	224(7)	1.8	0.0685

that infested points also had attacked trees in its vicinity. This was also the case for uninfested points. That is, although no attacked trees were present in the established uninfested points, attacked trees were present in close proximity to the points. Trees killed by unknown or other causes such as western spruce budworm defoliation were excluded from analysis. Few trees were killed by Douglas-fir beetle during or prior to 1991 (Table 1). The number of trees killed increased yearly through 1993 and then declined through 1995. A small increase was again noted in 1996. The trend was the same for both infested and uninfested points. Numbers of infested trees was always higher in the proximity of infested points. Overall Chi-square test for association between year of attack of Douglas-fir beetle-killed trees and plot status was significant ($\chi^2 = 14.539$, $df = 5$, $P < 0.013$). When live trees are included, 39.9% of all trees sampled were attacked during the outbreak in the vicinity of the infested points and 11.4% in the vicinity of the uninfested points. A Chi-square test in which trees attacked in 1993 were excluded from analysis indicated a lack of association between year of attack of Douglas-fir beetle-killed trees and plot status ($\chi^2 = 4.057$, $df = 4$, $P < 0.398$). Another Chi-square test in which attack data from all years except 1993, and attack data for 1993 were cross-tabulated with plot status was significant ($\chi^2 = 10.482$, $df = 1$, $P < 0.001$). These series of tests indicates that the significance in the overall Chi-

Table 4
Means (±SEM) for dead, infested, and live Douglas-fir trees within infested points, Pikes-San Isabel National Forest, CO, 1994–1995

Variable	DFB-killed	Infested	Live
N	409	94	350
Douglas-fir dbh (cm)	25.7 (0.5)	32.7 (1.1)	28.1 (0.6)
Douglas-fir total height (m)	10.2 (0.06)	12.1 (0.3)	11.0 (0.17)
Douglas-fir growth during last 5 year period (mm)	2.6 (0.05)	3.0 (0.09)	3.1 (0.06)
Douglas-fir growth during second-to-last 5 year period (mm)	2.9 (0.06)	3.3 (0.12)	3.7 (0.08)
Douglas-fir periodic growth rate	0.93 (0.01)	0.95 (0.03)	0.88 (0.02)
Douglas-fir growth rate in last 10 years (mm)	5.6 (0.11)	6.3 (0.18)	6.7 (0.12)
Douglas-fir matched growth (mm)	2.6 (0.05)	3.3 (0.12)	3.7 (0.08)

Table 5
Number of dead, infested, and live Douglas-firs, expected numbers, deviation and χ^2 contribution by crown position in points infested by the Douglas-fir beetle, Pikes-San Isabel National Forest, CO, 1994–1995[a]

Tree Status	Value	Crown Position			
		Dominant	Co-dominant	Intermediate	Totals
DFB -killed	Frequency	271	81	57	409
	Expected	136.3	136.3	136.3	
	Deviation	134.7	−55.3	−79.3	
	Cell χ^2	133.1	22.4	46.1	
Infested	Frequency	63	26	5	94
	Expected	31.3	31.3	31.3	
	Deviation	31.7	−5.3	−26.3	
	Cell χ^2	32.1	0.9	22.1	
Live	Frequency	218	88	44	350
	Expected	116.6	116.6	116.6	
	Deviation	101.4	−28.6	−72.6	
	Cell χ^2	88.2	7.0	45.2	
Totals		552	195	106	853

[a] Overall $\chi^2 = 397.1$; $df = 4$, $P < 0.005$.

square test was associated with peak tree mortality in 1993. These data also confirm that the outbreak had subsided by the time sampling was conducted.

3.2. Probability of infestation

Three different models to predict probabilities of infestation were built using the tree classification approach. Cross-validation estimates for the models ranged from 0.55 to 0.63, costs of misclassification for the different condition classes ranged from 0.36 to 0.40 for the infested condition and 0.38 to 0.50 for the uninfested condition, overall misclassification cost ranged from 0.75 to 0.90, number of terminal nodes was 2 or 4 and number of variables was 1 or 2 (Table 2).

In Model 1, the first split was made on percent basal area represented by Douglas-fir (PCDF). When PCDF $\leq 89.4\%$ of the total basal area, the model yields an intermediate node with an infested class frequency of 0.33 (Fig. 1a). This intermediate node is then split into two terminal nodes based on trees per hectare (TPH); when TPH ≤ 672 the probability of infestation is 0.29; when TPH > 672 the probability of infestation is 0.75. When PCDF $> 89.4\%$, another intermediate node is produced with an infested class frequency of 0.62; the node is then split into two more terminal nodes based on TPH. With TPH > 292 the probability of infestation was 0.71.

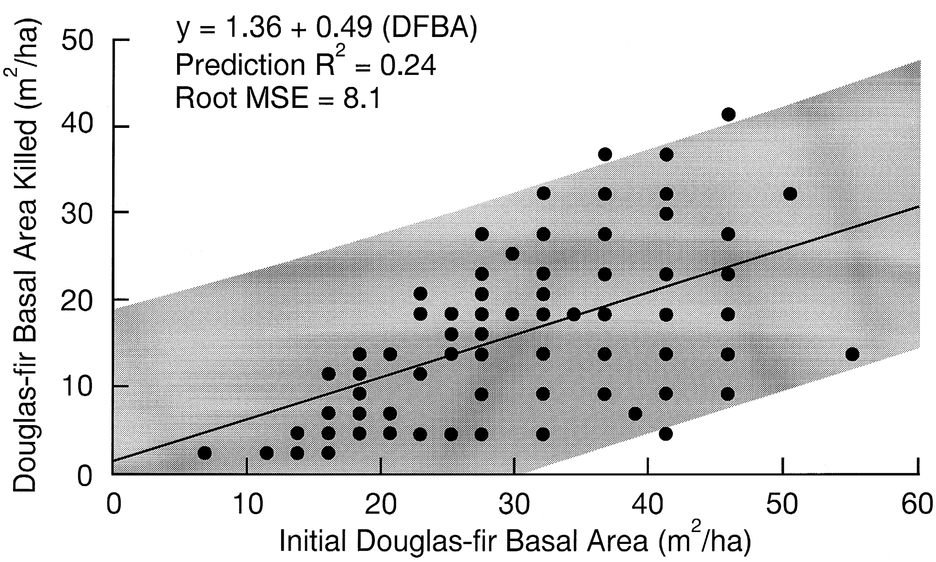

Fig. 2. Relationship between initial basal area of Douglas-fir and Douglas-fir basal area killed by the Douglas-fir beetle (33 hidden observations). Shaded area indicates 95% confidence intervals for individual observation prediction. Pikes-San Isabel National Forest, CO, 1994–1995.

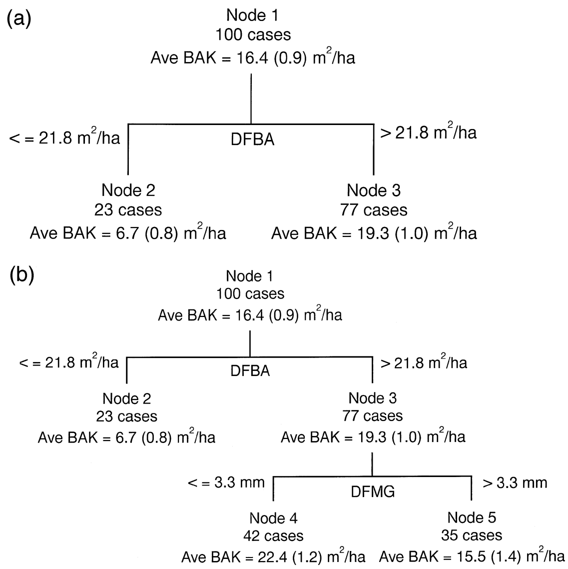

Fig. 3. Regression tree for estimating average mortality ($\pm$SEM) associated with the Douglas-fir beetle, (a) Model R1; (b) Model R2. Abbreviations are as follows: DFBA = Douglas-fir basal area (m^2/ha); BAK = Douglas-fir basal area killed by Douglas-fir beetle (m^2/ha); DFMG = Douglas-fir matched growth (mm). Pikes-San Isabel National Forest, CO, 1994–1995.

With TPH ≤ 292 the probability of infestation is 0.42.

Model 2 uses the first split observed in Model 1; but this time the split results in two terminal nodes. Higher PCDF results in a probability of infestation of 0.62; less host type results in a probability of infestation of 0.33 (Fig. 1b).

During the model construction process, it was noted that average growth rate during the last 5 years prior to the initiation of the outbreak (DFMG) was a good competitor variable to TPH. Therefore, TPH and PCDF were excluded and the result was Model 3. In Model 3, the only split is based on DFMG. In this case, growth equal to or less than 3.0 mm during that time frame results in a probability of infestation of 0.64; better growth results in a decrease in probability of infestation to 0.41 (Fig. 1c).

3.3. Infested and uninfested point characteristics

Normality tests indicated that the only normally distributed variables were stand density index and average phloem thickness of live Douglas-fir. Wilcoxon rank sum tests indicated significant differences ($P < 0.05$) between infested and uninfested points for average Douglas-fir dbh, average Douglas-fir periodic growth rate, trees per hectare, Douglas fir-basal area, percent basal area represented by Douglas-fir, and average Douglas-fir matched growth (Table 3).

3.4. Characteristics of infested trees

Contrasts between live and Douglas-fir beetle-killed trees indicated significant differences for average Douglas-fir dbh ($F = 89.3$, $P < 0.0018$), average Douglas-fir total height ($F = 15.23$, $P < 0.0001$), average Douglas-fir last 5 years' growth rate ($F = 54.86$, $P < 0.0001$), average Douglas-fir second-to-last 5 years' growth rate ($F = 58.47$, $P < 0.0001$), average Douglas-fir periodic growth rate ($F = 6.06$, $P < 0.0141$), average Douglas-fir last 10 years' growth rate ($F = 53.3$, $P < 0.0001$), and average Douglas-fir matched growth ($F = 164.79$, $P < 0.0001$); and significant differences between the mean of infested and Douglas-fir beetle-killed trees when compared to live trees for average Douglas-fir last 5 years' growth rate ($F = 16.23$, $P < 0.0001$), average Douglas-fir second-to-last 5 years' growth rate ($F = 28.88$, $P < 0.0001$), average Douglas-fir periodic growth rate ($F = 6.94$, $P < 0.0086$), average Douglas-fir last 10 years' growth rate ($F = 21.69$, $P < 0.0001$), and average Douglas-fir matched growth ($F = 61.33$, $P < 0.0001$) (Table 4).

Table 6
Number of terminal nodes, cross-validated relative error, prediction R^2, and Root MSE for tree regression models built to estimate mortality associated with the Douglas-fir beetle in infested points, Pikes-San Isabel National Forest, CO, 1994–95

Model	No. terminal nodes	Cross-validated relative error	Prediction R^2	Root MSE
Model R1	2	0.74 ± 0.07	0.26	34.2
Model R2	3	0.68 ± 0.1	0.32	31.5

Table 7
Empirically derived damage classes, tree regression criteria, average basal area killed ($\pm$SEM), and percent basal area Douglas-fir killed ($\pm$SEM) as derived from the regression tree models built to estimate mortality associated with the Douglas-fir beetle in infested points, Pikes-San Isabel National Forest, CO, 1994–95[a]

Model	Damage class	Criteria	Average basal area killed	Percent basal area Douglas-fir killed
R1	Low	DFBA ≤ 21.8	6.7 ± 0.8	38.1 ± 3.9
	High	DFBA > 21.8	19.3 ± 1.0	56.8 ± 2.9
R2	Low	DFBA ≤ 21.8	6.7 ± 0.8	38.1 ± 3.9
	Moderate	DFBA > 21.8 and DFMG > 3.3	15.5 ± 1.4	42.6 ± 3.6
	High	DFBA > 21.8 and DFMG ≤ 3.3	22.4 ± 1.2	68.7 ± 3.6

[a]DFBA = Douglas-fir basal area m^2/ha; DFMG = Douglas-fir matched growth (mm).

Cross tabulation and Chi-square analysis of tree status and crown positions within infested points, under the assumption that all crown positions are equally preferred, indicated an overall significant association between crown position and attacked or unattacked trees by the Douglas-fir beetle ($\chi^2 = 397.1$, $df = 4$, $P < 0.005$) (Table 5). Douglas-fir beetle exhibited preference in attacking dominant trees and less preference for co-dominant trees or intermediate trees.

3.5. Extent of mortality

Initial basal area of Douglas-fir was the best predictor variable of mortality associated with Douglas-fir beetle infestations. A simple linear equation, using Douglas-fir basal area (DFBA) as a predictor variable, resulted in a positive but weak correlation with amount of basal area affected with a prediction R^2 value of 0.24 ($P < 0.0001$) (Fig. 2). Positive slope indicates that an increase in 0.49 m^2/ha of DFBA results in mortality increases of a unit of Douglas-fir m^2/ha. This model allows estimation of potential mortality of Douglas-fir beetle with initial Douglas-fir basal area with a precision of about 16 m^2/ha of basal area.

A model (Model R1) produced with the tree regression approach indicates that with DFBA $\leq$ 21.8 m^2/ha, average basal area killed by Douglas-fir beetle was 6.7 m^2/ha (Fig. 3a). With DFBA > 21.8 m^2/ha, average basal area killed by Douglas-fir beetle was 19.3 m^2/ha. An alternate model (Model R2) used the same first split from Model R1 (Fig. 3b). The higher basal area condition, however, was an intermediate node, which was then split based on average Douglas-fir matched growth (DFMG) into two terminal nodes. With DFMG > 3.3, mm average Douglas-fir mortality was 15.5 m^2/ha; with DFMG ≤ 3.3 mm, average Douglas-fir mortality increased to 22.4 m^2/ha. Cross-validation error and root mean square was lower and prediction R^2 was higher for Model R2 (Table 6).

Mortality levels resulting from estimates of the tree regression approach were classified as low, moderate, and high for each of the two models built, and percent of host type basal area killed under each damage class calculated (Table 7). For Model R1, two damage classes were created. Low mortality resulted with DFBA ≤ 21.8 m^2/ha with average Douglas-fir mortality of 6.7 m^2/ha and 38% of the host type basal area killed by Douglas-fir beetle. High mortality resulted with DFBA > 21.8 m^2/ha with average Douglas-fir mortality of 19.3 m^2/ha and 57% of the host type basal area killed by Douglas-fir beetle. For Model R2, three damage classes were created. The low damage class was the same as in Model R1. With DFBA > 28.1 m^2/ha and DFMG > 3.3 mm the mortality class was moderate with average Douglas-fir mortality of 15.5 m^2/ha or 43% of the host type. With DFBA > 28.1 m^2/ha and DFMG ≤ 3.3 mm, the mortality class was high with average Douglas-fir mortality of 22.4 m^2/ha or 69% of the host type.

4. Discussion

Douglas-fir beetle population trend data indicate that beetle populations were present in the vicinity of infested and uninfested points throughout the duration of the outbreak. Infested and uninfested points were intermingled in a network in relatively close proximity to each other but more trees were attacked in the vicinity of infested points. This supports the assumption that uninfested points established during this study were exposed to Douglas-fir beetle during the outbreak but not attacked, and are likely to be a good representation of low probability of infestation conditions.

Probability of infestation Models 1 and 2 used percent of basal area represented by Douglas-fir as the initial splitting variable, which suggests that under the range of conditions sampled in this study, host type availability is an important factor in determining probabilities of infestation by the Douglas-fir beetle (Fig. 1a,b). Model 1 also used trees per hectare as splitting variable with higher tree densities resulting in higher probabilities of infestation. Other studies have demonstrated that high tree densities are associated with increased probabilities of infestation by mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in ponderosa pine, *Pinus ponderosae* Laws., (Schmid and Mata, 1992; Schmid et al., 1994; Olsen et al., 1996). Model 3 used Douglas-fir matched growth as a splitting variable, with poor growth resulting in a higher probability of infestation (Fig. 1c). As mentioned above Douglas-fir matched growth was a good competitor variable to trees per hectare, which emphasizes the intrinsic relationship between these. The analysis suggested that trees per hectare may be a better discriminating variable; but it may reflect reduced growth caused by high tree densities or defoliation events or both. Reductions in radial growth caused by western spruce budworm have also been documented (Alfaro et al., 1982; Carlson et al., 1983; MacLean, 1985; Van Sickle, 1987). This concept agrees with Lessard and Schmid (1990), whose study indicated that trees infested by the Douglas-fir beetle in Colorado exhibited declines in growth prior to infestation. They attributed the growth reductions to western spruce budworm defoliation prior to the onset of the Douglas-fir beetle outbreak. It appears that this is also the case in this study, since western spruce budworm populations had been active in the study area for several years. Bark beetle populations which have been found to exhibit positive responses to defoliation include the fir engraver *Scolytus ventralis* LeConte attacking grand fir, *Abies grandis* (Dougl.) Lindley, following defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough in the Blue Mountains, Oregon (Wright et al., 1979; Wright et al., 1984); the Douglas-fir beetle following defoliation by the Douglas-fir tussock moth also in the Blue Mountains, Oregon (Wright et al., 1984); and *Polygraphus rufipennis* (Kirby) attacking black spruce, *Picea mariana* (Mill.) B.S.P., following defoliation by the eastern spruce budworm, *Choristoneura fumiferana* (Clem) in Newfoundland, Canada (Bowers et al., 1996).

From a management point of view, Models 1 and 2 are about equal in terms of cross-validation accuracy of classification and costs of misclassification. Because of its simplicity, Model 2 would be more appropriate for operational use. Models 1 and 3, however, provide a better understanding of the biological processes driving Douglas-fir beetle populations because they indicate that reduced growth caused by high tree densities or defoliation events can foster high susceptibility to Douglas-fir beetle.

Significant differences detected in average Douglas-fir dbh between infested and uninfested points are not in agreement with reported literature. Furniss et al. (1979) indicated that Douglas-fir beetle tends to infest larger diameter trees in affected stands. Lessard and Schmid (1990) also suggest this, but based on observational evidence. The difference in average dbh of Douglas-fir between infested and uninfested points in this study is only 1.5 cm, which may not have biological significance. This may also be a function of the poor site quality of the study sites sampled, as indicated by site index values (Table 3). Douglas-fir stands in the Colorado Front Range generally grow in poor sites and usually do not attain large diameter classes characteristic of those in the Pacific Northwest. In the study area, trees do not attain diameters much larger than 35.6 cm. Therefore, there may not be enough of a range from which the beetles could discriminate.

When tree variables were examined for Douglas-fir beetle-killed, infested, and live trees within infested points; a trend in reduced growth was evident for all growth related variables except average Douglas-fir periodic growth ratio (Table 4). Douglas-fir beetle-killed trees exhibited reduced growth rate with infested trees exhibiting intermediate growth rate as compared to live trees. Douglas-fir beetle-killed trees were also slightly smaller in dbh and height than live trees. Douglas-fir beetle-killed trees exhibited reduced growth and dbh, both at the plot and at the individual tree level. Infested trees were somewhat larger in dbh and taller than live or dead trees which may indicate that larger trees were being attacked in the sampled stands toward the latter part of the outbreak. Periodic growth rate values were closer to 1.0 for Douglas-fir beetle-killed and infested trees. Lessard and Schmid (1990) reported periodic growth rate values of more than 1.0 for Douglas-fir beetle killed trees. Douglas-fir beetle may be selecting trees which had been stressed by budworm defoliation and are on the way to recovery when they fall victim to Douglas-fir beetle.

The linear regression analysis resulted in an equation to predict mortality associated with Douglas-fir beetle infestations. The relationship was weak but significant. The best predictor variable was Douglas-fir basal area. From the extent of mortality models built with the regression tree approach, Douglas-fir basal area and Douglas-fir matched growth were the best predictor variables. Model R1 has about the same predictive power as the linear regression model. Model R2, however, has better predictive ability but requires growth rate data. The damage classes obtained from the regression tree (Table 7) provide empirically developed damage categories that can assist in the rating of potential mortality associated with the Douglas-fir beetle. In many instances, this may be enough information to prioritize stands for potential treatment or management alternatives. Since the classification tree analysis for estimating probabilities of infestation indicated that host type availability was important in determining the likelihood of an infestation, it is not surprising that increased host type would also result in increased mortality. Higher basal area conditions also are more likely to contain more trees which are growing slow and therefore more trees for the beetle to successfully attack. Other studies have demonstrated that high basal areas are associated with increased ponderosa pine mortality caused by mountain pine beetle in Colorado (McCambridge et al., 1982) and amount of spruce mortality caused by spruce beetle in Alaska (Reynolds and Holsten, 1994, 1996).

(Furniss et al., 1979, 1981) presented a qualitative model to explain abundance and damage by the Douglas-fir beetle in the Northern Rockies. Furniss concluded that disturbances primarily windstorms and fire, contribute to increased Douglas-fir beetle activity but also snow-damage, defoliation, drought, and root disease further extend the outbreak. Furniss also concluded that the proportion of Douglas-fir in the stand, its density, and age were positively correlated with susceptibility. The outbreak sampled in this study developed after defoliation by the western spruce budworm had been active in the study area. In the Colorado Front Range, it seems that the primary disturbance agent, although not the only one, that triggers Douglas-fir beetle outbreaks is western spruce budworm defoliation. The mechanism appears to be that defoliation causes a reduction in growth rate with the Douglas-fir beetle then exploiting this condition, as shown in this study and Lessard and Schmid (1990). Webb and Karchesy (1977) showed that defoliation by the Douglas-fir tussock moth was proportionally related to reductions in overall starch content in Douglas-fir. Webb (1981) indicated that starch is a precursor of secondary compounds which are used in defense against herbivores. Wright et al. (1979) indicate that the removal of photosynthetic tissues by Douglas-fir tussock moth in grand fir, leads to a reduction in total sugars during the first year after defoliation and starch the second year after defoliation. Total soluble sugars and previous year's starches were positively correlated with monoterpene concentrations, suggesting that carbohydrates are needed for monoterpene production. They reported that reduced monoterpenes caused reduced resistance to the fir engraver, *S. ventralis* (LeConte), and a relationship between low starch levels and tree mortality associated with the fir engraver. This suggests an important role for the availability of carbohydrates in the synthesis of defensive compounds. Waring and Pitman (1980) suggested that availability of carbohydrate reserves directly controls host resistance to bark beetles. They proposed that resistant trees have carbohydrate resources available to produce large amounts of stemwood. That study indicated that lodgepole pines, *Pinus contorta* Dougl., with increased amount of stemwood required higher populations of attacking mountain pine beetles to kill a tree.

Other studies indicate that spruce beetle prefers slow growing hosts for attack (Watson, 1928; Hard et al., 1983; Hard, 1985). Mitchell et al. (1983) indicated that lodgepole pine thinned stands contained trees with increased vigor (measured as current growth in grams of stemwood/m^2 of crown leaf surface), which led to increased stand vigor and reduced mortality associated with mountain pine beetle. Although defoliation was not a factor with spruce beetle or with mountain pine beetle in those studies, it is possible that reduced growth caused by other stressors such as high tree densities may also reduce a tree's the ability to synthesize defensive compounds.

The conclusion by Furniss et al. (1979, 1981) that proportion of Douglas-fir in the stand and its density are important regulators of susceptibility was evident in this study. Percent basal area in Douglas-fir and trees per acre were two of the variables used in the tree classification models. The third variable which Furniss indicated as important was tree age. In this study, age was only sampled indirectly when site index measurements were taken from dominant or co-dominant live trees, so it was not a carefully considered variable.

In the rating system described in Weatherby and Thier (1993) likely mortality levels are based on stand basal area, proportion of stand basal area in Douglas-fir, average stand age, and average dbh of Douglas-fir sawtimber (> 22.9 cm). Stand basal areas higher that 57.4 m^2/ha, proportion of stand basal area in Douglas-fir over 50%, average stand age over 120 years, and average dbh of Douglas-fir in sawtimber over 25.4 cm result in the highest potential levels of mortality. Forest conditions described in this Colorado Front Range study area did not include comparable basal area levels or diameter classes. But, similarly, proportion of Douglas-fir basal area was an important factor.

The probability of infestation models presented in this study have moderate cross-validation estimates. This may be related to rather homogenous forest conditions within the study area. The extent of mortality models built with linear and regression trees have weak to moderate explanatory power. Root mean square values for the regression tree models were higher than that obtained with the linear regression approach. This suggests that although the regression tree models had about equal or improved R^2 values and may be attractive to use because of their simplicity, they also exhibit reduced precision in the estimates provided.

The models presented in this study are tools that land managers can use when there is need to rate stands for probabilities of infestation or extent of mortality associated with Douglas-fir beetle in terms of amount of host type killed or both. These models are most applicable to Colorado Front Range areas with forest conditions similar to the ones sampled. Site index measurements indicate that the average site index for all points established was 38 and there was no difference in site index between infested and uninfested points (Table 6). Site index ranged from 27 to 79. This suggests that models developed in this study may be more applicable to poor sites along the Colorado Front Range.

More importantly perhaps, this study helps extend our understanding of the mechanisms associated with the build-up of Douglas-fir beetle outbreaks in the Colorado Front Range. It also follows that although the Douglas-fir beetle has long been an important insect along the Colorado Front Range, it may be primarily a symptom that points to the need for better western spruce budworm management in forested landscapes.

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