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Performance of Three Mountain Pine Beetle Damage Models Compared to Actual Outbreak Histories

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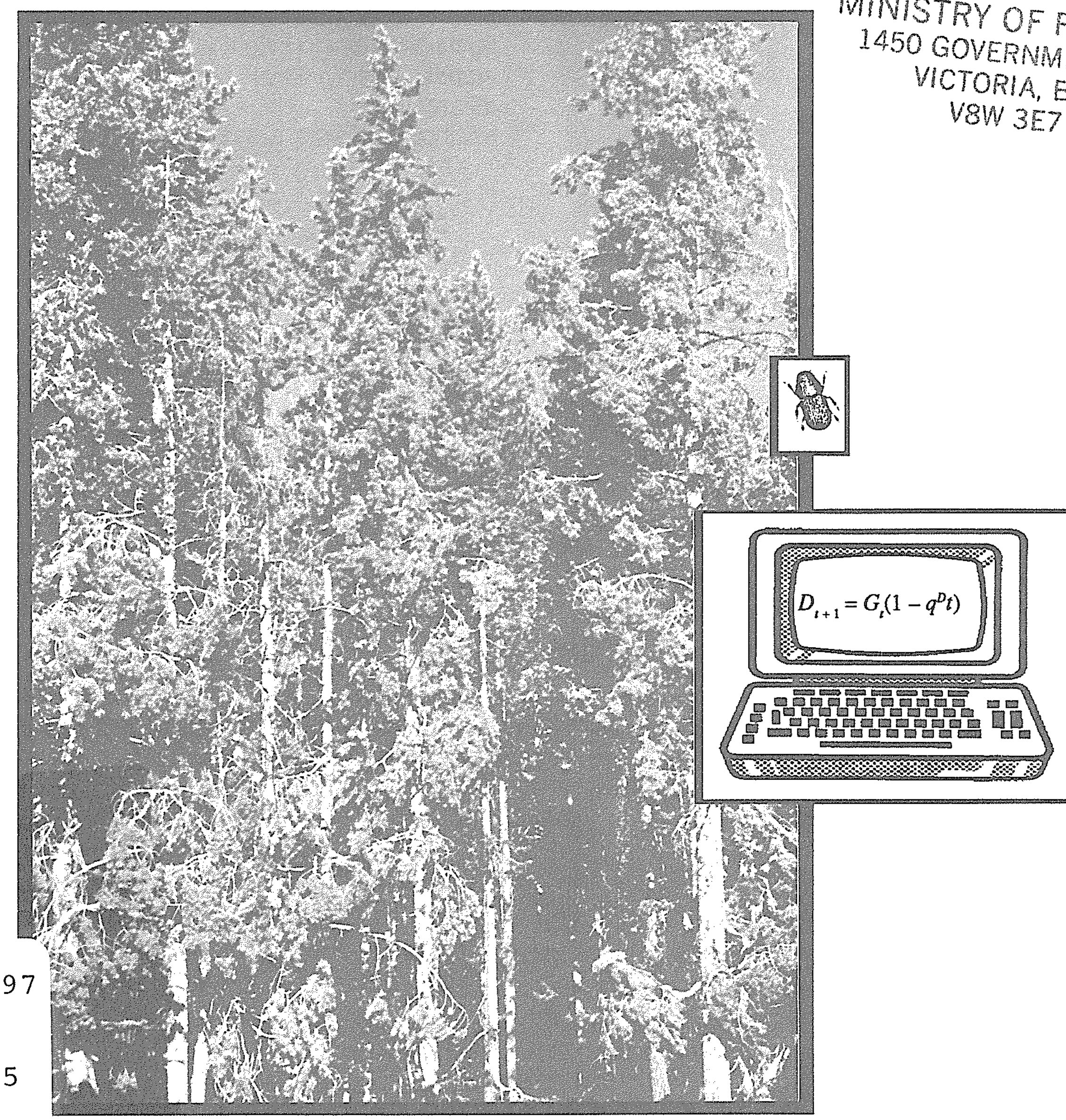

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RESEARCH SUMMARY

The importance of management planning to minimize losses to forest pests, especially mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine (*Pinus contorta*) stands, has been well recognized. To aid forest managers in estimating mountain pine beetle losses, damage models have been developed as extensions to the Prognosis Model for Stand Development (Prognosis Model). In evaluations of three mountain pine beetle extensions to the Prognosis Model, their predictions were compared to known histories of losses. These damage models predict volume lost to the mountain pine beetle and the diameter distribution of the volume lost. These model predictions were compared to actual mountain pine beetle outbreaks. The performance of the models was evaluated in terms of bias and standard deviation for the predicted volume lost to mountain pine beetle and the median diameter of the trees killed by the insect. Bias of models was also evaluated in relation to variables such as top height and relative density of the stands. The significant correlations varied with the different models. None of the models behaved best in all comparisons.

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INTRODUCTION

To aid forest managers in stand management of lodgepole pine (*Pinus contorta*) forests where mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) infestations are a potential threat, extensions of the Prognosis Model for Stand Development (Prognosis Model) have been developed. (See Wykoff and others 1982 for details of the Prognosis Model.) These model extensions predict effects of mountain pine beetle damage on stand development. Therefore, these models are candidates for management tools in silvicultural planning of forests. Whether a particular model is adequate for use depends on the unique context of each decision. A scheme for categorizing decisionmaking situations and a guide to evaluating model suitability is described in Newberry and Stage (1988). To apply this guide requires knowledge of model behavior expressed as bias and mean-square error. This paper provides these measures of behavior for three models representing losses to mountain pine beetle.

Three models that predict MPB losses in the Prognosis Model were evaluated: two versions of a rate-of-loss model (Bousfield in preperation; Cole and McGregor 1983) and a population dynamics model (Crookston and others 1978). The mountain pine beetle extension of the Prognosis Model allows the user to specify which type of MPB model is to be used to predict losses from the insect.

Rate-of-Loss Model

This model predicts the number of lodgepole pine killed by mountain pine beetle (Cole and McGregor 1983) in each 50-cm diameter class. This model calculates numbers of trees dying from independent calculations of the equation for each diameter class.

$$D_{t+1} = G_t(1 - q^{D}t)$$

in which

D_{t+1} = number of trees per hectare dying between time t and $t+1$ in the diameter at breast height (d.b.h.) class.
G_t = number of live trees per hectare at time t in the d.b.h. class.
q = probability of an individual tree surviving 1 year.

The values of q are defined in table 1 for each d.b.h. class.

Cole and McGregor (1983) noted that the model could overestimate tree mortality when compared to actual field conditions, but this behavior was not considered to be a serious problem in most cases. Bousfield and Oakes (in preparation) noted that the model failed to correctly predict mortality when a very high or very low number of trees per hectare was found in individual diameter classes.

Altered Rate-of-Loss Model

The original rate-of-loss model was modified by Bousfield to make q a function of stand density. Dense stands have lower q-values than more open stands. Survival probabilities (q) in the rate-of-loss model are raised to an exponent that is the ratio of G_t to a standard tree density for each diameter class (table 1).

The modification was based on data sets of 20 stands from the Gallatin and Kootenai National Forests measured at the conclusion of an MPB outbreak. Using data from 11 additional stands, the modification showed a model prediction error of 7.4 percent more volume killed than the actual amount, while the original mortality model predicted 53.9 percent more volume killed than the actual amount (Bousfield and Oakes in preparation). This modified mortality model will be referred to as the altered rate-of-loss model.

Table 1—Parameters of mountain pine beetle rate-of-loss models

D.b.h. class	Rate-of-loss model default D_0[1]	q	Altered rate-of-loss model standard tree density
Inches	*Trees/acre*		*Trees/acre*
2	0.0	1.0	150.0
4	.0	1.0	100.0
6	.0038	.9935	95.0
8	.0128	.982	66.0
10	.0206	.965	35.5
12	.0353	.909	16.5
14	.0500	.743	5.5
16	.1429	.309	3.0
18	.1500	.285	1.5
20+	.1500	.285	.8

[1]Based on Parker 1973, which used English units of measurement.

Population Dynamics Model

The population dynamics model was developed as a dispersal-aggregation model for mountain pine beetle in lodgepole pine stands (Crookston and others 1978). The model represents components of MPB flight, aggregation, attack, and death of lodgepole pine, reproduction of the beetle, and further dispersal of new beetles (Burnell 1977; Crookston and others 1978). This model is more complex than the rate-of-loss model, because it includes components that represent the beetle's life cycle and their interactions with the lodgepole pine hosts. Many parameters are available to adjust the population dynamics model to accurately predict losses in a specific region.

METHODS

Forest inventory data were obtained from the Northern Region, Forest Service, U.S. Department of Agriculture. Actual mortality caused by MPB was computed and then compared to the mortality predicted by each MPB model. Within the Northern Region, 58 stands with inventory data were located from various forests and research studies (table 2). Data used in our study came from four sources.

Kenneth Gibson, Northern Region entomologist, provided information on six permanent MPB population trend study areas throughout western Montana. The tree characteristics such as tree d.b.h. and heights were recorded on 30 variable-radius plots in each study area when the study was initiated. Insect damage codes were also recorded when the plots were established and on a yearly basis for several years thereafter. More details of these surveys are in published Forest Pest Management Reports (Gibson and others 1980; Gibson 1981, 1982, 1983, 1985).

Randall Gay, forester on the Gallatin National Forest, provided information on five permanent growth study plots within areas in that forest that were susceptible to MPB outbreaks. The field measurements for these plots also include tree d.b.h., tree height at establishment, and codes describing MPB-caused damage and death.

Wayne Bousfield, Northern Region entomologist (retired), provided stand information on 26 stands inventoried once after the completion of an MPB infestation. These stands were from the Kootenai and the Gallatin National Forests and inventoried using variable plot sampling procedures and the INDIDS damage coding system (Bousfield 1981). These stands were used by Bousfield to determine the altered rate-of-loss model.

Gene Amman, Intermountain Research Station research entomologist, provided data from a published study (McGregor and others 1987, background information in McGregor and Bennett 1980). These data were inventories from a test of thinning lodgepole pine stands. The set included 19 thinning treatments and two control plots.

Because the data were obtained from various researchers, we translated the coding and formats into a consistent form for use in the Prognosis Model and the MPB extension. Much of the field data were collected and recorded using the INDIDS system (Bousfield 1981). The INDIDS codes were converted for the Prognosis Model for use in a manner that was consistent with their original use. The

Table 2—Descriptions of the data sets analyzed in the study

Data set[1]	Location	Habitat type[2]	Slope[3]	Aspect	Latitude	Elevation	CCF[4]	Quadratic mean diameter	Basal area	Initial volume	Outbreak duration
						m		cm	m²/ha	m³/ha	Years
1	Beaverhead NF	*5	*	*	44	1,859	134	10.7	28	212	3
2	Kootenai NF	Abla/Mefe	2	SE	49	1,524	139	12.4	31	280	8
3	Lolo NF	Abla/Libo	2	Level	48	1,433	135	13.2	30	292	9
4	Flathead NF	Psme/Vagl	0	Level	48	1,219	127	12.7	28	288	8
5	Flathead NF	Abla/Clun	2	S	48.5	1,524	126	11.4	28	300	9
6	BLM (SW MT)	*	*	*	44	2,012	106	9.1	22	158	3
7	Gallatin NF	Abla/Libo	1	NE	45	2,073	72	7.4	16	146	5
8	Gallatin NF	Abla/Luhi	0	Level	44.5	2,012	132	7.1	27	187	8
9	Gallatin NF	Abla/Vasc	2	N	44	2,194	237	9.1	46	292	8
10	Gallatin NF	Abla/Vasc	2	Level	44	2,347	159	7.6	33	239	8
11	Gallatin NF	Abla/Vagl	4	NE	44.8	2,164	168	11.7	35	298	8
12	Gallatin NF	Abla/Vagl	5	E	44	2,194	107	12.7	23	212	10
13	Gallatin NF	Abla/Vagl	2	NE	44	2,134	94	10.9	20	177	10
14	Gallatin NF	*	*	*	44	*	102	17.5	24	223	10
15	Gallatin NF	Abla/Clun	1	S	44	2,134	116	12.9	28	270	10
16	Gallatin NF	Abla/Libo	0	Level	44	2,073	133	10.9	29	261	10
17	Gallatin NF	Abla/Vagl	4	NE	44	2,164	147	13.5	31	264	10
18	Gallatin NF	Abla/Mefe	2	NE	44	2,316	109	10.2	23	188	10
19	Gallatin NF	Abla/Clun	2	NE	44	2,073	78	9.6	17	142	10
20	Gallatin NF	Abla/Vagl	3	SE	44	2,164	146	16.5	35	376	10
21	Gallatin NF	Psme/Syal	6	SE	44	2,042	141	14.0	33	322	10
22	Gallatin NF	Abla/Mefe	1	SE	44	2,194	126	19.1	28	267	10
23	Gallatin NF	*	*	*	44	*	117	12.9	26	245	10
24	Gallatin NF	Abla/Luhi	0	Level	44	2,012	133	11.9	28	249	10
25	Gallatin NF	Abla/Libo	2	E	44	2,194	116	11.2	26	241	10
26	Gallatin NF	Abla/Vasc	2	N	44	2,194	133	10.9	27	200	10
27	Gallatin NF	Pial-Abla	1	E	44	2,073	90	10.9	21	199	10
28	Gallatin NF	Abla/Libo	3	N	44	2,134	91	9.9	19	157	10
29	Gallatin NF	Abla/Vasc	2	Level	44	2,347	172	11.7	37	331	10
30	Kootenai NF	Abla/Vaca	3	SE	44	1,372	121	13.5	29	287	10
31	Kootenai NF	Tshe/Clun	1	NE	44	1,036	146	21.3	38	391	10
32	Kootenai NF	Abla/Xete	3	SE	44	1,524	139	17.0	32	324	10
33	Kootenai NF	Abla/Libo	2	SW	44	1,524	123	11.9	30	254	10
34	Kootenai NF	Psme/Caru	0	SE	44	1,189	109	15.2	24	221	10
35	Kootenai NF	Psme/Libo	3	SE	44	1,341	115	11.9	25	215	10
36	Kootenai NF	Thpl/Clun	0	NW	44	1,585	161	12.2	35	296	10
37	Kootenai NF	Abla/Clun	4	SW	44	1,615	143	17.8	34	343	10
38	Lolo NF	Thpl/Clun	2	SE	48	1,280	119	10.7	26	233	7
39	Lolo NF	Thpl/Clun	1	Level	48	1,250	92	10.9	20	173	7
40	Lolo NF	Thpl/Clun	1	Level	48	1,250	113	10.4	26	257	7
41	Lolo NF	Thpl/Clun	1	N	48	1,250	114	9.1	24	201	7
42	Lolo NF	Abla/Clun	2	E	48	1,250	157	10.9	32	265	7
43	Lolo NF	Abgr/Xete	1	NE	48	1,250	123	10.4	27	256	7
44	Lolo NF	Abgr/Xete	1	W	48	1,219	132	10.4	28	233	7
45	Lolo NF	Abgr/Xete	1	NE	48	1,219	112	10.9	25	229	7
46	Lolo NF	Abgr/Xete	1	Level	48	1,280	139	12.9	30	273	7
47	Lolo NF	Abgr/Xete	2	E	48	1,250	112	14.0	24	231	6
48	Lolo NF	Abgr/Xete	3	N	48	1,250	125	13.2	28	263	5
49	Lolo NF	Abgr/Xete	1	S	48	1,219	145	12.4	31	275	7
50	Kootenai NF	Thpl/Clun	2	S	48	1,036	69	10.9	16	155	7
51	Kootenai NF	Thpl/Clun	2	S	48	1,036	66	12.4	15	139	7
52	Kootenai NF	Thpl/Clun	3	SW	48	1,219	138	16.0	30	272	7
53	Kootenai NF	Thpl/Clun	3	SW	48	1,219	105	15.7	23	207	7
54	Kootenai NF	Thpl/Clun	3	SW	48	1,219	87	14.2	20	199	7
55	Kootenai NF	Thpl/Clun	3	SW	48	1,219	87	17.8	20	183	7
56	Kootenai NF	Thpl/Clun	3	SW	48	1,219	127	17.3	28	247	7
57	Kootenai NF	Thpl/Clun	3	SW	48	1,219	99	16.5	23	216	7
58	Kootenai NF	Thpl/Clun	1	NE	48	1,250	174	15.7	40	376	7

[1]Contact person for data sets 1-6 is Ken Gibson, 7-11 is Randy Gay, 12-37 is Wayne Bousfield, 38-58 is Gene Amman.
[2]For details see Pfister and others (1977).
[3]Codes for slope are 0 = less than 5 percent, 1 = 6-15 percent, 2 = 16-25 percent, 3 = 26-35 percent, 4 = 36-45 percent, 5 = 46-55 percent, 6 = 56-65 percent.
[4]CCF = Crown competition factor (Krajicek and others 1961).
[5]* = Information unavailable from contact person. In Prognosis simulations, the default values were used (habitat type = Psme/Phma, slope = less than 5 percent, aspect = level, elevation = 1,158 m).

INDIDS codes for dead trees included the damage codes indicating MPB current beetle attack, last year's attack, older attack, and older secondary beetle attack. Trees having INDIDS codes such as strip attacks or unsuccessful attacks were considered as live trees. If damage codes attributed tree death to an older or unknown cause of mortality then it was noted as a different type of mortality than MPB caused. By differentiating mortality causes, it was possible to compare the MPB mortality predicted by the models with the actual MPB mortality.

In actual forecasting applications, one has only data for the start of a forecast period. Data sets provided by Gibson and Gay had initial conditions measured, and records of tree condition at the end of the outbreak were used directly. The plots that were measured only once at the end of the outbreak, provided by Bousfield and Amman, were backdated to represent the stand at the start of the time interval during which the recorded MPB mortality occurred.

To backdate the stand to the start of the time interval during which the recorded MPB mortality occurred, we estimated initial diameter for each tree as of the start of the time interval. Trees recorded as recent mortality were included as live trees. The Prognosis Model was used to estimate the initial diameter increment for the period equal to the duration of the infestation. These estimated increments are routinely produced by the model and are output in machine-readable format via the model's TREELIST option. The estimated past diameter increments for the trees that had survived the outbreak were subtracted from their diameters. The diameters of trees that had died were left unchanged. That is, we assumed no growth during the period on trees dying in the period.

Some may question the need for backdating in stands in which diameter increment seems rather insignificant (about 1 cm per decade). However, the diameter classes within which Cole and McGregor calculate their mortality probabilities are only 5 cm in width. Therefore, ignoring increment implies that 20 percent of trees within a diameter class are in the wrong class. Table 1 shows that in the larger classes that were well represented in the data, mortality probabilities can change substantially between classes. Therefore, errors in assigning trees to diameter classes will bias survival probabilities downward because there will be more trees in the denominator than is correct for the start of the period. The bias will be more severe in more rapidly growing or open stands.

It should be noted that Bousfield did not backdate the data used in the development of the altered rate-of-loss model. Much of his development of the altered model used the INDIDS system, which does not account for tree growth within a short (10-year) timeframe. Therefore, he used end-of-period diameter measurements to predict losses during the period. To verify that our modeling methods were consistent with those of Bousfield, we conducted Prognosis Model simulations with the original data provided by Bousfield. In these simulations, our estimates duplicated those of Bousfield.

Data entered into the Prognosis MPB Model included forest identification, habitat type, aspect, stand slope, and stand elevation (table 2). For four stands lacking information on these characteristics, the Prognosis Model defaults were used (Wykoff and others 1982). When using the population dynamics MPB model, an additional keyword describing the stand's latitude was also used.

COMPARISONS OF BEHAVIOR

The main concerns in testing the accuracy of the MPB models were to determine if the models were killing the proper number of trees and if the models did so in approximately the correct diameter distribution. To determine if the overall mortality was modeled correctly, the volume of lodgepole pine killed per hectare per year was multiplied by the number of years the outbreak lasted. This gave us an absolute measure of lodgepole pine volume lost per hectare per outbreak and allowed us to compare outbreaks of different time lengths.

The performance of the models was measured by bias defined as the mean of residual (observed − predicted) and standard deviation of the residual of the volume lost per outbreak. A well-behaved model would have a bias of zero and a low variance (as measured by the standard deviation of the residual). In addition, the root-mean square error (Root MSE) that includes both the squared bias plus the variance of estimates is provided.

The performance of the models was also measured by regressing the residuals on other variables, such as predicted losses of the original stand, top height of the original stand, and relative density of the original stand. Relative density is the basal area divided by the square root of the quadratic mean diameter (Curtis 1982). Evaluating these measures one would expect a well-behaved model to have no significant correlations between residuals and related variables and regression lines with a slope of zero.

To consider if the diameter distribution was predicted correctly, the median (50 percentile) diameter of predicted mortality volume was compared to the median diameter of the volume actually killed in the MPB outbreak. The residuals of the median diameter were computed and plotted against the

Table 3—Actual losses compared to model predictions for total cubic meters lodgepole pine lost per hectare per outbreak and for median diameter of the mortality trees

Model type	Volume Mean	Volume Standard deviation	Diameter Mean	Diameter Standard deviation	*n*
	- - - - - - m^3/ha - - - - - -		- - - - - - *cm* - - - - - -		
Actual losses	70.05	58.25	25.05	5.36	58
Original rate-of-loss	83.85	65.40	24.83	5.98	58
Altered rate-of-loss	53.10	44.05	26.70	4.44	58
Population dynamics	68.75	71.74	25.69	4.32	58

predicted values. Using the same statistics as for total volume lost, the performance of the models was also evaluated by the bias and standard deviation of the residual of the median diameter and by the correlation of the residuals to the predicted median diameter.

Losses in Volume Per Hectare Per Outbreak

The comparison of the predicted to actual mortality revealed variation between the models (table 3). The means of the cubic meters lodgepole pine lost per hectare per outbreak were significantly different from one another as indicated in a significant F test ($F = 3.62$, df = 3 and 228, alpha = 0.05). Considering the means of the residuals, the original rate-of-loss model overpredicted mortality by 19.7 percent, the altered rate-of-loss model underpredicted mortality by 24.2 percent, and the population dynamics model overpredicted mortality by 1.85 percent. Thus, on this basis alone, it appears that the population dynamics models had the least biased prediction of actual mortality. Unfortunately, such tests of significance lead one to accept a model if either the bias is small or if the unexplained variation is large.

Table 4 also lists the magnitude of the unexplained variation for each of the models as measured by the standard deviation of the residuals. All means had a relatively high standard deviation. For standard deviations of this magnitude and for a sample size of 58, the standard error of the estimated standard deviations would be about ±4 cubic meters/hectare/outbreak (Cochran 1953, p. 27). On the basis of the square root of the mean square error, the altered rate-of-loss model predicted volume lost better than the other two models.

Table 4—Comparison of residuals for the volume lost per outbreak and median diameters predicted of the mortality trees

Residuals	Volume Mean	Volume Standard deviation	Volume Root MSE	Diameter Mean	Diameter Standard deviation	Diameter Root MSE
	- - - - - - m^3/ha - - - - - -			- - - - - - *cm* - - - - - -		
Actual – original ROL	–13.80	50.01	51.88	0.23	2.52	2.53
Actual – altered ROL	16.95	45.69	48.73	–1.64	2.47	2.96
Actual – population dyn	1.30	63.37	63.38	–.64	2.43	2.51

When the residuals were plotted against the top height of the original stand, an unbiased relationship was found for the original and altered rate-of-loss model (table 5, fig. 1A-C). The residuals are significantly different from zero for the population dynamics model. Simple linear regression equations for residuals indicate that the original rate-of-loss model is slightly superior in this comparison of the models. The original rate-of-loss model regression equation had a slope closest to zero (table 5). The second term used in the regression equations notes the presence of thinning. The variable value was "1" if the plot had been thinned and a "0" otherwise. The nonsignificant *t*-ratios of this variable indicate that thinning appears to have little influence on the behavior of the model as evaluated by this statistical test.

When the residuals were plotted versus the predicted volume losses, both the original rate-of-loss model and the population dynamics model indicated a biased relationship (table 6, fig. 2A-C). The plots of residuals versus the predicted volume losses using the original rate-of-loss model and the population dynamics model both had slopes that were significantly different from zero. In this comparison the altered rate-of-loss model predicted volumes lost to MPB most accurately.

When the residuals were plotted versus relative density, the altered rate-of-loss model and the population dynamics model indicated significant biases (table 7, fig. 3A-C). Thus, the original rate-of-loss model was better behaved in this comparison.

Table 5—Relation of the residual errors of volume killed per hectare per outbreak to top height and thinning status

Predictor	Coefficient	Standard deviation	*t*-ratio	$s_{y.x}$	R^2	R^2(adj)
		Original rate-of-loss model				
Constant	44.38	63.16	0.70	50.36	0.022	0.0
TOP HEIGHT	–2.73	2.81	–.97			
THIN	6.85	13.77	.50			
		Altered rate-of-loss model				
Constant	104.00	57.00	1.82	45.44	.046	.011
TOP HEIGHT	–3.99	2.54	–1.57			
THIN	4.29	12.42	.35			
		Population dynamics model				
Constant	183.21	76.70	2.39*[1]	61.15	.102	.069
TOP HEIGHT	–8.31	3.41	–2.44*			
THIN	7.71	16.72	.46			

[1]* indicates a significant *t*-ratio at the 95 percent confidence interval.

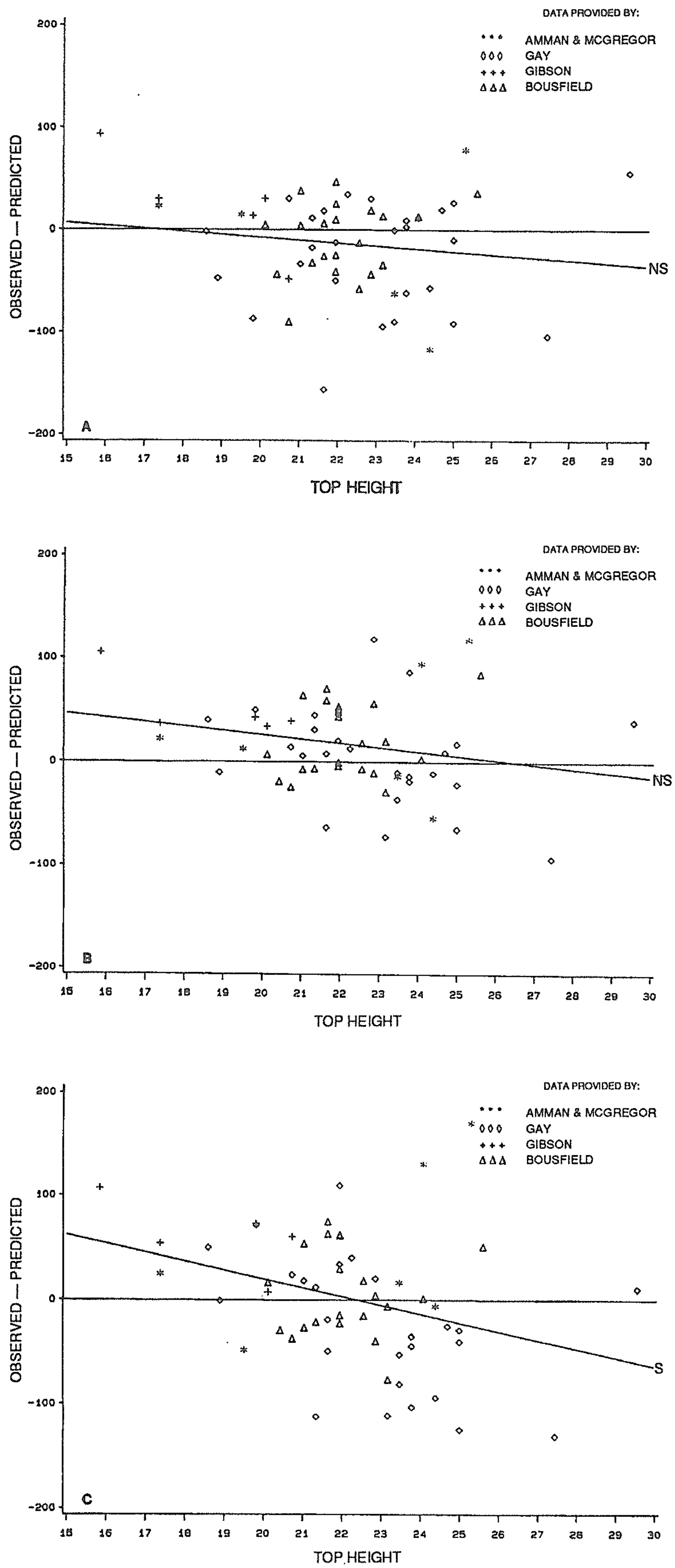

Figure 1—Residual plot of volume loss (cubic meters of lodgepole pine/hectare/outbreak) versus top height (meters) for (A) original rate-of-loss model, (B) altered rate-of-loss model, and (C) population dynamics model. Regression lines are drawn for unthinned case. Lines for thinned plots would be 6.85, 4.29, and 7.71 cubic feet per hectare lower. NS indicates a nonsignificant regression line. S indicates a significant regression line at the 95 percent confidence level.

Table 6—Relation of the residual errors of volume killed per hectare per outbreak to predicted volume killed and thinning status

Predictor	Coefficient	Standard deviation	*t*-ratio	$s_{y.x}$	R^2	R^2(adj)
		Original rate-of-loss model				
Constant	21.28	11.08	1.92	43.52	0.269	0.242
Predicted volume	–.40	.09	–4.46*[1]			
THIN	–3.87	12.15	–.32			
		Altered rate-of-loss model				
Constant	25.21	11.72	2.15*	45.93	.025	.01
Predicted volume	–.16	.14	–1.12			
THIN	.84	13.07	.06			
		Population dynamics model				
Constant	43.39	11.05	3.92*	49.72	.406	.384
Predicted volume	–.57	.09	–6.10*			
THIN	7.82	13.86	–.56			

[1]* indicates a significant *t*-ratio at the 95 percent confidence interval.

Table 7—Relation of the residual errors of volume killed per hectare per outbreak to relative density and thinning status

Predictor	Coefficient	Standard deviation	*t*-ratio	$s_{y.x}$	R^2	R^2(adj)
		Original rate-of-loss model				
Constant	–52.45	31.14	–1.68	50.14	0.030	0.004
Relative density	4.43	3.69	1.20			
THIN	11.58	14.16	.82			
		Altered rate-of-loss model				
Constant	–68.33	26.39	–2.59*[1]	42.48	.166	.136
Relative density	10.27	3.13	3.28*			
THIN	14.89	12.00	1.24			
		Population dynamics model				
Constant	–117.48	36.57	–3.21*	58.88	.167	.137
Relative density	14.20	4.34	3.27*			
THIN	22.83	16.63	1.37			

[1]* Indicates a significant *t*-ratio at the 95 percent confidence interval.

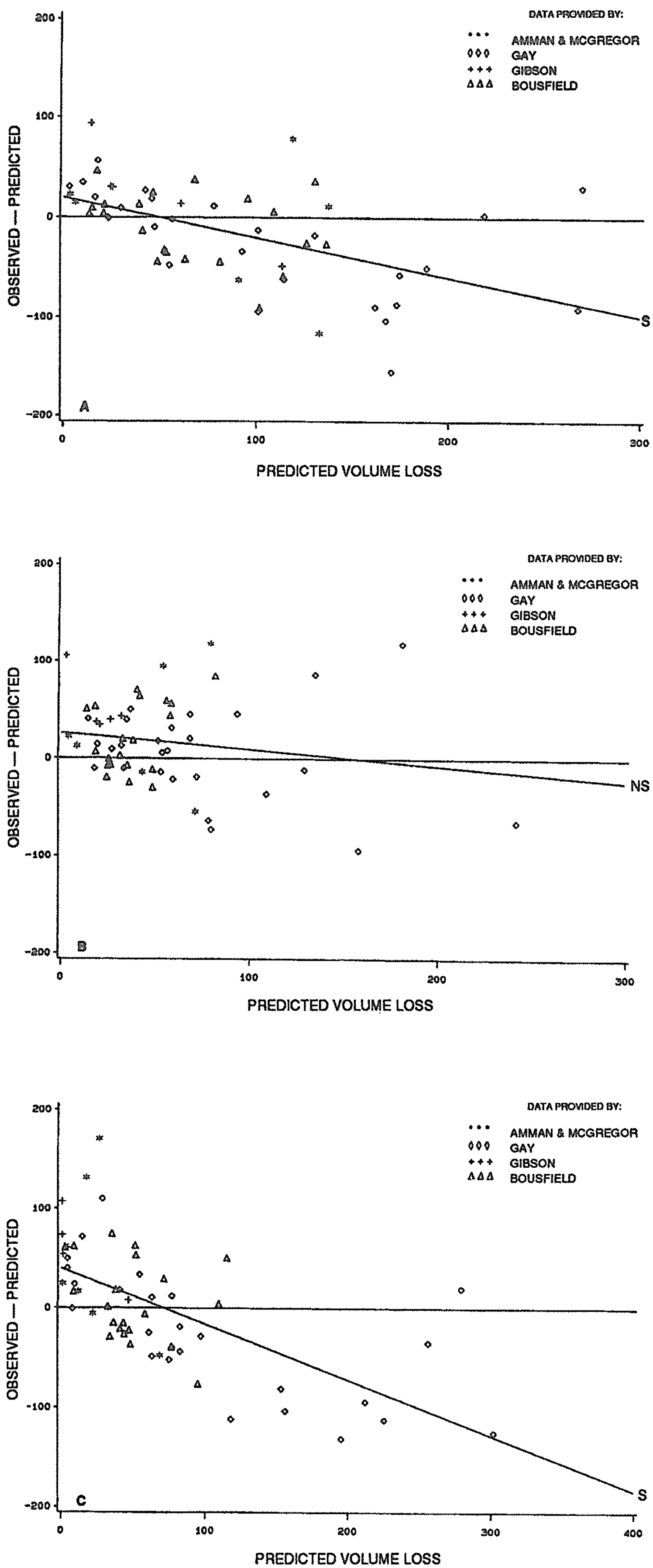

Figure 2—Residual plot of volume loss (cubic meters of lodgepole pine/hectare/outbreak) versus predicted volume loss (cubic meters of lodgepole pine/hectare/outbreak) for (A) original rate-of-loss model, (B) altered rate-of-loss model, and (C) population dynamics model. S indicates a significant regression line at the 95 percent confidence level. NS indicates a nonsignificant regression line at the 95 percent confidence level.

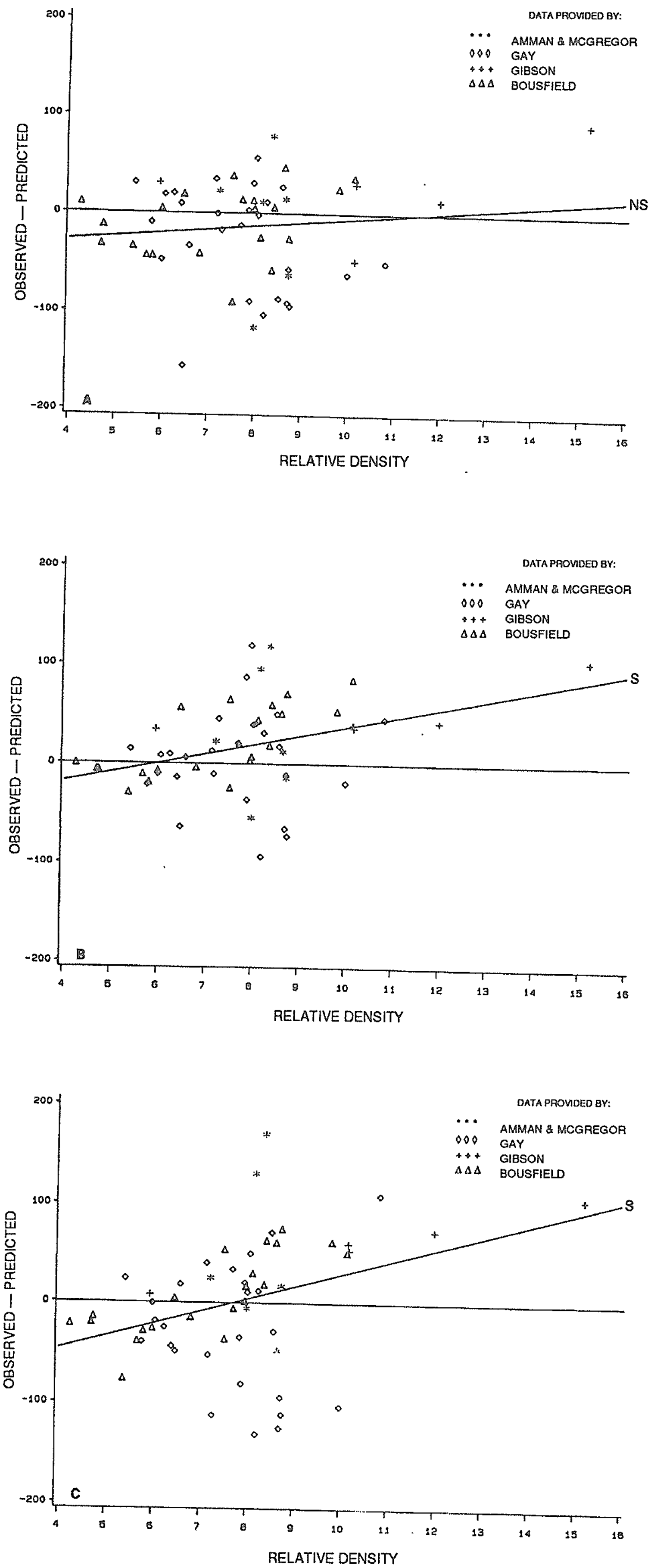

Figure 3—Residual plot of volume loss (cubic meters of lodgepole pine/hectare/outbreak) versus relative density (*BA/Dq***0.5) for (A) original rate-of-loss model, (B) altered rate-of-loss model, and (C) population dynamics model. NS indicates a nonsignificant regression line at the 95 percent confidence level. S indicates a significant regression line at the 95 percent confidence level.

Overall, the comparisons made to examine the volume of lodgepole pine lost per hectare per outbreak indicates that all three models appear to predict losses to MPB within an acceptable level. However, the original rate-of-loss model seems to predict losses slightly better than either the altered rate-of-loss model or the population dynamics model. It can be seen in the plot of the residuals against relative density that the altered rate-of-loss model appears to introduce some bias at lower stand densities.

Diameter Distribution of Losses

Comparing the average of the median diameter of the dead trees of each stand for each MPB model, the largest difference was 1.9 cm while the smallest difference was 0.58 cm. A one-way analysis of variance was performed on the median diameters of all stands using the different MPB models as treatment effects and found to be nonsignificant ($F = 1.59$, df = 3 and 228, alpha = 0.05). Examining the residual values of the median diameter of dead trees (table 3) indicates that all three models estimate the median diameter of the mortality trees relatively closely. The original rate-of-loss model slightly underestimated the median diameter while both the altered rate-of-loss model and the population dynamics model overestimated the median diameter of the mortality trees.

When the residual plots and regression equations were examined, the altered rate-of-loss model appeared to best predict the median diameter of dead trees (table 8, fig. 4A-C). The residuals of both the original rate-of-loss model and the population dynamics models indicated a slope significantly different from zero.

CONCLUSIONS

The results of these tests do not indicate that overall one model is clearly superior to another. The model that behaves best differs depending on the comparison criterion. However, both rate-of-loss models predict volume loss to MPB better than the population dynamics model does at its present state of calibration. Effects of thinning were insignificant for all of the models tested. Therefore, there is no reason to reject their use in managed stands based on these data. Obviously, there is room for improved model behavior in all cases examined. A substantial variation in the residuals for all models has not been explained by the present formulations. Future research needs to be conducted to reduce or explain this variation. For example, selecting the one parameter intended to represent stand vigor in the population dynamics model on a stand-by-stand basis reduced the standard deviation of volume residuals to one-tenth the values reported here. Further research on stand resistance may lead to an appropriate parameterization of this component of the population dynamics model. The current MPB damage models predict losses to within roughly 25 percent of the actual mortality.

We conclude that there is no reason to reject the original rate-of-loss model in favor of the altered version. The mixed results in the altered rate-of-loss model may be due to the lack of backdating in Bousfield's development of the model as opposed to our use of backdated data.

Table 8—List of regression equations fit through the residual plots for the median diameter of the mortality trees

Predictor	Coefficient	Standard deviation	*t*-ratio	$s_{y.x}$	R^2	R^2(adj)
		Original rate-of-loss model				
Constant	1.78	0.53	3.36*[1]	2.898	0.211	0.182
Predicted diameter	–.18	.05	–3.57*			
THIN	.24	.25	.97			
		Altered rate-of-loss model				
Constant	–1.65	.81	–2.04*	.972	.039	.004
Predicted diameter	.09	.07	1.15			
THIN	.29	.27	1.10			
		Population dynamics model				
Constant	–1.54	.78	–1.97*	2.950	.052	.018
Predicted diameter	.12	.07	1.60*			
THIN	.22	.26	.86			

[1]* indicates a significant *t*-ratio at the 95 percent confidence interval level.

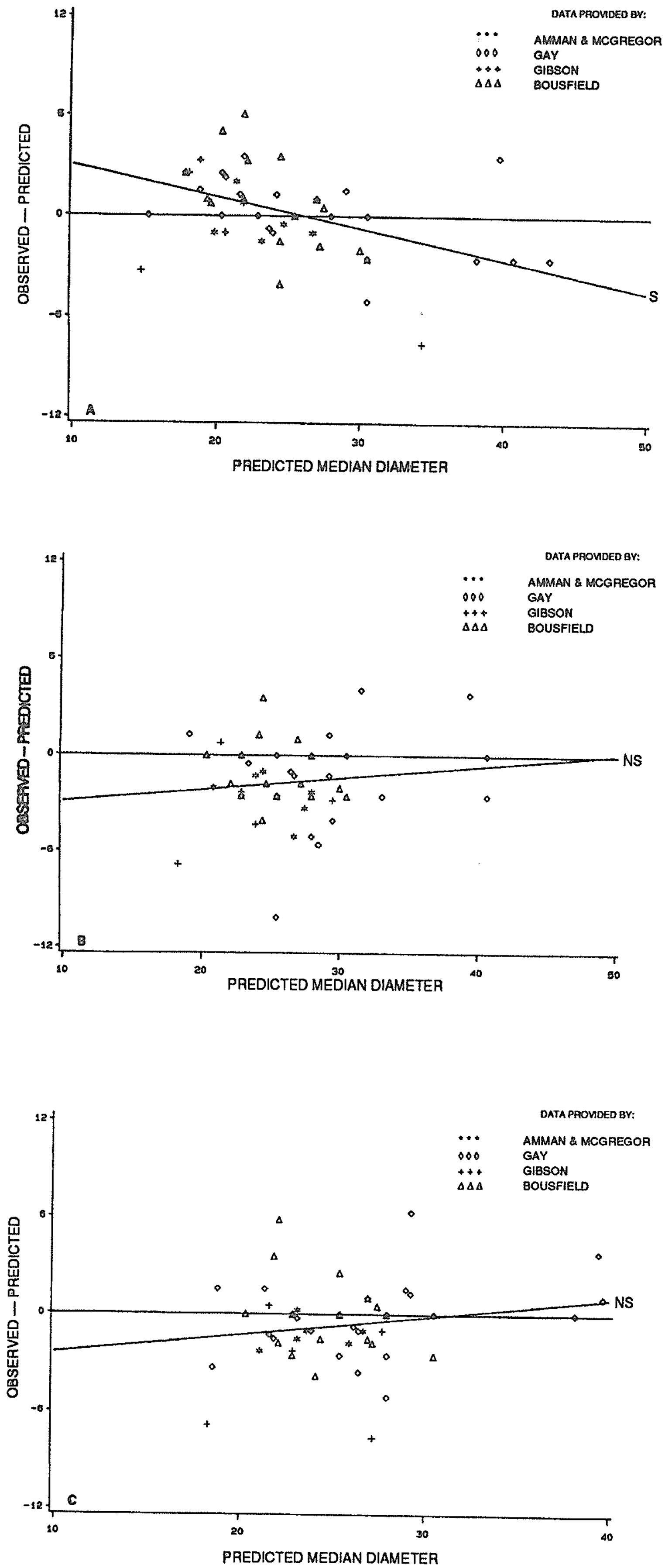

Figure 4—Residual plot of difference on median diameters (centimeters) versus predicted median diameter (centimeters) for (A) original rate-of-loss model, (B) altered rate-of-loss model, and (C) population dynamics model. S indicates a significant regression line at the 95 percent confidence level. NS indicates a nonsignificant regression line at the 95 percent confidence level.

It must also be noted that these models do not include emigration or immigration of mountain pine beetles between stands. The results may differ significantly if these elements are included in the modeling efforts.

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To aid forest managers in estimating mountain pine beetle (*Dendroctonus ponderosae* Hopkins) losses in lodgepole pine (*Pinus contorta*) stands, damage models have been developed as extensions to the Prognosis Model for Stand Development (Prognosis Model). In evaluations of three mountain pine beetle extensions to the Prognosis Model, their predictions were compared to known histories of losses. Evaluations included bias and standard deviation for the predicted volume lost to mountain pine beetle and the median diameter of the trees killed by the insect. Bias of models was also evaluated in relation to variables such as top height and relative density of the stands. The significant correlations varied with the different models. None of the models behaved best in all comparisons.

KEYWORDS: pest dynamics, tree mortality, yield estimation

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