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Integrated Control

of

Scolytid Bark Beetles

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LODGEPOLE PINE SELECTION BY MOUNTAIN PINE BEETLE IN RELATION TO GROWTH AND VIGOR FOLLOWING THINNING

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Abstract

Thinning stands of lodgepole pine (Pinus contorta Douglas var. latifolia Engelmann) is thought to increase vigor and thereby reduce susceptibility to mountain pine beetle (Dendroctonus ponderosae Hopkins). Partial-cut stands of lodgepole in the Kootenai and Lolo National Forests, Montana, U.S.A., provided opportunity (1) to determine growth response of 76- to 102-year-old lodgepole pines following thinning and (2) to test the hypothesis that vigor of residual trees infested and uninfested by beetles does not differ.

Lodgepole pine stands receiving different partial cutting treatments were sampled. Characteristics measured for trees within the sample were diameter at breast height (dbh), grams of stem wood per square meter of foliage, periodic growth ratio, and leaf area.

Trees in most treatments showed decreased growth the first year following thinning. The first year was followed by increased growth during the next 4 years.

Of the tree characteristics measured, only dbh was significantly different on both Forests between live trees and trees killed by mountain pine beetle; the latter were larger ($P < 0.001$). Active beetle infestations occurred in all stands prior to partial cutting and adjacent to stands following thinning. However, the low amount of mountain pine beetle infestation in partial-cut stands in the presence of poor growth response and vigor of residual trees suggests that factors other than tree vigor will regulate mountain pine beetle infestations in recently thinned lodgepole pine stands. The hypothesis is that change in stand microclimate is the principal factor.

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Introduction

Silvicultural methods to reduce losses from bark beetles traditionally are aimed at increasing tree vigor (Graham and Knight 1965; Keen 1958), thus making the trees better able to repel attacking beetles with copious resin flow (Reid, Whitney, and Watson 1967). Partial cutting to reduce losses of lodgepole pine, Pinus contorta Douglas var. latifolia Engelmann, to mountain pine beetle (MPB), Dendroctonus ponderosae Hopkins (Coleoptera: Scolytidae), has been effective (McGregor et al. 1987; Mitchell, Waring, and Pitman 1983; Cole, Cahill, and Lessard 1983; Cahill 1978; Hamel 1978). Early tests were based primarily on removing the large-diameter lodgepole in which MPB reproductive success is best (Amman 1969; Cole and Amman 1969; Reid 1963). More recent partial cutting tests of lodgepole pine (McGregor et al. 1987) included well-spaced thinnings that left large-diameter as well as small-diameter trees. Mountain pine beetle infestations in these partial-cut stands that left well-spaced trees of all sizes were reduced as much as that in earlier tests where only large-diameter trees were removed. Studies of growth response and various vigor indices of lodgepole pine in recently thinned (partial-cut) stands, as well as the response of MPB in thinned stands, challenge the role of tree vigor as the principal factor in preventing MPB infestations.

McGregor et al. (1987) found tree losses to MPB were significantly reduced in partial cutting treatments (4.0 to 38.6% of trees), compared to losses in unthinned check stands (73.1 to 93.8% of trees). Tree losses were ≤17% in all thinnings except spaced thinnings leaving 27.6 m^2/ha, which had losses of 38.6%. Populations were high in these areas where the partial cuts were done, as indicated by very heavy losses of trees in check stands and by catches of MPB in passive barrier traps (Schmitz et al. in press). These partial-cut stands (McGregor et al. 1987) provided opportunity to observe tree growth response and tree vigor changes in relation to susceptibility of MPB infestation.

Several tree and stand characteristics have been related to susceptibility of MPB infestations (Anhold and Jenkins 1987; Stuart 1984; Cole and McGregor 1983; Waring and Pitman 1980; Schenk, Mahoney, and Moore 1980; Mahoney 1978; Berryman 1978; Amman et al. 1977; Safranyik, Shrimpton, and Whitney 1974; Shrimpton 1973). Many of the variables measured for these methods are more appropriate for natural stands than for recently thinned stands. For example, variables related to tree competition as a precursor to MPB infestation would be inappropriate because thinning reduces numbers of trees below the level of intertree competition. These variables include crown competition factor (CCF) (Schenk, Mahoney, and Moore 1980; Berryman 1978) and stand density index (SDI) (Anhold and Jenkins 1987). The resinous response of trees to inoculation of blue-staining fungi (Ceratocystis clavigera [Robinson-Jeffrey and Davidson] Upadhyay) (Raffa and Berryman 1982; Shrimpton 1973) also is inappropriate because blue-stain inoculations did not distinguish lodgepole pine that were susceptible to MPB infestation in natural stands (Peterman 1977). Three tree characteristics that can be applied to thinned as well as natural stands are diameter at breast height (dbh) (Stuart 1984; Cole and McGregor 1983; Amman et al. 1977; Safranyik, Shrimpton, and Whitney 1974), periodic growth ratio (PGR), which is the current 5 years of radial growth divided by the previous 5 years of radial growth (Mahoney 1978), and grams of wood produced per square meter of foliage (Mitchell, Waring, and Pitman 1983).

Amman et al. (1977) and Cole and McGregor (1983) found dbh, and Stuart (1984) found quadratic mean diameter and number of growth rings in the outermost centimeter of radial growth, to be significant predictors of stand risk to MPB infestation. Mahoney (1978) found PGR an indicator of vigor and susceptibility to MPB infestation. Ratios of ≥0.9 suggest trees are resistant to beetle infestation; ratios <0.9 suggest susceptibility to infestation. As a measure of tree susceptibility, Waring and Pitman (1980) initially used the percentage of basal area contained in the most recent growth ring to total sapwood basal area. Trees having ≥15% of sapwood laid down in the current year were not attacked by MPB, trees having 8 to 15% might be attacked but not killed, and trees having <8% current sapwood basal area could be killed. Later, susceptibility classes were expressed as grams of stem wood produced per square meter of foliage. The three classes are: <50 g of wood per square meter of foliage, highly susceptible; 50 to 99 g, moderately susceptible; and ≥100 g, resistant to infestation (G. B. Pitman, personal communication, March 25, 1982). Grams of wood per square meter of foliage is thought to more closely approximate current tree vigor than do other measurements because it is based on diameter growth of the current year (Berryman 1982).

The objectives of this study were (1) to examine growth response of lodgepole pine following thinning and (2) to evaluate dbh, PGR, grams of wood per square meter of foliage, and leaf area as predictors of tree susceptibility to MPB following thinning.

Methods

Lodgepole pine were measured in partial cutting treatments that were established in late 1978 through early 1980 to test response of MPB to different intensities of thinning on the Kootenai and Lolo National Forests in western Montana (McGregor et al. 1987). The partial cutting treatments were replicated three times on each Forest: diameter limit thinnings consisted of all trees ≥25.4 or ≥30.5 cm dbh removed; spaced thinnings consisted of residual basal area 18.4, 23.0, and 27.6 m^2/ha; and untreated check stands. Stands ranged between 4.0 and 10.1 ha in size.

In June 1983, two stands in the Kootenai and one stand in the Lolo in each treatment were selected at random for study of tree susceptibility to MPB infestation. The stands were surveyed using two methods concurrently--variable radius plots (10 basal area factor = 2.3 m^2 of basal area/ha/tree) and usually two strips 20 m wide. Because the stands varied in size from 4 to 10 ha, sampling was proportional to size. The 10 BAF plots were about 50 m apart along the two strips through each stand. The first strip was about 25 m from one edge and parallel with the long axis of the stand. The second strip was about 50 m from the first strip. The number of 10 BAF plots ranged from 5 to

10, and the length of the strip from 350 to 700 m per stand. Residual stand structure was measured on the 10 BAF plots. The two live lodgepole pines closest to plot center were measured for dbh, and two increment cores were removed at random 180 degrees apart from each tree. Because of the low incidence of beetle infestation in thinned stands (see McGregor et al. 1987), the strip cruise was used to sample for trees killed by MPB. All beetle-killed trees on the strip were measured for the same characteristics listed for live trees. In June 1985, stands were again surveyed to determine tree losses to MPB and to determine growth response of surviving trees. Tree mortality was low in these years, consisting of 0.5 tree/ha in only one thinned stand in 1983 and no losses in 1984 in the Kootenai; an average of 1.4 tree/ha in all thinned stands in the Lolo in 1983 but no losses in 1984. To determine growth response of surviving trees, 23 stands were surveyed in 1985. These were two to three stands receiving each treatment on each Forest except the following, in which only one stand each was surveyed: 30.5 cm diameter limit and 23.0 m^2/ha in the Kootenai and 27.6 m^2/ha in the Lolo.

Increment cores were taken to a laboratory where radial growth and characteristics used for each of the tree vigor rating methods were measured.

Data consisting of dbh, grams of stem wood per square meter of foliage (= 0.15 m^2 foliage/cm^2 sapwood [Waring, Schroeder, and Oren 1982]), PGR, and leaf area were subjected to analysis of variance (ANOVA) and discriminant analysis. Discriminant analysis is a procedure that uses measurements on a series of characteristics to classify individuals into categories. Once a function has been developed to perform the classification, it can be used to place individuals of unknown origin in the category to which they most likely belong. The hypothesis tested was: characteristics of MPB-infested and uninfested trees do not differ. When ANOVA (SAS procedure GLM for unequal numbers) indicated significant differences, Tukey's Studentized Range Test was then used to determine significance among treatment means ($\alpha = 0.05$).

Chi-square was used to compare percentages of live and MPB-killed trees in each of three categories of grams of stem wood per square meter of foliage. The categories represented different susceptibility to MPB infestation (<50 = high; 50 to 99 = moderate; $\geq$100 = low). Differences in growth of residual lodgepole among treatments were analyzed using ANOVA of total radial stem growth for the 4 years before thinning (1975-1978), the 4 years after thinning (1981-1984), and difference in growth between the two.

Results

The sample consisted of 150 live trees and 152 dead trees in the Kootenai, and 123 live trees and 104 dead trees in the Lolo, for a total of 529 trees (number by treatment given in table 1). Tree age averaged 102 (sd = 6.8) in the Kootenai and 76 (sd = 10.9) in the Lolo.

Table 1. Diameter at breast height (dbh), grams of stem wood per square meter of foliage (wood), periodic growth ratio (PGR), and leaf area (leaf) for live and mountain pine beetle killed trees in lodgepole pine stands receiving different partial cutting treatments, Kootenai and Lolo National Forests, Montana, U.S.A.

Forest and treatment	Tree condition[1]	Numbers of trees	DBH (cm)		Wood (g)		PGR		Leaf	
			$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
KOOTENAI:										
25.4 cm diam. limit	1	30	21.6	3.74	29.06	13.78	1.16	0.32	26.1	9.6
	2	3	21.6	2.65	20.53	15.81	1.19	0.38	29.1	7.8
30.5 cm diam. limit	1	8	18.3	1.82	38.55	17.98	1.29	0.40	15.3	5.6
	2	43	22.5	3.44	38.06	17.70	1.19	0.43	25.9	11.7
18.4 m² BA/h	1	23	25.1	4.69	31.68	13.75	0.98	0.27	38.1	20.9
	2	23	29.3	5.44	29.32	13.76	1.02	0.30	43.7	17.7
23.0 m² BA/h	1	21	22.2	4.33	25.95	8.69	1.08	0.19	27.8	12.8
	2	29	28.1	3.92	31.14	21.35	0.86	0.21	37.1	13.6
27.6 m² BA/h	1	34	18.9	4.27	31.27	24.53	1.06	0.31	19.9	10.9
	2	34	24.5	4.47	39.04	34.22	1.03	0.30	35.8	16.9
Check	1	34	21.8	4.12	46.88	51.37	1.02	0.33	29.4	12.1
	2	20	25.0	4.01	31.84	11.52	1.04	0.23	34.0	13.2
LOLO:										
25.4 cm diam. limit	1	20	20.0	3.70	40.12	18.32	0.98	0.29	23.6	10.6
	2	1	24.6	--	50.60	--	0.82	--	37.6	
30.5 cm diam. limit	1	20	22.5	5.64	36.41	17.74	1.04	0.26	31.0	18.3
	2	36	23.5	3.20	38.91	15.56	1.08	0.37	31.3	10.5
18.4 m² BA/h	1	17	19.6	3.73	30.17	16.03	1.03	0.30	25.5	10.6
	2	13	25.4	3.74	17.75	8.08	0.91	0.23	39.6	16.7
23.0 m² BA/h	1	14	24.1	4.83	33.21	12.87	0.86	0.17	33.1	11.1
27.6 m² BA/h	1	18	21.6	3.42	33.64	15.36	1.20	0.47	35.7	11.0
	2	12	24.7	2.17	19.74	5.02	1.13	0.31	45.0	10.2
Check	1	34	19.7	3.42	45.52	24.12	0.97	0.24	26.4	8.8
	2	42	20.7	2.91	44.25	17.98	1.18	0.45	28.8	8.8

[1] 1 = live tree; 2 = killed tree.

Growth response

ANOVA did not detect a significant difference in growth either between Forests or among treatments before thinning nor after thinning ($P > 0.05$). Neither were the interactions between Forest and treatment significant (growth before treatment $P > 0.85$; growth after treatment $P > 0.31$). However, when the difference in growth between before and after treatment was analyzed by ANOVA, the Forests were significantly different ($P < 0.002$) (mean difference: Kootenai 0.15 cm; Lolo 0.03 cm). No significant differences were detected among treatments ($P > 0.15$) nor the Forest-treatment interaction ($P > 0.56$). In the Kootenai stands, radial growth of residual trees was slightly reduced or about the same in 1980 as in 1979, the year of most thinnings. Only trees in the 18.4 and 23.0 m^2 BA/ha treatments increased in growth the first year following thinning. However, most stands showed increasing growth trends starting in 1981 (figure 1).

The trend in radial growth in the Lolo stands, including untreated checks, also declined the first year following thinning, except for the 23.0 m^2 BA/ha treatment, which increased slightly (figure 2). Radial growth for most stands, including check stands, although not quite as large as in the Kootenai stands, generally increased from 1981 through 1984, except for a substantial decline in 1982.

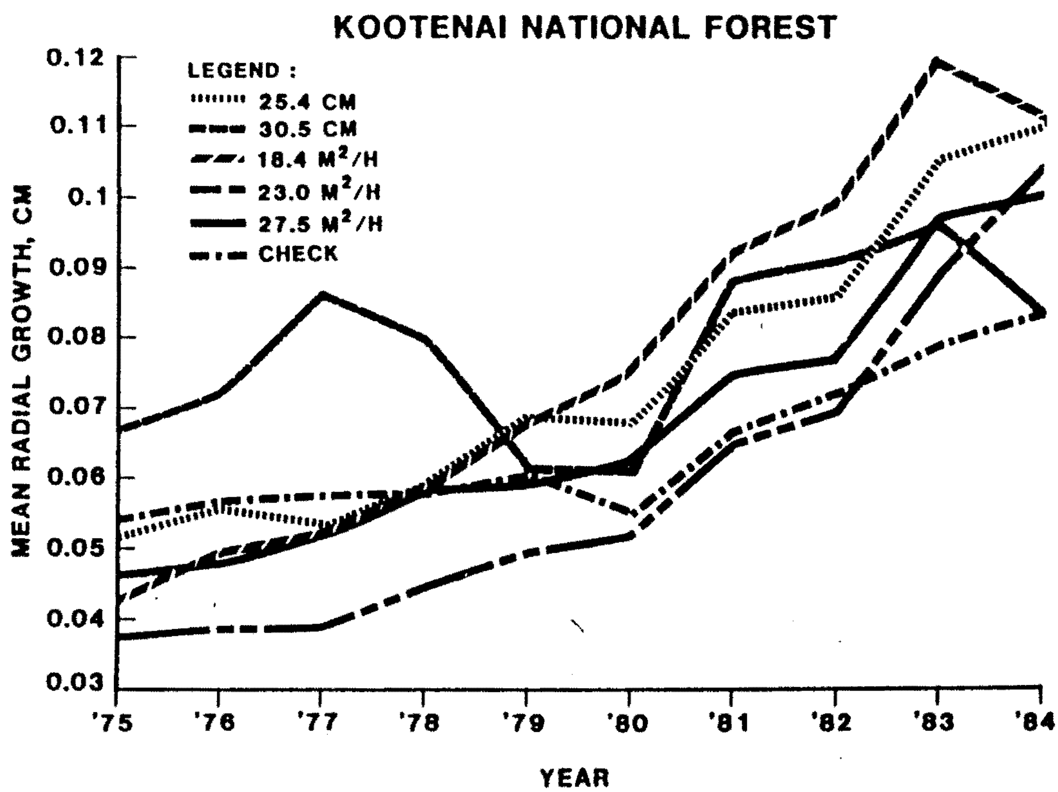

FIG. 1. Mean annual growth (radial) of lodgepole pine in partial cutting treatments applied in 1979 to reduce tree losses to mountain pine beetle, Kootenai National Forest, Montana. Curves are based on numbers of live trees shown for each treatment in table 1.

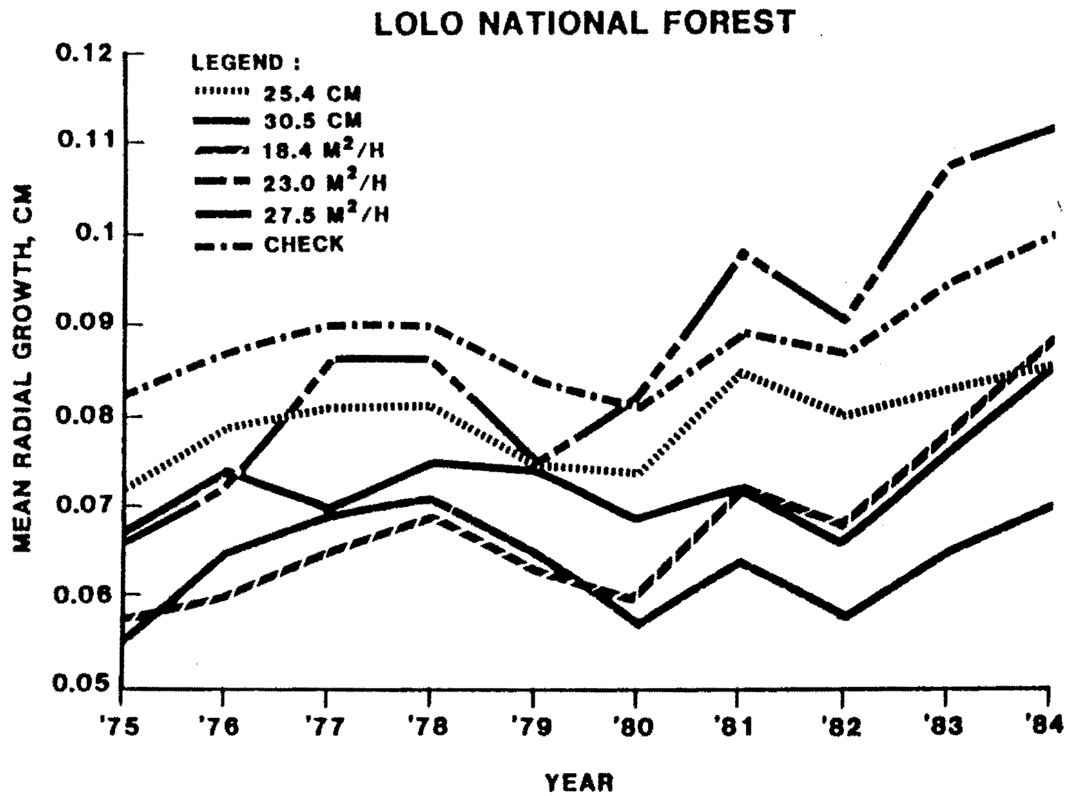

FIG. 2. Mean annual growth (radial) of lodgepole pine in partial cutting treatments applied in 1979 to reduce tree losses to mountain pine beetle, Lolo National Forest, Montana. Curves are based on numbers of live trees shown for each treatment in table 1.

Tree vigor

One-way ANOVA for the Kootenai revealed a significant difference in dbh ($P < 0.001$) between live trees ($\bar{x}$ = 21.5 cm) and MPB-killed trees ($\bar{x}$ = 25.3 cm). Neither grams of wood per square meter of foliage ($P > 0.57$) (live trees $\bar{x}$ = 34.1; dead trees $\bar{x}$ = 34.5) nor PGR ($P > 0.35$) (live trees $\bar{x}$ = 1.08; dead trees $\bar{x}$ = 1.05) were significantly different between live and MPB-killed trees. Average measurements of dbh, grams of wood per square meter of foliage, and PGR for live trees and trees killed by MPB in each cutting treatment are given in table 1.

ANOVA of data from the Lolo stands revealed significant differences in dbh ($P < 0.001$) (live trees $\bar{x}$ = 20.8 cm; dead trees $\bar{x}$ = 22.2 cm). Neither grams of wood per square meter of foliage ($P > 0.49$) (live trees $\bar{x}$ = 38.7; dead trees $\bar{x}$ = 38.4) nor PGR ($P > 0.82$) (live trees $\bar{x}$ = 1.01; dead trees $\bar{x}$ = 1.13) were significantly different between live and MPB-killed trees. The dbh of trees killed by MPB was greater than live trees in all silvicultural treatments in both the Kootenai and Lolo study areas, except the 25.4-cm diameter limit on the Kootenai, where diameters were the same, and the 23.0 m^2 BA/ha treatment on the Lolo, where no trees killed by MPB occurred in our sample.

Growth efficiency between live and MPB-killed trees was examined further by analyzing the percentages that fell in three susceptibility classes. None of the thinning treatments in either the Kootenai or Lolo showed a significant difference (Chi X^2 P >0.05). When all treatments were combined in the Kootenai stands, 86.7 and 88.2% of the live and killed trees, respectively, fell in the highly susceptible category (<50 g of stem wood/m^2 of foliage) compared to 77.4 and 77.2% of live and MPB-killed trees, respectively, in the Lolo stands. Two of the five sampled trees on the Kootenai and one of the two trees on the Lolo that produced ≥100 g of wood/m^2 of foliage were killed by MPB (one produced 215 g the year it was killed) (table 2).

The one-way ANOVA of characteristics between infested and uninfested trees gave probabilities for larger F-values ranging between 0.7 and 0.0001 for dbh in all treatments. Only the probability for dbh in the 25.4-cm diameter limit thinning exceeded 0.1 (table 3). Grams of stem wood per square meter of foliage had a probability <0.1 in only one treatment (18.4 m^2 BA/ha), PGR had probabilities <0.1 in two treatments (23.0 m^2 BA/ha and check), and leaf area had probabilities <0.1 in the three spaced thinnings (18.4, 23.0, and 27.6 m^2 BA/ha). The discriminant analysis (Wilk's Lambda) showed four treatments with probabilities <0.05 (the three spaced thinnings and the check).

Characteristics of dead trees were their larger dbh and greater leaf area than in live trees in all treatments. Grams of stem wood per

Table 2. Number of lodgepole pine, alive and killed by mountain pine beetles,[1] in three classes of susceptibility to MPB infestation based on grams of stem wood produced per square meter of foliage (<50 = highly susceptible; 50-99 = moderately susceptible; ≥100 = not susceptible) in partial cutting treatments on the Kootenai and Lolo National Forests, Montana, U.S.A., 1983

Forest		Grams of stem wood produced per square meter					
		<50		50-99		≥100	
		No.	%	No.	%	No.	%
Kootenai	Live	130	86.7	17	11.3	3	2.0
	Dead	134	88.2	16	10.5	2	1.3
Lolo	Live	106	77.4	30	21.9	1	0.7
	Dead	108	77.2	31	22.1	1	0.7
Combined	Live	236	82.2	47	16.4	4	1.4
	Dead	242	82.9	47	16.1	3	1.0

[1]No significant differences by Chi X^2 ($P \leq 0.05$).

Table 3. Probability of >F for discriminant analysis

Treatment	One-way ANOVA DBH	Grams of wood	PGR	Leaf area	Multivariate Wilk's Lambda
25.4 cm diam. limit	0.7092	0.7092	0.7092	0.7092	0.7092
30.5 cm diam. limit	.0560	.7013	.7895	.5273	.1420
18.4 m^2 BA/h	.0001	.0693	.7320	.0229	.0001
23.0 m^2 BA/h	.0001	.5823	.0151	.0292	.0001
27.6 m^2 BA/h	.0001	.7197	.4789	.0001	.0001
Check	.0787	.4671	.0303	.2676	.0448

square meter of foliage and PGR were greater in three treatments and less in three treatments, but not necessarily the same treatments. Given the characteristics observed in live trees, percentages of live trees in each treatment that would be correctly classified as live ranged between 64.0 and 74.3%, whereas 0.0 to 45.2% of the dead trees would have been classified incorrectly as live. Given the characteristics for dead trees, the percentages of dead trees in each treatment that would have been correctly classified as dead ranged between 54.8 and 100%, whereas 26.9 to 36% of the live trees would have been classified incorrectly as dead (table 4). The averages for all treatments show that 69.4% of the live trees had characteristics of live trees, whereas 30.6% of live trees had characteristics of dead trees as defined in the discriminant function. Averages show 75% of dead trees had characteristics of dead trees, and 25% of dead trees had characteristics more closely related to live trees.

A large squared distance between the means of the standardized value for the discriminant function indicates it is easy to discriminate between the groups. The squared distance is a function of the group means and the pooled variances and covariances of the variables (Afifi and Clark 1984). The pairwise squared distances, based on dbh, grams of wood, PGR, and leaf area, between live and MPB-killed trees (table 5) showed greatest distances occurred in the spaced thinnings (18.4, 23.0, and 27.6 m^2 BA/ha) and least distance in the check stands. Distances in the diameter limit thinnings were intermediate, with the 30.5-cm diameter limit thinning having a value close to the check.

Discussion

Growth response

The lack of significance (P >0.05) in growth among treatments on the Kootenai and Lolo before treatment suggests that all stands were fully using the site. The lack of significance (P >0.05) among

Table 4. Classification of live and MPB-killed lodgepole pine by the discriminant function

Treatment	Tree condition[1]	Live	Dead	Dead tree characteristics
		- - Percent - -		
25.4 cm diam. limit	1	64.0	36.0	
	2	0.0	100.0	>DBH <GMS >PGR >LA
30.5 cm diam. limit	1	71.4	28.6	
	2	39.2	60.8	>DBH >GMS >PGR >LA
18.4 m² BA/h	1	67.5	32.5	
	2	27.8	72.2	>DBH <GMS <PGR >LA
23.0 m² BA/h	1	74.3	25.7	
	2	13.8	86.2	>DBH >GMS <PGR >LA
27.6 m² BA/h	1	73.1	26.9	
	2	23.9	76.1	>DBH >GMS <PGR >LA
Check	1	66.2	33.8	
	2	45.2	54.8	>DBH <GMS >PGR >LA
Average	1	69.4	30.6	
	2	25.0	75.0	>DBH -- -- >LA

[1]1 = live tree; 2 = killed tree.

treatments following treatment suggests that not enough time had elapsed for growth differences commensurate with stocking to occur.

None of the stands could be considered vigorous. The average ages of 102 and 76 for the lodgepole pines in the Kootenai and Lolo, respectively, are past the age when maximum tree response to MPB infestation could be expected (Shrimpton 1973). In addition, trees were growing at a slow rate prior to and for several years following thinnings. Although average radial growth of trees in some stands increased 100% by the fourth year following partial cutting (for example, 23.0 m² BA/ha on the Kootenai), this was only an increase of 0.5 mm or less radial growth.

The first year following thinning, most stands showed a slight reduction in growth, which is attributed to "thinning shock." Because thinning tends to improve moisture availability in thinned stands, Donner and Running (1986) suggested that a negative growth response following thinning is probably caused by reduced photosynthetic capacity related to loss of shade leaves after exposure to full sunlight. During this first year (1980), growth probably was limited to root and shoot growth, because radial trunk growth is the last to occur (Waring 1983).

Table 5. Pairwise squared distance of the discriminant function for live and MPB-killed trees

Treatment	Distance
25.4 cm diam. limit	0.6155
30.5 cm diam. limit	0.3513
18.4 m^2 BA/h	1.7043
23.0 m^2 BA/h	2.1662
27.6 m^2 BA/h	1.3393
Check	0.3177

An increase in radial growth started the second year following thinning in all stands, including checks, in both the Kootenai and Lolo, probably because of increased moisture following thinning. Increased diameter growth following thinning can be expected in nearly all ages and densities of lodgepole stands that have not lost their physiological capability to recover from stagnation (Cole 1975). The greater growth response on the Kootenai than on the Lolo probably can be attributed to more productive sites on the Kootenai as defined by Pfister et al. (1977). Mountain pine beetles killed a few trees in most stands but at a rate much less than in untreated check stands in the Kootenai during 1980-1982, with little or no loss in 1983-1984 (McGregor et al. 1987). On the Lolo, most stands did not lose trees to MPB in 1980 even though tree growth declined and large numbers of beetles were flying through the stands, as indicated by trap catches (Schmitz et al. in press). Beetles then killed a few trees in 1981-1983 as growth rates increased. In 1984, no losses to MPB occurred, even in check stands, as the infestation declined throughout the general area (McGregor et al. 1987).

Tree vigor ratings

In the discriminant analysis, five of the six treatments yielded probabilities for F of $\leq$0.08. Data from the one treatment (25.4-cm diameter limit) that had a high probability (P >0.7) contained only four trees killed by MPB. A larger sample probably would have resulted in a probability more in line with other treatments. The close correlation of F probabilities obtained by the one-way ANOVA for dbh and those for the multivariate analyses (Wilk's Lambda) suggest dbh is the most discriminating of the four variables. Therefore, tree diameter was the most consistent indicator of lodgepole pine susceptibility to MPB infestation in recently thinned stands as well as in natural stands (Amman 1985; Stuart 1984; Safranyik, Shrimpton, and Whitney 1974; Cole and Amman 1969). The attraction to large-diameter trees is consistent with behavioral studies in the laboratory that demonstrate beetle attraction to large, dark silhouettes (Shepherd 1966) and observations in the field (Cole and Amman 1969) that show MPB consistently select the largest diameter trees in a stand each year over the life of an infestation. The infestation of lodgepole of large diameter has been related to thick phloem--food of developing larvae--found in large trees, in contrast to thin phloem found in small trees (Amman 1978; 1969). This attraction holds even in the presence of less vigorous trees, as determined by PGR and growth efficiency, which could have been infested by the large numbers of beetles that passed through the stands as measured by trapping (Schmitz et al. in press).

Grams of stem wood produced per square meter of foliage had only one significant F-value (P <0.07), and it appears to offer little use in distinguishing trees susceptible to MPB infestation. Beetles infested trees in three susceptibility classes (high, moderate, and low) in about the same proportion as they occurred in the stands in both areas. Mitchell, Waring, and Pitman (1983) stated that MPB rarely attack and kill trees that produce 100 g or more of wood/m² of foliage and did not attack trees producing over 150 g of wood. In our study, trees that produced ≥100 g of wood were rare, accounting for only 1.2% of the total. However, three (one produced 215 g of wood/m² of foliage) of the seven trees producing over 100 g of wood were killed by MPB.

Two treatments had PGR's with significant F-values (P <0.02 and <0.03) but were not consistent. In one case, trees killed by MPB had PGR's larger than those of live trees; in the other case, the reverse occurred. Therefore, PGR appears to offer little value in discriminating between trees that will and will not be infested by MPB. Similar findings were reported for southeastern Idaho (Amman 1985) and southcentral British Columbia (Shrimpton and Thomson 1983). There was a lack of selection by MPB for trees in any of the susceptibility classes defined by Pitman (personal communication, March 25, 1982) for growth efficiency and those classes defined by Mahoney (1978) for PGR in western Montana, as well as in southeastern Idaho (Amman 1985). Stuart (1984) also found growth efficiency and PGR to be poor predictors of stand risk to MPB infestation. This lack of selection suggests that beetles are responding to other factor(s) in the stands.

Leaf area was added in the discriminant analysis even though a high degree of correlation with dbh was expected. Probabilities for >F were generally larger than those for dbh, and only three were <0.1. Therefore, the effect of leaf area on the multivariate analysis was somewhat different than that of dbh and is probably related to pretreatment stand densities that would have affected length and width of live crown. The lack of discrimination in the 25.4-cm diameter limit thinning is probably due to the low number of MPB-killed trees in the sample (four).

Overall, the tree characteristics measured in this study discriminated successfully between live trees and trees killed by MPB in 69 to 75% of the cases. Diameter at breast height was the principal discriminator.

The pairwise generalized distance between live and MPB-killed trees was greatest in the spaced thinnings, intermediate in diameter limit thinnings, and least in the check. These distance differences are probably related to tree spacing. In the spaced thinnings, beetles probably are more selective of the tree they initially infest. Because of large distances between trees, other trees--for example, those of small diameter--are not included in the aggregation center created by pheromones from attacking beetles (Geiszler and Gara 1978). Therefore, a larger average tree diameter for killed trees is maintained. In contrast, partial-cut stands and check stands that have large or clumpy residual tree density also have short distances between trees. Therefore, small-diameter trees in the vicinity of large-diameter trees initially selected by MPB for infestation become included in the MPB aggregation center and also are infested. Consequently, the pairwise generalized distance for live and MPB-killed trees is much smaller in stands that are dense or in which trees are unevenly spaced.

Following partial cutting, most of the Kootenai and Lolo stands still should have been susceptible to MPB infestation. Average dbh of most stands (McGregor et al. 1987) exceeded the 20.3 cm specified in Amman et al. (1977) and Safranyik, Shrimpton, and Whitney (1974), grams of wood per square meter of foliage for most trees (82.6%) was in the highly susceptible category of <50 g, and PGR was <0.9 in many trees. However, tree losses were greatly reduced in treated stands ranging between 4.0 to 38.6%, compared to untreated check stands where losses were 73.1 to 93.8% (McGregor et al. 1987). Therefore, dbh, tree vigor measured by grams of wood per square meter of foliage, PGR, and leaf area appear to have little to do with the immediate decline in tree losses following thinning. Because both grams of wood per square meter of foliage and PGR are ratios, results can be deceiving. For example, ratios can be large even though trees are growing slowly and have little foliage. Such trees have thin phloem and little cross-sectional sapwood, and if such a tree is infested by MPB, little food is available to developing larvae and the tree dries excessively. Thus, larval survival and beetle production are low. Conversely, large-diameter trees of more open stands can have low foliage-sapwood ratios and PGR's, but because of thick phloem and large cross-sectional areas of sapwood, they have great potential for producing beetles. Such trees also have high potential for resin production and resistance to MPB infestation as determined by tree response to fungal inoculation (Shrimpton 1973). Kaufmann and Ryan (1986) illustrated the ratio problem. They found suppressed and overtopped lodgepole pine had growth efficiencies equal to the highest efficiencies observed for dominant, codominant, and intermediate trees. Hungerford (1987) found no significant difference in the foliage: sapwood area ratio in lodgepole stands ranging from 2,900 to 17,800 stems/ha. The search for a general relationship to explain forest insect outbreaks is a noble endeavor (Christiansen, Waring, and Berryman 1987), but to expect low growth efficiency of host trees to apply to all bark beetle problems ignores much of bark beetle ecology (Waters, Stark, and Wood 1985; Coulsen 1979; Rudinsky 1962). Alteration of stand microclimate probably is the key factor causing the immediate reduction in tree loss to MPB. Graham and Knight (1965) discussed microclimate as a limiting factor for some species of forest insects. This is a topic of another paper in this symposium (Bartos).

Thinning results in greater insolation, light intensity, wind movement, and reduced humidity. At constant temperature, higher light intensities and temperature caused MPB to attempt flight with greater frequency than at lower light intensities (Shepherd 1966). Higher light intensity and temperature in thinned than in unthinned stands probably caused few beetles to stop in thinned stands and may have caused many beetles to avoid the stand entirely (Schmitz et al. in press). Therefore, change in microclimate probably is more important than tree vigor in reducing tree losses to MPB in thinned stands. Studies of MPB infestation need to be continued to elucidate the roles and interactions of tree vigor, tree diameter, and stand microclimate, particularly in managed stands.

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