Susceptibility of lodgepole pine to infestation by mountain pine beetles following partial cutting of stands

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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 (*i*) to determine growth response of 76- to 102-year-old lodgepole pines following thinning and (*ii*) to test the hypothesis that vigor of residual trees infested and uninfested by beetles does not differ. Lodgepole pine stands receiving different partial cutting prescriptions were sampled. Characteristics measured for trees within the sample were diameter at breast height, grams of stem wood per square metre of foliage, periodic growth ratio, and leaf area. Trees in most treatments showed decreased growth the 1st year following thinning. The 1st 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 the mountain pine beetle; the latter were larger ($P < 0.001$). The low amount of mountain pine beetle infestation in all 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. We hypothesize change in stand microclimate is the principal factor.

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On pense généralement que l'éclaircie des peuplements de Pin tordu (*Pinus contorta* Douglas var. *latifolia* Engelmann) contribue à augmenter la vigueur et ainsi à diminuer la susceptibilité au dendroctone (*Dendroctonus ponderosae* Hopkins). Des coupes partielles effectuées dans des peuplements de Pin tordu des forêts nationales de Kootenai et de Lolo, au Montana, ont donné l'opportunité (*i*) d'étudier la réponse de croissance de peuplements de Pin tordu âgés de 76 à 102 ans à l'éclaircie et (*ii*) de vérifier l'hypothèse voulant que la vigueur des arbres résiduels infestés ou non par le dendroctone ne diffère pas. On a ainsi sondé divers peuplements de Pin tordu ayant été traités suivant différentes prescriptions de coupes partielles. Les caractéristiques d'arbres mesurées étaient le diamètre à hauteur de poitrine (dhp), le poids en grammes du bois du fût par mètre carré de feuillage, le ratio de croissance périodique et la surface foliaire. Avec la plupart des traitements, la croissance des arbres a diminué durant l'année qui a suivi l'éclaircie. Durant les 4 années subséquentes cependant, la croissance a augmenté. Parmi les caractéristiques mesurées, seul le dhp était significativement différent pour les deux forêts entre les arbres vivants et ceux qui avaient été décimés par le dendroctone; les premiers étaient plus gros ($P < 0{,}001$). Le degré plutôt faible d'infestation par le dendroctone dans tous les peuplements caractérisés par une faible réponse de croissance et une faible vigueur des arbres résiduels semble indiquer que des facteurs autres que la vigueur des arbres influencent les infestations du dendroctone dans les peuplements de Pin tordu récemment éclaircis. Nous pensons que des modifications du microclimat des peuplements pourraient constituer le facteur principal.

[Traduit par la revue]

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 et al. 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), was first tested in 1972 near Granby, Colorado (Cahill 1978). Treatment consisted of removing large-diameter trees, which favor high beetle production because of the thicker phloem (food of developing larvae) (Amman 1972). This treatment resulted in losses of 1 to 2%, whereas tree losses to MPB in unthinned stands were over 30%. Additional tests using various forms of partial cutting also greatly reduced losses to MPB (Cole et al.

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TABLE 1. Diameter at breast height (dbh), grams of stem wood per square metre of foliage (wood), periodic growth ratio (PGR), and leaf area 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[a]	No. of trees	Dbh (cm)		Wood (g)		PGR		Leaf area	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Kootenai										
25.4 cm diameter limit	1[a]	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 diameter 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 m^2 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 m^2 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 m^2 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 diameter 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 diameter 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 m^2 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 m^2 BA/h	1	14	24.1	4.83	33.21	12.87	0.86	0.17	33.1	11.1
27.6 m^2 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

[a] 1, live tree; 2, killed tree.

1983; Hamel 1978; McGregor et al. 1987). Mitchell et al. (1983) observed reduced tree losses to MPB in old thinnings established in lodgepole pine for growth and yield studies.

McGregor et al. (1987) found tree losses to MPB were significantly reduced in partial cutting treatments (4.0 to 38.6% of trees), compared with 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 in the Kootenai, which had losses of 38.6%.

Several tree and stand characteristics have been related to susceptibility of MPB infestation (Amman et al. 1977; Berryman 1978; Cole and McGregor 1983; Mahoney 1978; Safranyik et al. 1974; Schenk et al. 1980; Shrimpton 1973; Stuart 1984; Waring and Pitman 1980). Many of the items measured for these methods are more appropriate for natural stands than for recently thinned stands. For example, the methods of Schenk et al. (1980) and Berryman (1978) use crown competition factor (CCF), which in thinned stands is reduced below the level of intertree competition. The method of Shrimpton (1973) used the resinous response of trees to a blue-staining fungus (*Ceratocystis clavigera* (Robinson-Jeffrey and Davidson) Upadhyay) that is normally carried by MPB. Raffa and Berryman (1982) attempted to quantify the relation between host resistance and beetle attack behavior. They reported no relation between tree resistance and rate of resin flow, rate of resin crystallization, monoterpenes, or current growth rate of trees but found that trees resistant to fungal inoculation formed greater quantities of resin than susceptible trees. However, Peterman (1977), in a field test, found visual estimates of response to inoculation unreliable in distinguishing trees susceptible from those not susceptible to mountain pine beetle infestation. Three tree characteristics that can be applied to thinned as well as natural stands are diameter at breast height (dbh) (Amman et al. 1977; Cole and McGregor 1983; Safranyik et al. 1974; Stuart 1984), periodic growth ratio (PGR) (Mahoney 1978), and grams of wood produced per square metre of foliage (Mitchell et al. 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 of MPB infestation. Mahoney (1978) found PGR an indicator of vigor and susceptibility to MPB infestation. PGR measured at breast height is the current 5 years of radial growth divided by the previous 5 years of radial growth. 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 areas. 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 less than 8% current sapwood basal area could be killed. Later, susceptibility classes were expressed as grams of stem wood produced per square metre of foliage. The three classes are as follows: <50 g of wood/m^2 foliage, highly susceptible; 50–99 g, moderately susceptible; and ≥100 g, resistant to infestation (G. B. Pitman, personal communication). Grams

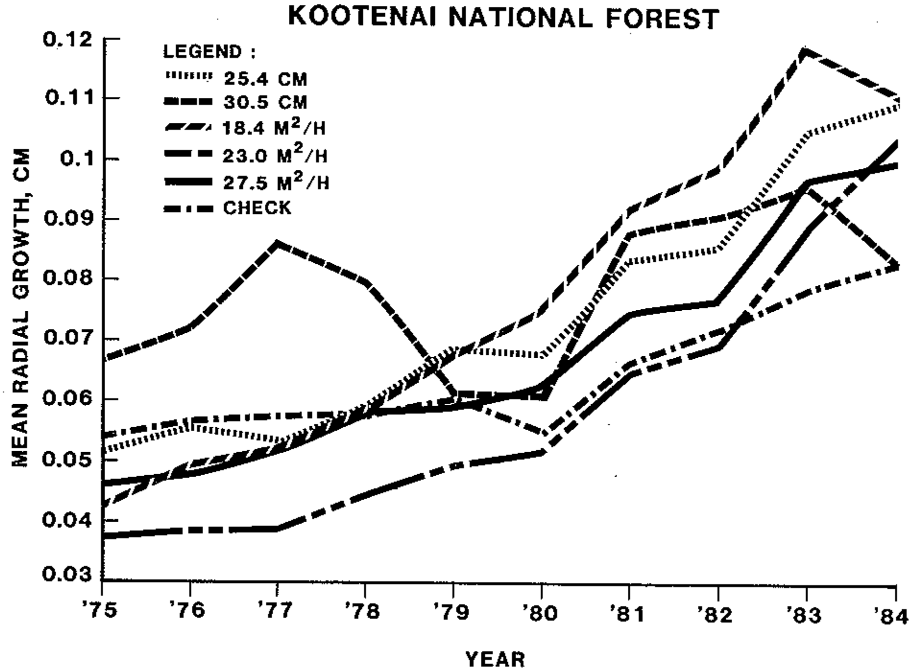

FIG. 1. Mean annual growth (radial) of lodgepole pine in partial cutting treatments applied in 1979 to reduce tree losses to mountain pine beetle, Kootenai National Forest, Montana. Curves are based on numbers of live trees shown for each treatment in Table 1.

of wood per square metre 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 our study were (*i*) to examine growth response of lodgepole pine following thinning and (*ii*) to evaluate dbh, PGR, grams of wood per square metre of foliage, and leaf area as predictors of tree susceptibility to MPB following thinning.

Methods

For our study we used 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 (McGregor et al. 1987). The partial cutting treatments were replicated three times on each forest: (*i*) diameter limit thinnings consisted of all trees ≥25.4 and ≥30.5 cm dbh removed; (*ii*) spaced thinnings consisted of residual basal area 18.4, 23.0, and 27.6 m^2/ha; (*iii*) 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 (BAF)) 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 ca. 50 m apart along the two strips through each stand. The first strip was ca. 25 m from one edge and parallel with the long axis of the stand. The second strip was ca. 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° 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 and an average of 1.4/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 the 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 in Missoula where radial growth and characteristics used for each of the tree vigor rating methods were measured.

Data obtained from live and MPB-killed trees (dbh, grams of stem wood per square metre of foliage (0.38 m^2 foliage/cm^2 sapwood; Waring et al. 1982)), PGR, and leaf area were subjected to 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 this procedure, it can be used to classify individuals of unknown origin into the category to which they most likely belong. The hypothesis tested was that 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 used to determine significance among treatment means ($\alpha = 0.05$).

χ^2 was used to compare percentages of live and MPB-killed trees in each of three categories of grams of stem wood per square metre of foliage. The categories represented different susceptibility to MPB infestation (<50, high; 50–99, moderate; ≥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, 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.

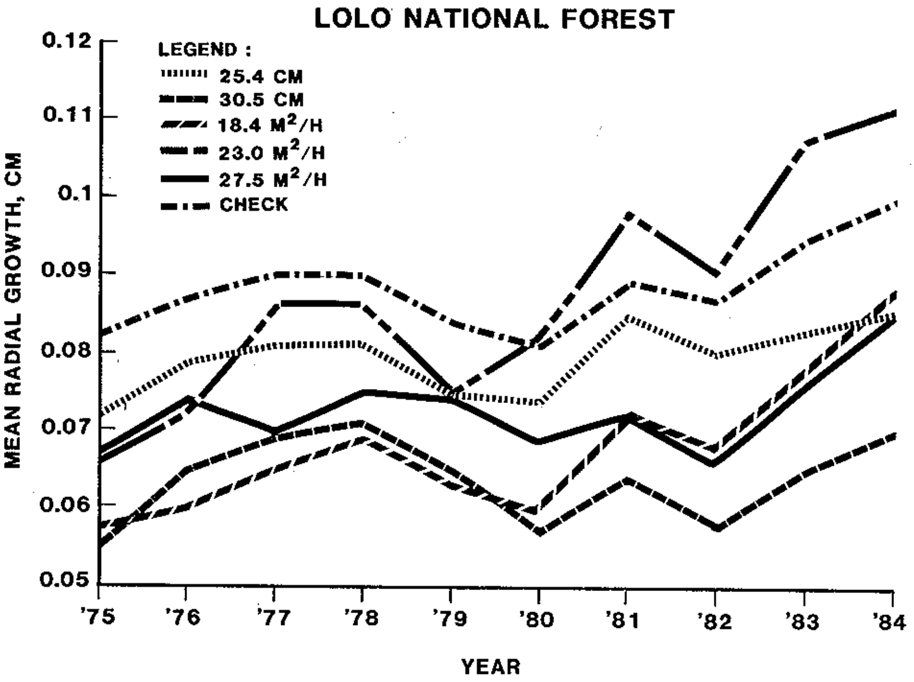

FIG. 2. Mean annual growth (radial) of lodgepole pine in partial cutting treatments applied in 1979 to reduce tree losses to mountain pine beetle, Lolo National Forest, Montana. Curves are based on numbers of live trees shown for each treatment in Table 1.

Growth response

ANOVA did not detect a significant difference in growth either between Forests or among treatments before thinning or 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). Significant differences were not detected among treatments ($P > 0.15$) or 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 1979, the year of most thinnings. Only trees in the 18.4 m^2 BA/ha and 23.0 m^2/ha treatments increased in growth the 1st year following thinning. However, most stands showed increasing growth trends starting in 1981 (Fig. 1).

The trend in radial growth in the Lolo stands, including untreated checks, also declined the 1st year following thinning, except for the 23.0 m^2/ha treatment, which increased slightly (Fig. 2). Radial growth for most stands, including check stands, although not quite as large as in the Kootenai stands, showed an upward trend from 1981 through 1984, with a substantial decline in 1982.

Tree vigor

One-way analyses of variance 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 metre 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 metre of foliage, and PGR for live and trees killed by MPB in each cutting treatment are given in Table 1.

TABLE 2. Number of lodgepole pine, alive and killed by mountain pine beetles,[a] in three classes of susceptibility to MPB infestation in partial cutting treatments on the Kootenai and Lolo National forests, Montana, U.S.A., 1983

	Stem wood produced (g/m^2)					
	$<50^b$		50–99^c		$\geq 100^d$	
	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

[a] No significant differences by χ^2, $\alpha = 0.05$.
[b] <50 g/m^2, highly susceptible.
[c] 50–99 g/m^2, moderately susceptible.
[d] ≥ 100 g/m^2, not susceptible.

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 metre 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, which had no trees killed by MPB that fell within our sample.

Growth efficiency between live and MPB-killed trees was examined further by analyzing the percentages that fell in

TABLE 3. Probability of $>F$ for discriminant analysis

Treatment	One-way ANOVA				Multivariate (Wilk's λ)
	DBH	Grams of wood	PGR	Leaf area	
25.4 cm diameter limit	0.7092	0.7092	0.7092	0.7092	0.7092
30.5 cm diameter limit	0.0560	0.7013	0.7895	0.5273	0.1420
18.4 m^2 BA/h	0.0001	0.0693	0.7320	0.0229	0.0001
23.0 m^2 BA/h	0.0001	0.5823	0.0151	0.0292	0.0001
27.6 m^2 BA/h	0.0001	0.7197	0.4789	0.0001	0.0001
Check	0.0787	0.4671	0.0303	0.2676	0.0448

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

Treatment	Tree condition	% live	% dead	Dead tree characteristics[a]
25.4 cm diameter limit	Live	64.0	36.0	
	Dead	0.0	100.0	>dbh, <g/m^2, >PGR, >LA
30.5 cm diameter limit	Live	71.4	28.6	
	Dead	39.2	60.8	>dbh, >g/m^2, >PGR, >LA
18.4 m^2 BA/h	Live	67.5	32.5	
	Dead	27.8	72.2	>dbh, <g/m^2, <PGR, >LA
23.0 m^2 BA/h	Live	74.3	25.7	
	Dead	13.8	86.2	>dbh, >g/m^2, <PGR, >LA
27.6 m^2 BA/h	Live	73.1	26.9	
	Dead	23.9	76.1	>dbh, >g/m^2, <PGR, >LA
Check	Live	66.2	33.8	
	Dead	45.2	54.8	>dbh, <g/m^2, >PGR, >LA
Average	Live	69.4	30.6	
	Dead	25.0	75.0	>dbh, — — >LA

[a] dbh, diameter at breast height; g/m^2, grams of stem wood per square metre of foliage; PGR, periodic growth ratio; LA, leaf area.

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

Treatment	Distance
25.4 cm diameter limit	0.6155
30.5 cm diameter 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

three susceptibility classes. None of the thinning treatments in either the Kootenai or Lolo showed a significant difference (χ^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 with 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 analyses of variance 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 (Table 3). Only the probability for the 25.4 cm diameter limit thinning exceeded 0.1. Grams of stem wood per square metre of foliage had $P < 0.1$ in only one treatment (18.4 m^2 BA/ha), PGR had $P < 0.1$ in two treatments (23.0 m^2 BA/ha and check), and leaf area had $P < 0.1$ in the three spaced thinnings (18.4, 23.0, and 27.6 m^2 BA/ha). The discriminant analysis (Wilk's λ) showed four treatments with $P < 0.05$ (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 square metre 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 closer to the check than the 25.4 cm.

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 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 very 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 4th year following partial cutting (for example, 23.0 m^2 BA/ha on the Kootenai), this was only an increase of 0.5 mm or less radial growth.

During the 1st year following thinning, most stands showed a slight reduction in growth, which we attribute to "thinning shock." Because thinning tends to improve moisture availability in thinned stands, Donner and Running (1986) suggest 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 1st year (1980), growth probably was limited to root and shoot growth, because radial trunk growth is the last to occur (Waring 1983). An increase in radial growth started the 2nd 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). MPB 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 (R.F. Schmitz, unpublished data). MPB 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 ≤ 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 λ) 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; Cole and Amman 1969; Stuart 1984). The attraction to large-diameter trees is consistent with behavioral studies demonstrating beetle attraction to large, dark silhouettes in the laboratory (Shepherd 1966), and field observations (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 1969, 1978). 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 (R.F. Schmitz, unpublished data).

Grams of stem wood produced per square metre of foliage had only one significant F-value ($P < 0.07$) and appears to offer little value 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 et al. (1983) stated that MPB rarely attack and kill trees that produce 100 g or more of wood per square metre of foliage and did not attack trees producing over 150 g of wood. In our study, three (one produced 215 g of wood/m^2 of foliage) of the seven trees producing over 100 g of wood were killed by MPB.

Two treatments had PGRs with significant F-values ($P < 0.02$, $P < 0.03$) but were not consistent. In one case, trees killed by MPB had PGRs 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 south central British Columbia (Shrimpton and Thomson 1983). There was a lack of selection by MPB for trees in any of the susceptibility classes defined by G. B. Pitman (personal communication) for growth efficiency and those defined by Mahoney (1978) for PGR in western Montana, as well as in southeastern Idaho (Amman 1985). This lack of selection suggests that beetles are responding to other factor(s) in the stands. Stuart (1984) also found growth efficiency and PGR to be poor predictors of stand risk to MPB infestation.

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 less than 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 and trees killed by

MPB in 69 to 95% 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 as to the tree they initially infest. Because of large distances between trees, other trees (e.g., those of small diameter) are not included in the aggregation center created by pheromones from attacking beetles, an idea proposed by Geiszler et al. (1980). 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 et al. (1974). Grams of wood per square metre of foliage for most trees 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 and 38.6%, compared with 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 metre of foliage, PGR, and leaf area appear to have little to do with the immediate decline in tree losses following thinning. We believe alteration of stand microclimate is the key factor causing the immediate reduction in tree loss to MPB. Microclimate as a limiting factor for some species of forest insects was discussed by Graham and Knight (1965).

Mitchell et al. (1983) considered the idea that open stands were unacceptable to MPB but dismissed it because one thinned stand in their study failed to respond with increased growth efficiency and became infested by MPB. However, the average diameter (23.2 cm) in that stand exceeded any other stand in their study by 2.6 cm. As shown in our study and others (Amman 1985; Cole and McGregor 1983; Stuart 1984), diameter is an overriding factor in tree selection by MPB, and because of time since thinning, the stand may have developed a suitable microclimate.

Thinning results in greater insolation, light intensity, wind movement, and reduction in humidity. At constant temperature, higher light intensities and temperatures 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 cause few beetles to stop in thinned stands and may cause many beetles to avoid the stands entirely (R.F. Schmitz, unpublished data). Therefore, we offer the hypothesis that change in microclimate when thinning lodgepole pine is more important than tree vigor in reducing tree losses. When crowns of lodgepole increase in size following thinning, shade and accompanying microclimate slowly change to create an environment conducive to MPB infestation. Anhold and Jenkins (1987) explored the application of stand density index (Reineke 1933) to hazard rate lodgepole stands infested by MPB. They observed greatest mortality at relatively low SDI values of 125 to 150, and hypothesize that trees are starting to come under stress because crowns are beginning to touch or close. In view of the great reduction in tree losses to MPB following thinning without a concomitant increase in vigor in our study, we suspect that the SDI levels identified by Anhold and Jenkins (1987) occur at about the same time stand microclimate becomes attractive to MPB. We predict greater attention to changes in microclimate, not just tree growth, will be needed in future managed stands to assess susceptibility to MPB infestation. Of course, beetles are less likely to be found at an endemic level in a thinned (managed) stand, and therefore for an infestation to start, beetles may need to migrate from adjacent unmanaged stands into managed stands. Stands that were thinned some years ago but now offer a microclimate attractive to MPB will probably be vulnerable even though trees are growing well.

The role of tree vigor in preventing successful beetle infestation will continue to be debated, but as yet it appears no satisfactory way has been devised to measure vigor. If the methods now used do indeed measure vigor, then the MPB seems to be ignoring tree vigor. Studies of MPB infestation need to be continued in partial cut lodgepole pine stands to elucidate the role and interactions of tree vigor, tree diameter, and stand microclimate.

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