Effect of partial cutting treatments of lodgepole pine stands on the abundance and behavior of flying mountain pine beetles

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Passive barrier traps deployed at three heights above ground were used to determine the effect of five intensities of partial cutting of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) and two unthinned check stands on response of flying mountain pine beetles (*Dendroctonus ponderosae* Hopkins) from 1980 to 1983 on two sites in western Montana. Percentages of mountain pine beetles caught 4 years after thinning were significantly greater in the least severely thinned (27.6 m^2 basal area/ha) treatment (27%) and the unthinned check (28%) than in the 25.4 cm diameter limit (8%) and the 23.0 m^2 basal area/ha (7%) thinnings ($P < 0.05$). Numbers of mountain pine beetles trapped in the 18.4 m^2 basal area/ha thinning did not differ significantly from other treatments. The proportions of mountain pine beetles caught at three trapping heights differed significantly ($P < 0.05$), totaling 63, 28, and 9% at midbole, midcrown, and 1.8 m above ground, respectively. Fewer trees were killed in relation to the numbers of mountain pine beetles trapped in the most severely thinned stands. However, tree mortality rates could not be attributed to thinning-induced changes in tree vigor. These findings, and the preference of flying mountain pine beetles for the midbole stratum, suggest that stand environment is an important factor regulating the severity of tree killing.

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Des pièges passifs ont été installés à trois hauteurs au-dessus du sol et ont servi à déterminer l'effet de cinq degrés de coupe partielle dans des peuplements de Pin à feuilles tordues (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) et de l'absence de coupe dans deux peuplements témoins sur la réponse du dendroctone (*Dendroctonus ponderosae* Hopkins) de 1980 à 1983 dans deux localités de l'ouest du Montana. La proportion de dendroctones capturés 4 ans après l'éclaircie était plus élevée de façon significative dans le peuplement ayant été éclairci le moins fortement avec une surface terrière prélevée de 27,6 m^2/ha (27%) et dans le témoin non éclairci (28%) que dans la coupe à diamètre minimum d'utilisation de 25,4 cm (8%) et dans l'éclaircie à 23,0 m^2/ha (7%) ($P < 0,05$). Le nombre des insectes capturés dans l'éclaircie à 18,4 m^2/ha ne différait pas des autres traitements de façon significative. Les nombres des insectes capturés aux trois hauteurs de capture différaient de façon significative ($P < 0,05$) totalisant 63, 28 et 9% pour le milieu du tronc, le milieu de la cime et 1,8 m au-dessus du sol, respectivement. Toutes proportions gardées, moins d'arbres ont été tués en liaison avec le nombre d'insectes capturés dans les peuplements les plus fortement éclaircis. Toutefois, le taux de mortalité des arbres n'a pas pu être attribué aux modifications de leur vigueur provoquées par l'éclaircie. Ces résultats, ainsi que la préférence pour le dendroctone de voler au niveau du milieu du tronc, indiquent que l'environnement du peuplement constitue un facteur important affectant la sévérité de la mortalité des arbres.

[Traduit par la revue]

Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) continues to be the major source of lodgepole pine mortality in stands in the United States throughout Montana, Idaho, Utah, Wyoming, Colorado, and Oregon, and in western Canada (Loomis et al. 1985; Sterner and Davidson 1982). Although methods exist for suppressing MPB infestations, including logging, application of insecticides, and felling and burning, none are particularly well suited for suppressing outbreaks over the extensive area currently infested. Environmental constraints on the use of chemical controls and clear-cutting, and the difficulty of harvesting, milling, and marketing the tremendous volumes infested, prompted a large-scale test of an alternative management strategy. The strategy was based on a preventive approach suggested by results from previous research. The intent was to reduce stand hazard by partial cutting to deprive the beetle of its preferred host material, thereby limiting tree killing and preventing MPB populations from building to outbreak levels (McGregor et al. 1987).

The strategy was based on the knowledge that the beetle prefers large-diameter trees which have the thickest phloem and therefore produce more beetles per unit area of bark

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TABLE 1. Characteristics of stands selected for monitoring in-flight populations of the mountain pine beetle

Cutting treatment	Area (ha)	No. of trees killed/ha before treatment (1976–1979)	Lodgepole pine after treatment		Basal area after treatment (m^2)	
			dbh (cm)	No./ha	Lodgepole pine	All species
25.4 cm diam. limit						
Lolo unit 4	7.7	38.0	17.8	758.6	20.7	24.3
Kootenai unit B6	7.3	0.5	18.8	805.6	30.3	37.9
30.5 cm diam. limit						
Lolo unit 3	6.9	41.8	20.6	602.9	21.3	23.4
Kootenai unit H5	5.7	26.7	23.4	462.1	17.0	20.9
18.4 m^2 residual BA/ha						
Lolo unit 1	6.1	2.4	20.3	269.3	8.0	18.4
Kootenai unit B4	6.5	4.9	23.1	331.1	14.5	17.2
23.0 m^2 residual BA/ha						
Lolo unit 11	6.1	1.2	21.6	494.2	18.6	23.9
Kootenai unit B3	7.7	3.7	19.1	780.9	22.7	22.7
27.6 m^2 residual BA/ha						
Lolo unit 6	6.9	16.3	18.8	897.0	28.9	29.8
Kootenai unit B8	7.3	28.4	26.9	170.4	10.6	25.5
Untreated checks						
Lolo						
Unit 7A	8.5	12.1	21.1	879.7	30.8	31.0
Unit 18	6.1	96.8	20.3	672.1	21.8	30.1
Kootenai						
Unit B10	9.3	430.3	20.3	1477.7	49.6	55.6
Unit B11	10.1	396.2	20.3	1314.6	49.6	56.5

than small-diameter trees (Amman 1972). Removal of the larger trees limits MPB survival and prevents populations from building to outbreak proportions. The most recent test of partial cutting prescriptions consisted of removing from different stands all lodgepole pine with diameter at breast height (dbh) of 17.8, 25.4, and 30.5 cm and larger; prescriptions leaving 18.4, 23.0, and 27.6 m^2 basal area (BA) per hectare were also tested (McGregor et al. 1987). The first 5 years' results following cutting showed greatly reduced tree killing by the MPB in the thinned stands compared with the uncut checks. There were no significant differences in tree losses among partial cut treatments. Posttreatment mortality of lodgepole pine 12.7 cm dbh and larger to MPB averaged 4–38.6% in these thinned stands compared with 73.1–93.8% in the untreated checks (McGregor *et al.* 1987).

The objective of this study was to determine the effect of thinning on the abundance and behavior of dispersing MPB in the treated stands following treatment. The findings summarize results recorded from 1980 to 1983 in five partial cutting treatments and uncut check stands that were replicated on two national forests, Lolo National Forest near Thompson Falls, Montana, and Kootenai National Forest near Libby, Montana (McGregor et al. 1987).

Little is known about the influence of stand environment on the flight and host selection behavior of the MPB. What has been documented has been observed during outbreaks in uncut stands. The fact that the beetle kills the largest-diameter lodgepole pines remaining in infested stands during successive years of an outbreak is well documented (Hopping and Beal 1948; Cole and Amman 1969). This observation agrees with laboratory measures of host selection behavior that show the beetle is attracted to large, dark silhouettes (Shepherd 1966) and vertical cylinders (Gray et al. 1972; Schönherr 1976). The beetle's apparent preference for large-diameter trees is such that it will attack these trees even when intermingled smaller trees are baited with components of the beetle's aggregative pheromone (Rasmussen 1972). Some investigators have suggested that the height of the upright silhouette is more important than the width (Borden et al. 1986). Flight height above ground appears to be independent of either ambient temperature or wind speed (Gray et al. 1972). Measurement of the time of arrival of the MPB at attractive log sections revealed that peak flight periods occur in late afternoon and coincide with prestorm conditions; micrometeorological studies have shown that the air mass beneath the canopy is most stable at this time (Fritschen 1984; Edson 1978). The role of the MPB's pheromone as a chemical messenger to aid in host selection and to induce and terminate mass attack on lodgepole pine has been conclusively demonstrated in the field (Pitman 1971; Borden et al. 1983, 1986). Preliminary measures of flight behavior of the MPB in lodgepole pine stands in Montana and Wyoming following cutting suggested that (*i*) beetles were most abundant just beneath the canopy, and (*ii*) while present in about equal numbers in thinned and unthinned stands, beetles killed more trees in unthinned stands (Schmitz et al. 1980). These findings prompted the longer-term test described in this paper, which included a broader range of thinning treatments to determine how stand density affects the dispersion of the MPB.

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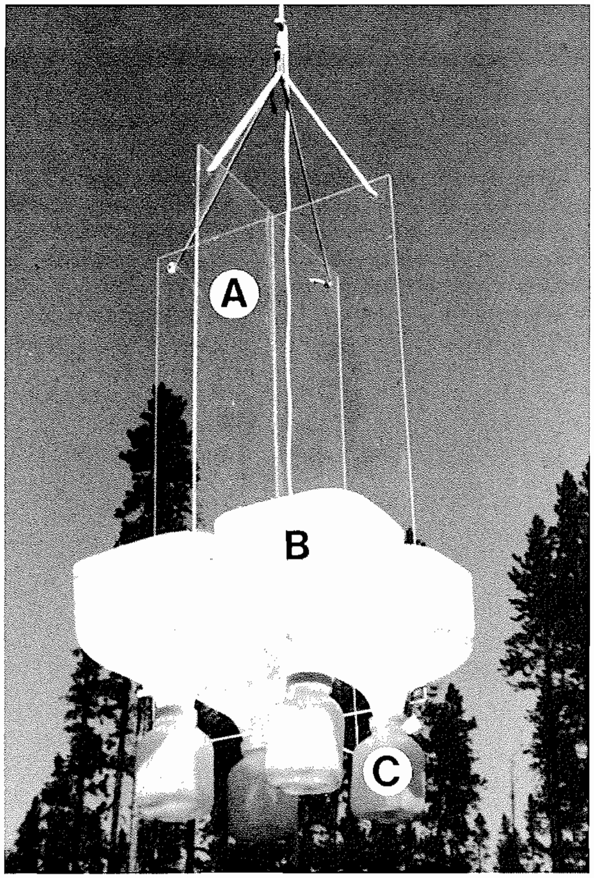

FIG. 1. Omnidirectional passive barrier trap consisting of two Plexiglas panels positioned at right angles (A), four funnel-like collectors bolted to the base of the panels (B), and four plastic bottles to contain trapped insects (c).

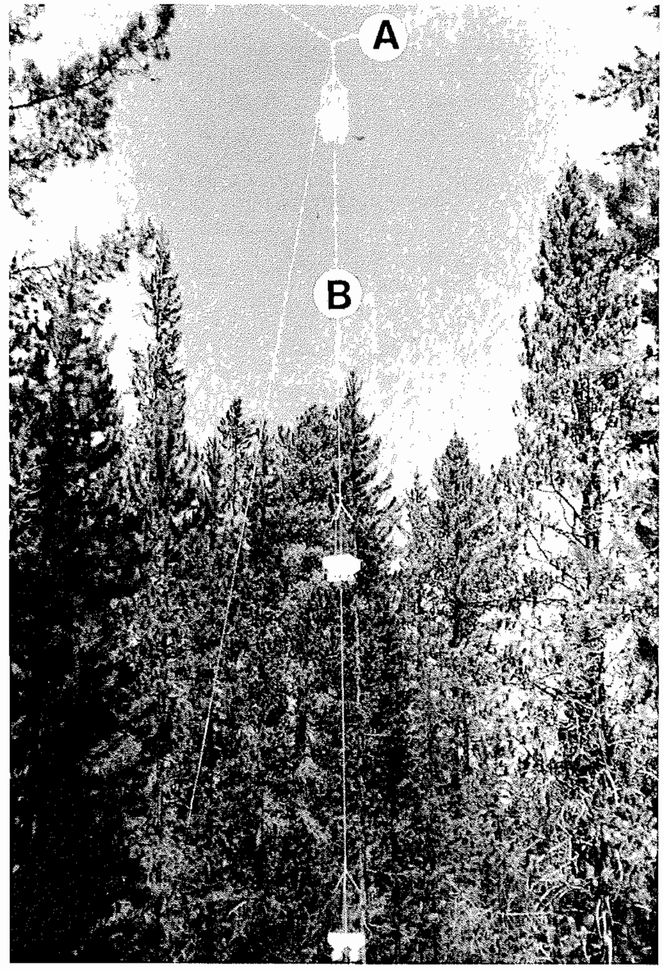

FIG. 2. Deployment of omnidirectional passive barrier trap, showing horizontal support line with pulley for attachment of vertical line (A), and vertical line used to raise and lower traps, with traps attached (B).

Methods and materials

Mountain pine beetle flight was monitored in the study stands in western Montana. The Kootenai sites were approximately 129 km northwest of the Lolo sites. Elevations of the test stands on the Kootenai Forest ranged from 1036 to 1219 m, and those on the Lolo from 1146 to 1406 m. These stands were selected because they had been partially cut to test the effectiveness of a partial cutting strategy that removed the larger-diameter trees to modify stand density and spacing to reduce tree killing by the MPB (McGregor et al. 1987). Beetle flight behavior and abundance were evaluated in five partial cutting treatments: two diameter-limit cuts (all trees 25.4 and 30.5 cm dbh and larger removed) and three basal area cuts which left 18.4, 23.0, and 27.6 m^2 residual basal area per hectare. Also evaluated were two unthinned check stands in each test area (Table 1) (McGregor et al. 1987). One replicate of each thinning treatment and two uncut check stands were selected for monitoring on each forest. Within each forest, stands selected for monitoring were as close to one another as possible to ensure that each treatment was exposed to MPB populations of similar density. However, to ensure that stands selected for thinning were similar in age, average diameter, and species composition, it was sometimes necessary to select stands from different locales within a forest. Overall, the distance between treatments on the Kootenai Forest was less than that on the Lolo.

Treatments on the Kootenai were clustered within three adjacent drainages. One drainage (Benefield) contained four (18.4, 23.0, and 27.6 m^2 BA/ha and 25.4 cm diameter limit) of the five thinning treatments and two uncut check stands monitored for beetle abundance. The four treated stands were situated so that no treatment was more than 270 m from a check stand. The remaining thinning (30.5 cm diameter limit) was approximately 4 km by air from this cluster. Treatments monitored within the Lolo Forest were divided between two areas, with five of the treatment blocks (18.4 and 27.6 m^2 BA/ha, 25.4 and 30.5 cm diameter limit, and the uncut check) clustered in the Mantrap drainage, while the 23.0 m^2 BA/ha and one uncut check were in the Fishtrap and Beartrap drainages, approximately 4.3 and 5.8 km by air, respectively, from the Mantrap cluster.

Annual stand surveys initiated before the partial cuts were made revealed the MPB had killed trees in all the test stands in which MPB were to be trapped (Table 1). Currently infested trees were removed in 1979, when the partial cuts were completed and before trapping was undertaken. All treatments were in place beginning with the 1980 flight period.

Omnidirectional passive barrier traps were used to monitor the number of beetles in flight from 1980 to 1983 (Schmitz 1984). Traps consisted of two clear Plexiglas panels (30 cm wide by 57 cm high) at right angles to one another (Fig. 1). This design provides a total intercepting surface above the funnels of 0.72 m^2, accounting for the fact that a single panel may intercept beetles approaching from opposing directions. The traps were supported by a single vertical line suspended from a pulley attached to a horizontal line supported by the crowns of two adjacent trees. The horizontal line was positioned in the tree crowns with a bow and arrow or line gun (Schmitz 1984). Three traps were attached to a vertical line at each of two locations (six traps per stand) within each of the 10 treated stands and 4 uncut checks. The traps were positioned at midcrown (midway between the extremities of the live crown), at midbole (mid-

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TABLE 2. Numbers of mountain pine beetles trapped, by treatment and year, in the Kootenai and Lolo national forests, Montana, 1980–1983

Treatment	*N*	1980		1981		1982		1983		Total		Forests combined (1980–1983)		Transformed means†
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
25.4 cm diam. limit														
Kootenai	1	19	8	34	9	3	4	4	11	60	8			
Lolo	1	3	6	3	8	0		12	14	18	9			
												78	8	1.733*b*
30.5 cm diam. limit														
Kootenai	1	59	26	42	12	0		0		101	15			
Lolo	1	8	17	5	13	9	28	10	12	32	16			
												133	15	2.140*b*
18.4 m^2 residual BA/ha														
Kootenai	1	36	16	44	12	17	24	13	35	110	17			
Lolo	1	6	12	3	8	1	3	14	16	24	12			
												134	15	2.217*ab*
23.0 m^2 residual BA/ha														
Kootenai	1	9	4	11	3	16	23	9	24	45	6			
Lolo	1	9	19	4	10	2	6	0		15	7			
												60	7	1.675*b*
27.6 m^2 residual BA/ha														
Kootenai	1	44	19	124	35	12	17	2	5	182	26			
Lolo	1	19	39	14	36	5	16	26	30	64	31			
												246	27	2.868*a*
Uncut checks														
Kootenai														
1		57		72		15		13		157	18			
2		69		133		29		6		237	27			
Average		63.0	27	102.5	29	22.0	32	9.5	25	197.0	28			
Lolo														
1		4		15		23		16		58	23			
2		3		4		7		32		46	18			
Average		3.5	7	9.5	25	15.0	47	24.0	28	52.0	25			
Average for forests combined		66.5		112.0		37.0		33.5						
												249*	28	
													100	2.857*a*
All treatments combined														
Kootenai	7	230	33	357.5	52	70	10	37.5	5	695	100			
Lolo	7	48.5	23	38.5	19	32	16	86	42	205	100			
Forests combined		278.5	30	396	44	102	12	86	14	900	100	900		
Mean‡		2.560*a*		2.771*a*		1.929*b*		1.734*b*						

*Total includes mean for number of MPB caught in two check treatments for each forest.
†Values followed by same letter are not significantly different ($P > 0.05$); Tukey's Studentized range critical value = 4.117.
‡Values followed by same letter are not significantly different ($P > 0.05$); Tukey's Studentized range critical value = 3.701.

way between the ground and the bottom of the live crown), and at the bottom (about 1.8 m above ground level) (Fig. 2). To ensure that traps were in position throughout the flight period, bark samples were periodically removed from infested trees within the study areas to assess brood development and project the earliest date of adult emergence.

An analysis of variance was performed for the numbers of MPB caught (transformed: $(n + 1)^{1/4}$). The model used was a four-way factorial with forest, year, treatment, and trapping height as the four factors. Tukey's Studentized range test was used to test for significant difference among means.

Results

Abundance by treatment

Analysis of variance revealed that the total numbers of beetles caught among treatments after 4 years for both areas combined were significantly different ($P < 0.0013$). Based on the numbers of beetles caught, Tukey's Studentized range test showed the treatments separated into two groups (Table 2). One group, in which the fewest beetles were caught, included the basal area thinning of intermediate severity (23.0 m^2 BA/ha) and the two diameter-limit thin-

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TABLE 3. Relationship of number of mountain pine beetles trapped and estimated in-flight populations to number of residual lodgepole pine killed, by treatment, at Lolo and Kootenai national forests, Montana, 1980–1983

	Lolo National Forest						Kootenai National Forest					
	Residual trees killed/ha		Total MPB trapped*		Estimated no. of MPB in flight/ha†	Ratio of trees killed to estimated MPB in flight	Residual trees killed/ha		Total MPB trapped		Estimated no. of MPB in flight/ha	Ratio of trees killed to estimated MPB in flight
Treatment	No.	%	No.	%			No.	%	No.	%		
Diam. limit												
25.4 cm	65	8.6	18	7	48 768	1:750	96	11.9	60	7	162 560	1 : 1693
30.5 cm	105	17.5	32	12	86 699	1:825	42	9.0	101	11	273 642	1 : 6515
Residual BA												
18.4 m^2/ha	13	4.7	24	9	65 024	1:5001	10	3.0	110	12	298 026	1 : 29 802
23.0 m^2/ha	55	11.1	15	6	40 640	1:739	31	4.0	45	5	121 920	1 : 3932
27.6 m^2/ha	243	27.0	64	25	173 397	1:713	115	67.7	182	20	493 098	1 : 4288
Uncut check												
1	365	41.4	58	23	116 501	1:319	1047	70.8	157	18	425 365	1 : 406
2	423	62.9	46	18	167 978	1:397	918	69.8	237	27	642 111	1 : 699
Total	1269		257	100			2259	100.0	892	100		

*Derived from the number caught in six passive barrier traps, each with 0.72 m^2 of trapping surface. Two sets of three traps each were positioned within each treatment at three heights (1.8 m above ground, midbole, and midcrown).

†Assumes that the number of MPB flying in each square metre of untrapped air at that stratum was the same as the number caught per unit area of trap surface (0.72 m^2). Total intercepting surface used to derive the estimate was equivalent to that represented by two imaginary vertical planes positioned at right angles, with their point of intersection at the plot center and extending across the width of the treatment area. The estimate accounted for vertical stratification of the catch by assuming an average tree height of 30 m and that the catch at the basal, midbole, and midcrown positions was representative of a 10-m stratum at each of those positions.

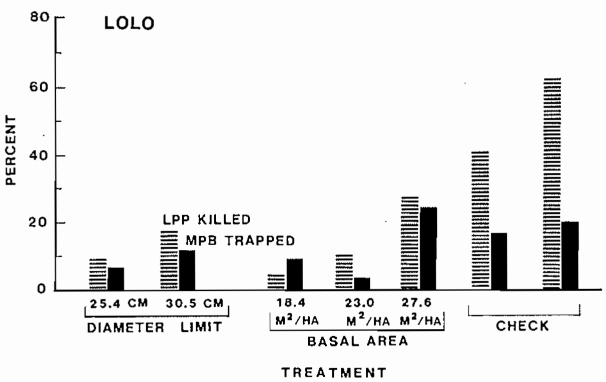

FIG. 3. Total percentages of mountain pine beetles (MPB) caught per treatment compared with percentages of residual lodgepole pine (LPP) killed per treatment following thinning, Lolo National Forest, Montana, 1980–1983.

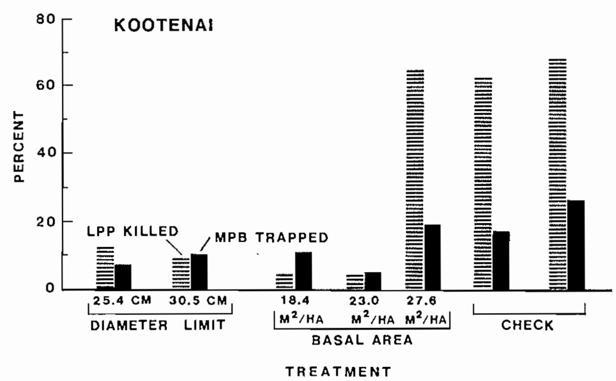

FIG. 4. Total percentages of mountain pine beetles (MPB) caught per treatment compared with percentages of residual lodgepole pine (LPP) killed per treatment following thinning, Kootenai National Forest, Montana, 1980–1983.

nings (≧25.4 and 30.5 cm). The combined catch for both forests revealed that only 30% of all beetles caught were trapped in these treatments (Table 2). In addition, there was little variation in the percentages of MPB caught by treatment between forests. The check and 27.6 m^2 BA/ha thinning made up the other group of treatments, in which the greatest percentage of beetles (55%) was caught (Table 2). Again, the variation in numbers of MPB caught by treatment between forests was minimal. The number of MPB caught in the 18.4 m^2 BA/ha thinning did not differ significantly from numbers on the other four treatments.

Abundance by year

Analysis of variance showed there was a significant difference in the total combined catch of MPB by year ($P < 0.0001$). Tukey's Studentized range test revealed that the total catch during the 1st year of trapping (1980) was not significantly different from that for the 2nd year (1981) (Table 2). However, the catch recorded for these first 2 years (1980, 1981) differed significantly from that recorded during the last 2 years (1982, 1983) (Table 2). Comparison of the numbers of beetles caught in all treatments during the 4-year study revealed that MPB population levels at the Lolo test site remained constant during the first 3 years (1980–1982), but more than doubled during the 4th year, indicating that populations had yet to reach their peak abundance (Table 2). This trend differs from that recorded at the Kootenai site, where more than half of all MPB trapped were caught during the 2nd year (Table 2). The combined annual catch at the Kootenai site declined thereafter, suggesting population levels had peaked.

Abundance versus damage

The percentages of the residual stand killed from 1980 to 1983 by treatment are compared with the percentages of MPB caught during the same period in Figs. 3 and 4. In general, the greatest percentages of MPB were trapped in the 27.6 m^2 BA/ha thinning (26–31%) and uncut checks

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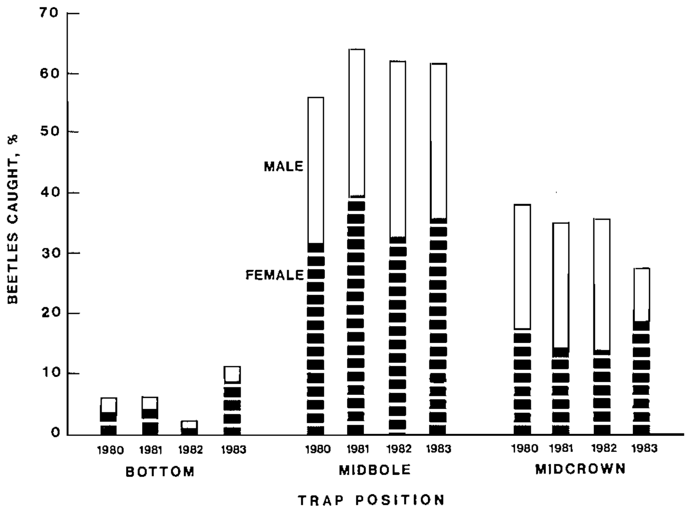

FIG. 5. Percentages of mountain pine beetles caught by traps positioned at three heights above ground, Lolo National Forest, Montana, 1980–1983.

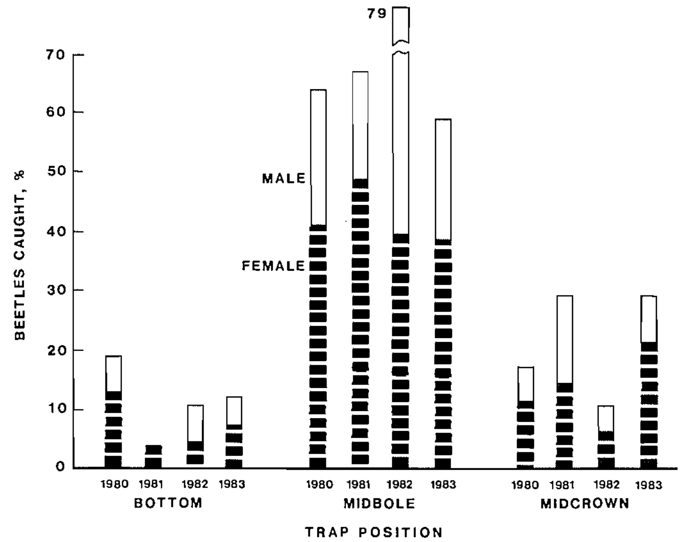

FIG. 6. Percentages of mountain pine beetles caught by traps positioned at three heights above ground, Kootenai National Forest, Montana, 1980–1983.

(25–28%) treatments. The greatest percentages of residual trees killed, ranging from 27 to 67.7% in the 27.6 m^2 BA/ha thinning and from 41.4 to 70.8% in the checks, were also recorded in these two treatments (Table 3).

In contrast, the percentages of residual trees killed in the 23.0 m^2 BA/ha and 25.4 cm diameter thinning treatments, where fewest beetles were trapped, were among the smallest, ranging from 4.0 to 11.9% (Table 3). The 18.4 m^2 BA/ha thinning, while not significantly different from the other treatments in number of MPB, was the only treatment with fewer trees killed. Residual trees killed in this treatment were 4.7 and 3.0% per hectare on the Lolo and Kootenai forests, respectively. The percentage of trees killed in the 18.4 m^2 BA/ha thinning at the Kootenai site was only 1 less per hectare than that recorded from the 23.0 m^2 BA/ha thinning, and approximately one-quarter of the percentage recorded from the 25.4 cm diameter thinning treatment (Table 3).

Comparison of the percentages of residual trees killed with the percentages of MPB trapped in thinned and unthinned stands revealed that the percentage of trees killed in the thinned treatments was less than might have been expected (Figs. 3 and 4). The one exception was the 27.6 m^2 BA/ha thinning, the least severe of the thinned basal area thinning treatments. Comparison of MPB abundance and tree killing in the 27.6 m^2 BA/ha thinning treatments showed that the proportion of MPB trapped to the number of residual lodgepole pine killed was nearer that found in the unthinned checks (Figs. 3 and 4). The percentage of trees killed compared with the percentage of beetles caught was considerably greater at the Kootenai site in the 27.6 m^2 BA/ha thinning and check treatments. The fewest MPB were caught in the 23.0 m^2 BA/ha thinnings at both sites, but the resultant tree killing at the Kootenai site was proportionately greater than that recorded at the Lolo site (Figs. 3 and 4). More MPB were trapped in the 18.4 m^2 BA/ha than in the 23.0 m^2 BA/ha thinning treatments at both sites. The percentages of trees killed in the 18.4 m^2 BA/ha thinning treatments in the two forests were almost identical. However, based on the percentages of MPB trapped, this was far less than might have been expected when compared with the other treatments, especially the checks and the 27.6 m^2 BA/ha thinning (Figs. 3 and 4).

The relationship of estimated MPB in flight to residual lodgepole pine killed in the two forests is shown in Table 3. Overall, the ratio of residual trees killed to the estimated number of MPB in flight was less in the thinned stands than in the unthinned check stands within each forest. Although the 27.6 m^2/ha thinning and check treatments caught significantly more beetles than the 23.0 m^2/ha and 30.5 cm diameter thinning treatments, the ratio of residual trees killed to MPB trapped for the two sets failed to show a difference of similar magnitude.

Height of flight

An analysis of variance showed a significant difference in numbers of MPB caught among the three trapping heights ($P < 0.0001$). Tukey's Studentized range test revealed that the numbers of MPB trapped differed significantly for the three trapping heights ($P < 0.05$). Most MPB were caught at the midbole position at both sites (Figs. 5 and 6). The average for the midbole for the 4 years was 65% at the Lolo site and 61% at the Kootenai site. Beetles were next most abundant at midcrown, with 23% of the 4-year total caught at the Lolo location and 33% at the Kootenai location. Fewest were caught at the lowest trap, with a 4-year average of 12% at the Lolo site and 6% at the Kootenai site. Variation in the MPB catch by position was minimal between years. In years when the catch at midbole increased (1981 at Lolo and 1982 at Kootenai), the number trapped at midcrown decreased proportionately. Similarly, when the catch at midbole declined (1980 at Lolo and 1983 at Kootenai), the numbers of MPB trapped at midcrown tended to increase proportionately.

Overall, proportionately more females than males were caught. The mean sex ratio for all treatments combined at the Lolo site was 1.6 females per male, and the range was 1.1–1.7 females per male during the 4 years. Corresponding ratios at the Kootenai site were 1.4:1 (4-year mean), with a range of 1.1–2.1. There was no apparent treatment effect on sex ratio.

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Discussion

Abundance by treatment

Significantly more MPB were trapped in stands that were thinned least severely. The 27.6 m^2 BA/ha thinning and unthinned checks caught 27 and 28%, respectively, of all MPB trapped, while the 25.4 cm diameter limit and 23.0 m^2 BA/ha thinning caught the fewest MPB, 8 and 7%, respectively. Earlier, a preliminary trapping experiment in lodgepole pine stands in the Gallatin National Forest suggested MPB flew through thinned and unthinned stands with about equal frequency (Schmitz et al. 1980). This tentative conclusion was based on only two seasons of trapping in stands that were thinned using guidelines based on diameter limits rather than basal area. The more comprehensive findings derived from 4 years of trapping in both diameter limit and basal area thinnings suggest that residual stand structure may influence the number of flying MPB within a stand. Unfortunately, the limited replication and variation in stand structure among replicates of the same treatments limit the specific inferences that can be made regarding the influence of stand structure on the abundance of flying MPB populations. Nevertheless, comparison of the characteristics of the residual stands suggests that for the most part, the average diameter of the 27.6 m^2 BA/ha thinning and unthinned checks was greater than 20.3 cm, exceeding those of the 25.4 cm diameter limit and 23.0 m^2 residual BA/ha treatments that were, with one exception, less than 20.3 cm. Lodgepole pine stands are known to be particularly susceptible to MPB when tree diameters are 20.3 cm or larger (Cole and Amman 1969; Hopping and Beal 1948; Safranyik et al. 1974). Tests to determine the effects of thinning on tree vigor and susceptibility to MPB in Oregon also showed that stands with large average tree diameter sustained appreciable mortality (Mitchell et al. 1983). In general, the residual BA of all species was also greater in the 27.6 m^2 BA/ha thinning and check treatments, where significantly more MPB were trapped. Finally, the highest percentages of MPB overall were trapped in those treatments that resulted in residual stands with both a large average stand diameter and a high basal area for all species.

The fact that considerably more MPB were trapped in the 18.4 m^2 BA/ha thinning treatment at the Kootenai site than on the same treatment at the Lolo site may have been due in part to the larger average dbh of the lodgepole pine at the Kootenai site. The larger MPB catch may also have been the result of the position of this particular treatment. It was within 50 m of check unit 1, in which the third highest number of MPB (157) were trapped over the 4 years.

Distribution of trees within the residual stand may also influence MPB abundance. In a larger-scale test of the effect of partial cutting on MPB, which included the treatments reported in this study, tree killing was recorded more frequently in locations where the trees that remained were left in clumps rather than spaced evenly throughout the stand (McGregor et al. 1987). This situation occurred more frequently in treatments based on diameter limits or in the least severely thinned treatment, which left a residual basal area of 27.6 m^2/ha.

Abundance by year

Comparison of the number of MPB trapped annually showed that the differences in catch among treatments remained relatively constant throughout the 4 years of trapping. The 25.4 cm diameter limit and 23.0 m^2 BA/ha thinning, in which significantly fewer beetles were trapped than in the 27.6 m^2 BA/ha thinning and unthinned checks after 4 years, also had the smallest percentage catch in 1980 (Table 2). In contrast, the 27.6 m^2 BA/ha thinning and unthinned check treatments were among the highest, except for the Lolo check treatments. These comparisons show that the overall pattern of beetle abundance in these two groups of treatments was established the 1st year following thinning, when all previously infested trees had been removed by thinning, except on the unthinned checks. During 1981, the same overall pattern of abundance existed in the two groups. During 1982 and 1983, the magnitude of the difference in overall numbers of MPB trapped in the two sets of treatments was less. This may have been due in part to the fact that MPB populations at the Kootenai site peaked during 1981 and declined thereafter, while populations at the Lolo site doubled during the 4th year, suggesting that they had yet to reach maximum abundance.

Abundance versus damage

Tree killing was most severe in the unthinned checks and least severely thinned (27.6 m^2 BA/ha) treatments, where the highest percentages of MPB were trapped. McGregor et al. (1987) concluded that the level of tree killing associated with the six treatments was similar to that reported earlier from a larger-scale test of partial cutting to reduce losses to MPB. This test included the two replicates of the six treatments used in this study, but did not include measures of MPB abundance. These researchers found that although there were no significant differences in tree killing among partial cutting treatments, losses to MPB were greatly reduced, regardless of the type and severity of partial cutting, compared with uncut check stands. The check stands had significantly more mortality than all partial cut treatments except the 27.6 m^2 BA/ha thinning treatment at the Kootenai site (McGregor et al. 1987).

Some investigators have attributed reductions in tree killing in thinned stands to an increase in tree resistance to MPB attack following thinning (Mitchell et al. 1983). Yet standard measures of tree vigor (dbh, grams of stemwood per square metre of foliage, periodic growth ratio, and leaf area) applied to trees in the residual stands in this test for 4 years following cutting failed to detect increased vigor as a major reason for the differences in tree killing between treatments (Amman et al. 1988).

Comparison of the estimated, rather than the actual, number of MPB in flight with the number of trees killed revealed that in the thinned treatments the severity of tree killing was often less than might be expected on the basis of the ratio of trees killed to estimated MPB populations in the unthinned checks. For example, the estimated number of MPB in flight for the 25.4 cm diameter limit treatment in the Kootenai Forest was approximately 25–38% of the numbers estimated to be in flight in the two check treatments. Yet the number of trees killed in the 25.4 cm diameter limit treatment was only 9–10% of that in the checks.

Height of flight

Most MPB were trapped at midbole height throughout the 4 years of the study, followed by midcrown height and then 1.8 m above ground. Results from an earlier preliminary test showed that most MPB were caught at midbole, but that the next highest total was caught 1.8 m above

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ground rather than at midcrown (Schmitz et al. 1980). The difference is due in large part to the short (2-year) duration of the preliminary test. For example, the second most abundant catch in the Gallatin Forest in 1978 was recorded 1.8 m above ground, while in 1979 it was recorded at mid-crown. These findings emphasize the value of continuing such trapping experiments for more than 2 years. The more recent findings confirm that the beetle prefers to fly within a particular stratum within the forest canopy. The reason for such stratification is unknown, although airborne semiochemicals are known to regulate the MPB's orientation to its host (Borden et al. 1986). In addition, some investigators have suggested that stand density (more specifically, the distance between boles of trees 20.3 cm dbh or larger) governs the ability of the MPB to switch its attack from the initially attacked tree to a surrounding tree (Geiszler and Gara 1978). Geiszler and Gara (1978) believe the switch is triggered by the sequential effects of aggregative and anti-aggregative pheromones. They contend that beetles select the adjacent tree on the basis of tree diameter and distance from the initially attacked tree. Accordingly, they suggest that thinning guidelines based on appropriate tree spacing may reduce tree killing by bark beetles.

Micrometeorological measurements within the forests have shown that on clear days, sunlight absorbed by the upper canopy heats the surrounding air and creates instability in the air within the upper canopy above the preferred stratum, while at the same time causing an inversion in the stem zone characterized by more stable air (Chapman 1967; Fares et al. 1980). Inversions tend to be more pronounced in dense stands than in more open stands (Fares et al. 1980; Fritschen 1984). Tests to measure movement of aerosols below a dense canopy on a sunny day have found that the aerosol was trapped beneath the canopy until it flowed to a point where the canopy was less dense or there was a small opening (Fares et al. 1980). These data suggest that conditions which create unstable air beneath the canopy may disrupt the orientation of bark beetles to attractive odor plumes which guide them to suitable hosts (Fares et al. 1980).

The disproportionate reduction in trees killed in relation to the number of beetles trapped in the most severely thinned treatments, failure to detect changes in stand vigor that account for the differences in tree killing, and the apparent preference of flying MPB for the midbole stratum suggest that stand environment may be an important regulator of the severity of tree killing by the MPB. The role of stand density in regulating air movement suggests that thinning may alter the stand environment to such a degree that some stimuli which orient the MPB to suitable stands and trees are no longer perceptible. The importance of stand density to host selection behavior has not generally been recognized (Chapman 1967; Fares et al. 1980). Definitive studies are under way that will more precisely define the importance of stand microenvironment to the susceptibility of lodepole pine stands to infestation by the MPB.

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