

## WHY PARTIAL CUTTING IN LODGEPOLE PINE STANDS REDUCES

### LOSSES TO MOUNTAIN PINE BEETLE

Gene D. Amman

**ABSTRACT:** Thinning stands of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) greatly minimized tree losses to mountain pine beetles (*Dendroctonus ponderosae* Hopkins). Although losses were reduced immediately following thinning, trees did not respond with increased growth until the second year after thinning. Tree losses in partial cut stands were more closely related to large tree diameter than to tree vigor indices.

Beetles were trapped in thinned stands for several years after thinnings were completed but were infesting only a few of the residual trees. The altered microclimate of the stands is suspected of being the factor most likely affecting beetle behavior.

Thinning lodgepole pine stands increased light intensity, wind movement, insolation, and temperature. Temperatures on the south exposure of tree trunks and of soil were significantly higher in thinned than unthinned stands.

#### INTRODUCTION

Silvicultural methods to reduce losses from bark beetles traditionally are aimed at decreasing tree competition and increasing tree vigor (Graham and Knight 1965; Keen 1958), thus making the trees better able to repel attacking beetles with copious resin flow (Reid and others 1967). To test partial cutting of mature lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) stands to reduce tree losses to mountain pine beetles (*Dendroctonus ponderosae* Hopkins [Coleoptera: Scolytidae]) (MPB), large-diameter trees were removed from stands on Bureau of Land Management lands near Granby, CO, in 1972 (Cahill 1978). Large-diameter trees favor high beetle production because they have thicker phloem (food of developing larvae) than that found in small-diameter trees (Amman 1972). This treatment resulted in losses to MPB of 1 to 2 percent, whereas tree losses in unthinned stands were 39 percent. Diameter limit cuts on the Gallatin

Paper presented at the Symposium on the Management of Lodgepole Pine to Minimize Losses to Mountain Pine Beetle, Kalispell, MT, July 12-14, 1988.

Gene D. Amman is Principal Entomologist, Mountain Pine Beetle Population Dynamics Research Work Unit, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Ogden, UT.

National Forest near West Yellowstone, MT, showed similar reductions in tree losses to MPB (Hamel 1978). Partial cutting tests on the Shoshone National Forest in northwest Wyoming, consisting of (1) diameter limit thinnings that removed all trees 7, 10, or 12 inches and larger d.b.h., (2) spaced thinnings leaving the 50 best trees per acre, and (3) untreated check stands, resulted in losses of less than 1 percent of trees in partial cut stands, compared to 4 percent in check stands the first year following cutting (Cole and others 1983). Five years after the partial cuts were made on the Shoshone National Forest, tree losses to MPB ranged between 0.3 to 7 percent in partial cut stands, compared to 27 percent in unthinned check stands (fig. 1) (Amman and others 1988a). Partial cutting tests on the Kootenai and Lolo National Forests in northwest Montana included (1) diameter limit thinnings that removed either all trees 10 or 12 inches and larger d.b.h., (2) spaced thinnings that left residual basal areas of 80, 100, or 120 ft<sup>2</sup> BA/a, and (3) check stands. Five years after these partial

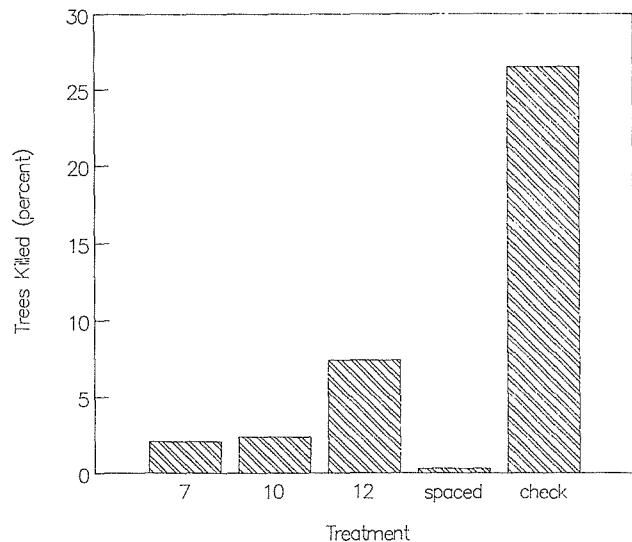


Figure 1--Percent lodgepole pine killed by mountain pine beetles in different partial cutting treatments, Shoshone National Forest, WY, 1981 to 1985 (from Amman and others 1988a). Treatments indicate diameter limit cuts in which all trees 7, 10 or 12 inches and larger d.b.h. were removed; spaced thinnings in which the 50 best trees per acre remained; and untreated check.

cuts were made, tree losses were less than 17 percent in all partial cut stands except those that left 120 ft<sup>2</sup> BA/a, where losses were 38 percent. Losses were 73 and 94 percent, respectively, in the Kootenai and Lolo check stands (fig. 2) (McGregor and others 1987). Lodgepole pine losses to MPB also were much reduced in thinnings established 7 to 15 years prior to evaluation of tree losses to MPB in Oregon (Mitchell and others 1983b). Tree losses in the Oregon thinnings averaged 9 percent, compared to 19 percent in unthinned check stands.

Following partial cutting of lodgepole pine stands on the Kootenai, Lolo, and Shoshone National Forests, observations were made of: (1) response of MPB determined by trapping the beetles, and (2) changes in radial growth and vigor indices of residual trees in relation to susceptibility of MPB infestation. A third item, differences in microclimate of thinned and unthinned stands as they relate to MPB infestation, was determined on the Wasatch National Forest in northeastern Utah.

#### BEETLE RESPONSE TO PARTIAL CUT STANDS

Little is known about the influence of stand environment on the flight and host selection behavior of MPB. What is known has been documented 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 (Cole and Amman 1969; Hopping and Beall 1948). 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 and others 1972; Schönherr 1976). The

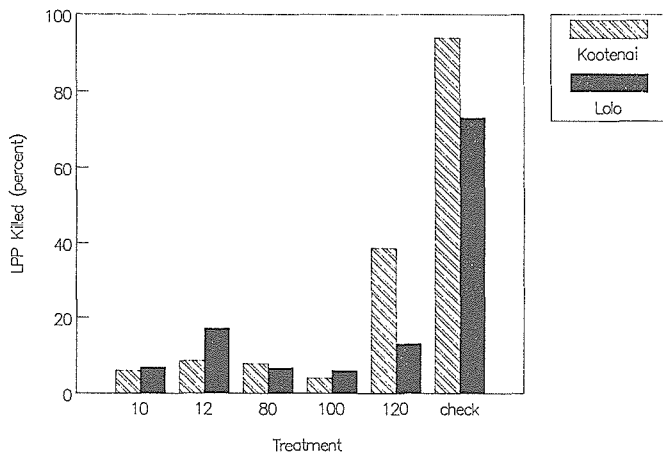


Figure 2--Percent lodgepole pine (LPP) killed by mountain pine beetles in different partial cutting treatments, Kootenai and Lolo National Forests, MT, 1980 to 1984 (from McGregor and others 1987). Treatments indicate diameter limit cuts in which all trees 10 or 12 inches and larger d.b.h. were removed, spaced thinnings leaving 80, 100, or 120 ft<sup>2</sup> BA/a, and untreated check.

beetle's apparent preference for large-diameter trees is such that it will infest these trees even when intermingled smaller trees are baited with components of the beetle's aggregative pheromone (Rasmussen 1974).

To study how stand density affects the dispersion of MPB in partial cut stands of lodgepole pine, omnidirectional passive barrier traps were used to monitor numbers of MPB in flight (Schmitz and others 1980; Schmitz and others, in press). Traps consisted of two clear Plexiglas panels with funnels and containers at the base of the panels to entrap the beetles that flew into the panels. Each trap had a total intercepting surface above the funnels of 7.75 ft<sup>2</sup> (Schmitz 1984). Three of these traps were hung on a single nylon cord supported on a horizontal line between the crowns of two adjacent trees. Traps on the line were positioned so they corresponded to midcrown, midbole, and about 6 ft above ground (fig. 3). Two such lines were hung in each stand monitored for beetle flight.

In earlier work on the Gallatin National Forest near West Yellowstone, MT, Schmitz and others (1980) found that most MPB flew in the midbole area. Beetles were caught with about equal frequency in thinned and unthinned stands, but more trees were infested in unthinned stands (Hamel 1978). Numbers of beetles caught among treatments after 4 years on the Kootenai and Lolo National Forests were significantly different

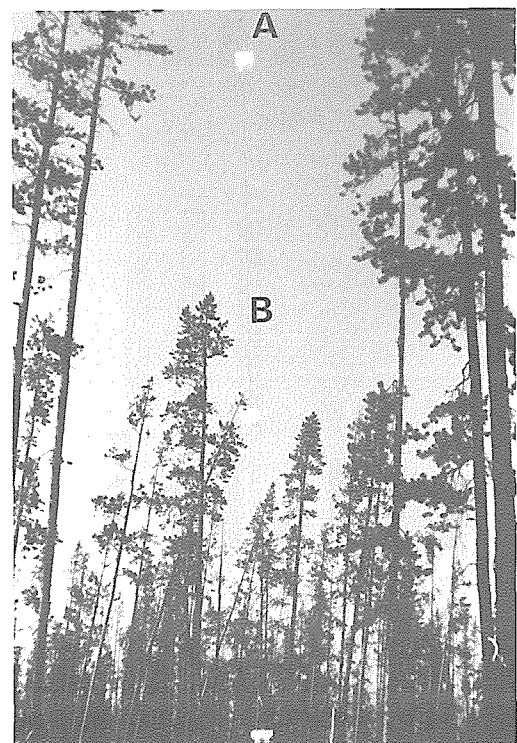


Figure 3--Omnidirectional passive barrier traps used to catch flying beetles: (A) horizontal support line with pulley for attachment of vertical line; (B) vertical line used to raise and lower traps, with three traps attached.

among partial cutting treatments (fig. 4). The treatments separated into two groups. Group one had the fewest beetles and included stands having 100 ft<sup>2</sup> BA/a of residual basal area and the 10-inch diameter limit cut. Group two consisted of the 120 ft<sup>2</sup> BA/a and the check stands, which had the greatest tree densities. The other two treatments, consisting of 80 ft<sup>2</sup> BA/a and the 12-inch diameter limit cut, did not differ significantly from group one or group two. In general, the greatest numbers of beetles were trapped in group two stands, and the greatest numbers of trees were killed in these stands (Schmitz and others, in press). Comparison of percentages of residual trees killed with MPB trapped between thinned and unthinned stands revealed the percentage of trees killed in the thinned treatments was proportionately less than might have been expected, based on the number of

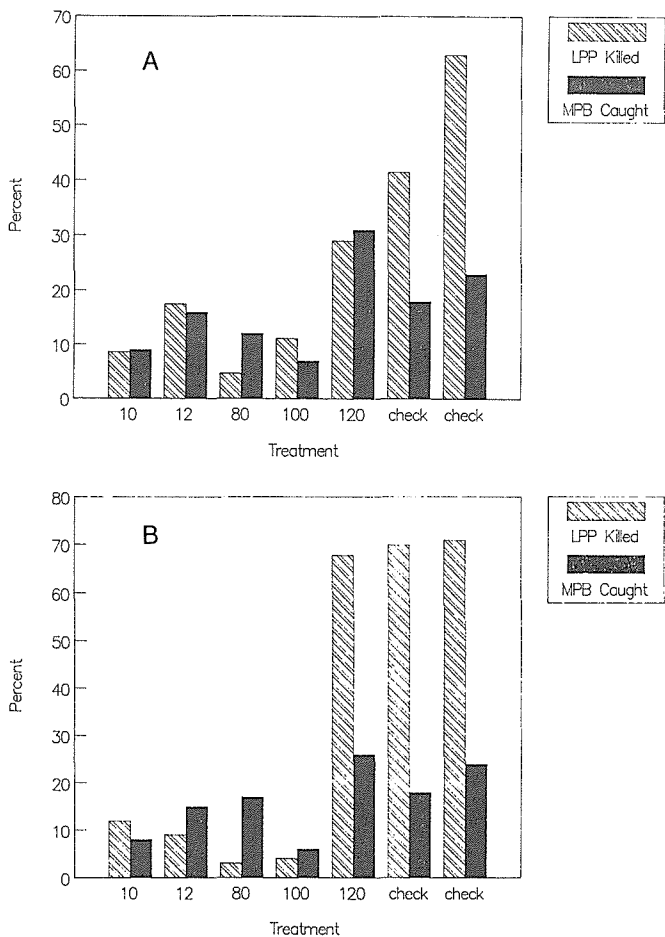


Figure 4--Percentage of total mountain pine beetles (MPB) caught per treatment compared with percentage of residual lodgepole pine (LPP) killed per treatment following thinning in the (A) Lolo and (B) Kootenai National Forests, MT, 1980 to 1983 (from Schmitz and others, in press). Treatments indicate diameter limit cuts in which all trees 10 or 12 inches and larger d.b.h. were removed, spaced thinnings leaving 80, 100, or 120 ft<sup>2</sup> BA/a, and untreated check.

MPB trapped. Overall, the ratio of estimated MPB in flight per tree killed was greater in thinned stands than in unthinned check stands (fig. 5). As on the Gallatin National Forest (Schmitz and others 1980), most MPB were caught in midbole traps (fig. 6) (Schmitz and others, in press). The loss of fewer trees in thinned stands than in unthinned stands proportional to the numbers of flying beetles suggests that many beetles were not stopping to infest trees in thinned stands.

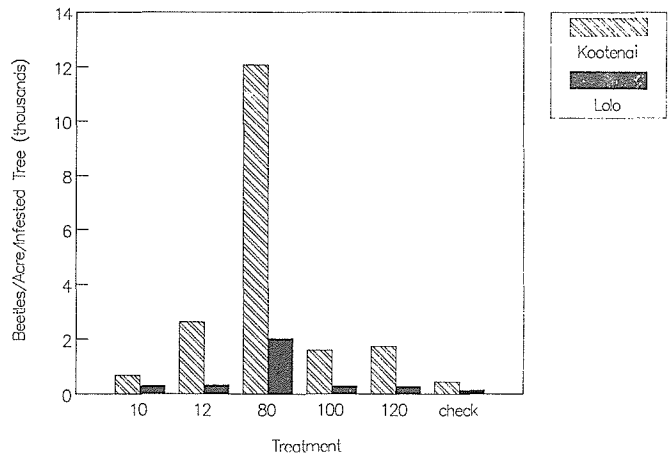


Figure 5--Ratio of estimated inflight beetles (MPB) per acre for each tree killed by mountain pine beetles in partial cutting treatments on the Kootenai and Lolo National Forests, MT (from Schmitz and others, in press). Treatments indicate diameter limit cuts in which all trees 10 or 12 inches and larger d.b.h. were removed, spaced thinnings leaving 80, 100, or 120 ft<sup>2</sup> BA/a, and untreated check.

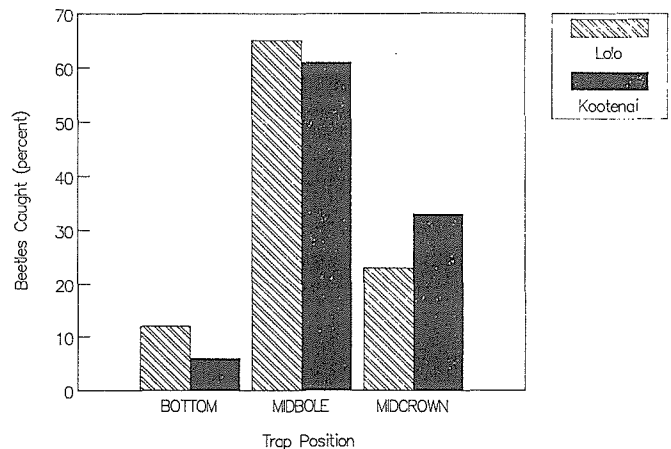


Figure 6--Percentage of mountain pine beetles (MPB) caught by trap position in the Lolo and Kootenai National Forests, MT, 1980 to 1983 (from Schmitz and others, in press).

GROWTH RESPONSE FOLLOWING PARTIAL CUTTING

Radial growth of residual trees in the Kootenai stands was slightly reduced or about the same in 1980 as in 1979, the year of most thinnings. Only trees in the 80 and 100 ft<sup>2</sup> BA/a treatments increased in growth the first year following thinning. Most stands showed increasing growth trends starting in 1981 (fig. 7) (Amman and others 1988b).

The trend in radial growth in the Lolo stands, including untreated checks, also declined the first year following thinning, except for the 100 ft<sup>2</sup> BA/a treatment, which increased slightly (fig. 8). 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 the exception of a sharp decline in 1982.

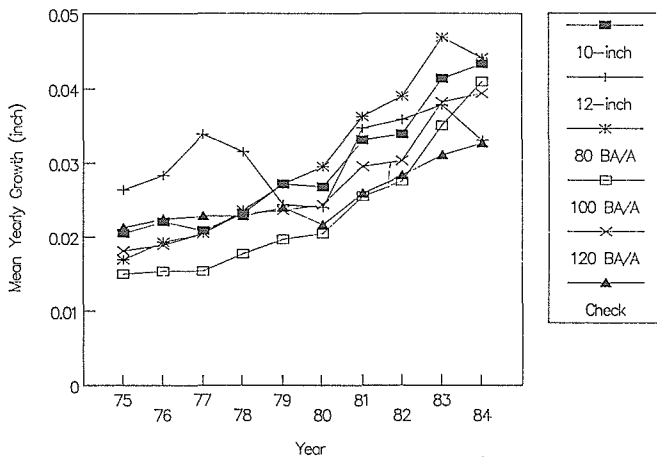


Figure 7--Mean annual growth (radial) of lodgepole pine in partial cutting treatments applied in 1979 to reduce tree losses to mountain pine beetle, Kootenai National Forest, MT (from Amman and others 1988b).

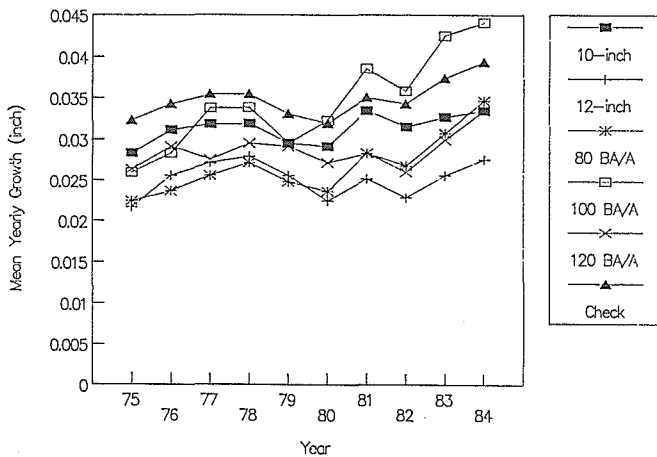


Figure 8--Mean annual growth (radial) of lodgepole pine in partial cutting treatments applied in 1979 to reduce tree losses to mountain pine beetle, Lolo National Forest, MT (from Amman and others 1988b).

In the Shoshone National Forest, significant radial growth occurred following thinning in 1979 and 1980 (fig. 9). None of the treatments showed decline in growth following thinning, although a slight flattening of the growth curve occurred for the 7-inch and 10-inch diameter limit cuts between 1979 and 1980. Check stands showed a decline in growth during this period. Trees in all treatments, including the checks, had substantial live crown, with averages ranging between 46 and 63 percent of total tree height. However, only the check stands did not respond with a significant increase in radial growth, but the trend in growth was up. Apparently, reductions in numbers of trees caused by MPB were not large enough to provide as rapid growth response as partial cutting treatments on the Kootenai and Lolo National Forests. Extensive tree mortality in check stands on the Kootenai and Lolo resulted in significant growth response of residual trees.

Five years after partial cuts were made on the Kootenai and Lolo National Forests, none of the stands were considered vigorous. Lodgepole pines, with average ages of 102 and 76 years on the Kootenai and Lolo, respectively, and 100 on the Shoshone, are past the age when maximum resin response to MPB infestation could be expected (Shrimpton 1973). Trees were growing at a slow rate prior to and for several years after thinnings were completed. Although average radial growth of trees in some stands increased 100 percent by the fourth year following thinning, this was only an increase of 0.02 inch.

The first year following thinning, most stands showed a slight reduction in growth. 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

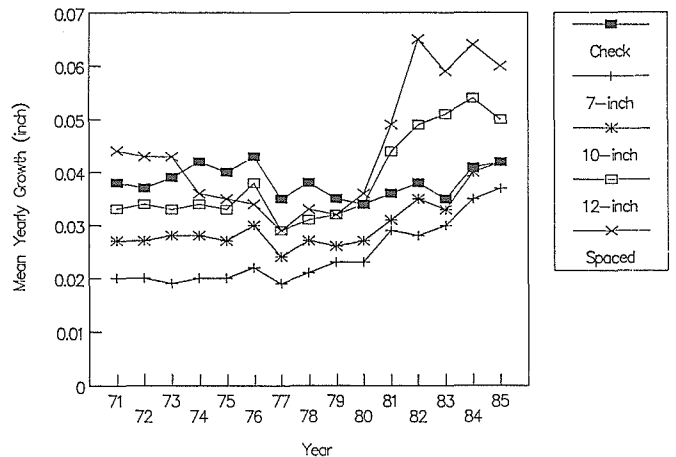


Figure 9--Mean annual growth (radial) of lodgepole pine in partial cutting treatments applied in 1979 and 1980, Shoshone National Forest, WY (from Amman and others 1988a).

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). An increase in radial growth started the second year following thinning in all stands, including checks, on the Kootenai, Lolo, and Shoshone, 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). Reduced tree losses to MPB following partial cutting should not have occurred on the basis of tree growth because growth was so small.

#### TREE VIGOR FOLLOWING PARTIAL CUTTING

Several tree and stand characteristics have been related to susceptibility of MPB infestation (Amman and others 1977; Berryman 1978; Cole and McGregor 1983; Mahoney 1978; Safranyik and others 1974; Schenk and others 1980; Shrimpton 1973; Stuart 1984; Waring and Pitman 1980). Many of the variables measured for these methods are more appropriate for natural stands than for recent partial cut stands. For example, variables related to tree competition as a precursor to MPB infestation would be inappropriate, since thinning reduces numbers of trees below the level of intertree competition. These variables include crown competition factor (CCF) (Schenk and others 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, since 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 (d.b.h.) (Amman and others 1977; Cole and McGregor 1983; Safranyik and others 1974; Stuart 1984), 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 and others 1983b). These three risk-rating methods were applied to trees in partial cuts on the Kootenai, Lolo, and Shoshone National Forests. Comparisons were made between the characteristics of trees killed by MPB and adjacent live trees, using 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 this, it can be used to classify individuals of unknown origin into the category to which they most likely belong. Diameter at breast height was found to be the most discriminating of the variables measured (table 1). PGR and grams of wood per square meter of foliage were larger in trees killed by MPB in half of the partial cuts, and larger in surviving trees in the other half of the partial cuts. Therefore, these characteristics were not useful in discriminating between susceptible and nonsusceptible trees in the partial cut stands (Amman and others 1988b). The discriminant function showed that 69.4 percent of live trees had characteristics of live trees, whereas 30.6 percent of live trees had characteristics of dead trees. In contrast, 75 percent of dead trees had characteristics of dead trees and 25 percent had characteristics more closely related to live trees (table 2). 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 d.b.h., grams of wood, PGR, and leaf area, between live and MPB-killed

Table 1--Probability of >F for discriminant analysis

Treatment	One-way ANOVA			Multivariate	
	DBH	Grams of wood	PGR	Leaf area	Wilk's Lambda
10-inch diam. limit	0.7092	0.7092	0.7092	0.7092	0.7092
12-inch diam. limit	0.0560	0.7013	0.7895	0.5273	0.1420
80 ft <sup>2</sup> BA/a	0.0001	0.0693	0.7320	0.0229	0.0001
100 ft <sup>2</sup> BA/a	0.0001	0.5823	0.0151	0.0292	0.0001
120 ft <sup>2</sup> BA/a	0.0001	0.7197	0.4789	0.0001	0.0001
Check	0.0787	0.4671	0.0303	0.2676	0.0448

Table 2--Classification of live and MPB-killed lodgepole pine by the discriminant function

Treatment	Tree condition	Live	Dead	Dead tree characteristics
		-- Percent --		
10-inch diam. limit	Live	64.0	36.0	>DBH <GMS >PGR >LA
	Dead	0.0	100.0	
12-inch diam. limit	Live	71.4	28.6	>DBH >GMS >PGR >LA
	Dead	39.2	60.8	
80 ft <sup>2</sup> BA/a	Live	67.5	32.5	>DBH <GMS <PGR >LA
	Dead	27.8	72.2	
100 ft <sup>2</sup> BA/a	Live	74.3	25.7	>DBH >GMS <PGR >LA
	Dead	13.8	86.2	
120 ft <sup>2</sup> BA/a	Live	73.1	26.9	>DBH >GMS <PGR >LA
	Dead	23.9	76.1	
Check	Live	66.2	33.8	>DBH <GMS >PGR >LA
	Dead	45.2	54.8	
Average	Live	69.4	30.6	>DBH -- -- >LA
	Dead	25.0	75.0	

trees (table 3) showed greatest distances occurred in the spaced thinnings (80, 100, and 120 ft<sup>2</sup> BA/a) and least distance in the check stands. Distances in the diameter limit thinnings were intermediate, with the 12-inch diameter limit thinning having a value close to the check.

On the Shoshone National Forest, not enough trees were killed by MPB for comparisons to be made between characteristics of killed and surviving trees. However, observations on surviving trees show grams of wood produced per square meter of foliage was still well below the 100-g level dividing susceptible from nonsusceptible trees 5 years after partial cuts were made (Amman and others 1988a). PGR's for all partial cuts exceeded the average for resistant trees, being

1.0 or greater at the start of the test and steadily increasing following partial cutting, even in the check stands, which had losses exceeding 30 percent of the trees.

Following partial cutting, stands should still have been susceptible to MPB infestation, based on vigor indices. Average d.b.h. of most stands exceeded the 8 inches specified by Amman and others (1977) and Safranyik and others (1974); grams of wood per square meter of foliage for most trees were still in the highly susceptible category of less than 50 g; and PGR was less than 0.9 in many trees on the Kootenai and Lolo but not on the Shoshone National Forest. However, tree losses were much reduced. Even though trees had not yet responded with greatly increased vigor, the much reduced losses following partial cutting, when compared to uncut check stands, suggest that some factor other than tree vigor is involved. Bartos and Amman (1989) suggest that stand microclimate is responsible, being altered by the partial cutting treatments.

Table 3--Pairwise squared distance of the discriminant function for live and mountain pine beetle killed trees

Treatment	Distance
10-inch diam. limit	0.6155
12-inch diam. limit	0.3513
80 ft <sup>2</sup> BA/a	1.7043
100 ft <sup>2</sup> BA/a	2.1662
120 ft <sup>2</sup> BA/a	1.3393
Check	0.3177

While grams of wood per square meter of foliage was not a good measure of tree susceptibility to MPB infestation in Montana and Wyoming, Mitchell and others (1983b) found this to be a good predictor of lodgepole susceptibility to MPB infestation in stands on the Deschutes National Forest in Oregon. The stands had been thinned 7 to 15 years before the infestation. In that length of time, most stands had exceeded the 100 g of wood per square meter of foliage that separates susceptible from nonsusceptible stands.

Although stand microclimate was considered as a possible cause for differences in beetle behavior among the Oregon stands, it was not studied (Mitchell and others 1983b).

Quantitative and qualitative changes in resins following partial cutting were not explored in the Kootenai, Lolo, and Shoshone stands, as was done in thinned loblolly pine stands in the southern United States in relation to bark beetle attack (Matson and others 1987; Nebeker and Hodges 1983). Nebeker and Hodges (1983) found total monoterpene content did not change with time or treatment. However, greatest terpene increase occurred in trees receiving basal wounds during the thinning operation. This they attributed to stimulation caused by the wounding. Matson and others (1987) observed greater resin production in residual trees in thinnings than in unthinned stands 6 years after treatment. Because of small changes in growth of lodgepole pine in our partial cutting treatments immediately and even 5 years after partial cutting treatment, substantial increase in resin production seems unlikely. This observation, coupled with the slow radial growth and slow change in tree vigor of residual trees, suggests that factors other than tree vigor are governing whether beetles remain in the partial cut stands to infest trees. The most likely factor is change in microclimate as a result of the partial cuts.

MICROCLIMATE OF STANDS AND TREES  
IN PARTIAL CUT STANDS

Partial cutting lodgepole pine stands causes subtle changes not only in incident radiation, temperature, and light (Reifsnyder and Lull 1965), but also in wind speed. These climatic changes brought about by thinning may have profound effects on MPB activity. The effects of extremely high (Patterson 1930) and low temperatures (Somme 1964; Yuill 1941) on MPB have been reported. However, an optimum zone for temperature and other microclimatic factors has not been defined. Microclimate was measured and compared for thinned and unthinned stands located at 9,400 ft (latitude 41 °N) on the Wasatch National Forest in northeastern Utah (Bartos and Amman 1989).

Microclimatic factors measured in thinned and unthinned stands in northern Utah were: temperature of the outer and inner bark of live trees, air temperature, soil temperature, solar radiation, and wind speed, using either an automatic recording device and thermocouples or an infrared thermometer. The inner bark (phloem) temperature was consistently 2 to 4 °F higher in the thinned than in the unthinned stand. The outer bark (surface) temperature on the south side was 2 to 5.5 °F higher in the thinned than in the unthinned stand (fig. 10). Less difference was observed on the north sides between thinned and unthinned stands. However, temperatures were 5.5 to 7 °F higher on the south than north sides. These differences are consistent with those reported by Powell (1967) in British Columbia. In addition, he found temperatures of infested

trees are higher than those of live trees. Powell (1967) reported subcortical temperatures were occasionally 95 °F or higher on south sides. Bartos and Amman (1989) reported an average difference of 4 °F between north and south sides during the hours of 10 a.m. to 2 p.m., with maximum temperature being 22 °F higher in the thinned than unthinned stand. Temperatures on north sides of trees in thinnings would not deter beetle attack. Cooler temperatures on north sides apparently offer more favorable physical environment for attacking MPB. MPB attack

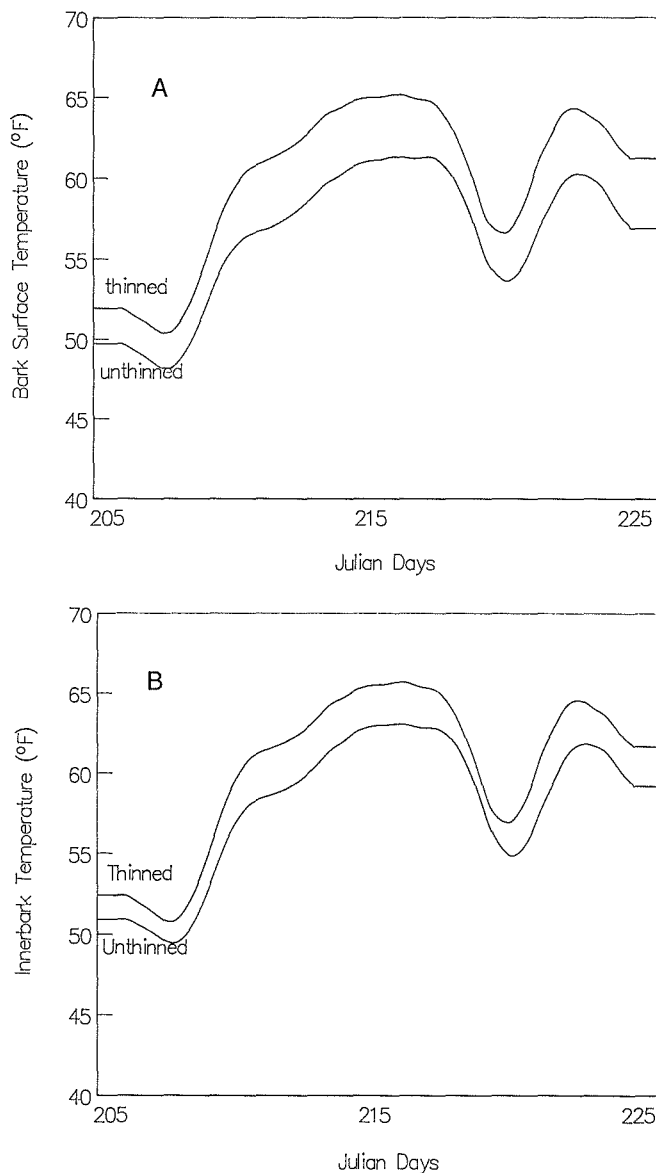


Figure 10--Smoothed curves for a 17-day time period in 1986 contrasting (A) bark surface temperatures and (B) innerbark temperatures on the south side of two lodgepole pine trees between a thinned and unthinned stand (from Bartos and Amman 1989).

densities are higher on north sides (Reid 1963; Shepherd 1965), and when trees are strip attacked, the attacks usually occur on north and east sides (Mitchell and others 1983a).

The effect of temperature could be more subtle than simply creating a direct inhospitable environment for MPB attack. MPB may have evolved behavior to avoid situations where beetle brood are not likely to survive. In thinned stands, high temperatures are not likely to be lethal to any MPB stage (Safranyik 1985). However, where tree temperatures are a few degrees above those of trees in unthinned stands, MPB may proceed too far in their development before winter, thus entering winter in stages that are very susceptible to freezing--for example, the pupal stage--as observed by Reid (1963) and Amman (1973).

The increased wind speed and air turbulence in thinned compared to unthinned stands could disrupt the pheromone communication system of MPB. More sunlight penetrated the canopy in the thinned than unthinned stands (fig. 11), resulting in significantly higher soil temperatures.

Increased soil temperatures, averaging 9 °F higher in the thinned than in the unthinned stand (Bartos and Amman 1989), increase convection currents (Rosenberg and others 1983) and air turbulence that could disrupt pheromone plumes and resultant MPB communication (fig. 12). In addition, wind speed is greater in thinned than unthinned stands (fig. 13), thus possibly further complicating pheromone communications. MPB response to pheromones is more predictable at wind speeds under 3 mph, but a few beetles fly at wind speeds of 4.5 mph. Twice as many males as females fly at wind speeds in excess of 2.4 mph (Gray and others 1972).

In dense stands, sunlight is absorbed by the upper levels of the tree canopy that in turn heat the surrounding air, creating instability in the air within the upper canopy. This creates an inversion in the stem zone that is characterized by more stable air (Chapman 1967; Fares and others 1980). Inversions tend to be more pronounced in dense stands than in sparse ones (Fares and others 1980; Fritschen 1984). Aerosol movement below a dense canopy on a sunny day is trapped beneath the canopy until it flows to a point where the canopy is sparse or has an opening (Fares and others 1980). Solar energy penetrating through canopy openings to the forest floor heats the ground and adjacent air, which becomes buoyant and rises through the canopy opening, carrying the aerosol with it (Fares and others 1980). The aerosol or pheromone plume will be torn apart in the faster, more turbulent air currents that occur above the canopy. Therefore, when MPB infest a tree in a thinned stand, canopy density usually is insufficient to trap the pheromone and move it intact horizontally to attract other beetles. Rather, the pheromone rises through the canopy on convection currents and is dispersed above the canopy. Schmitz and others (in press) concluded that most MPB fly in the bole area beneath the canopy, where the pheromone communication system would be most effective.

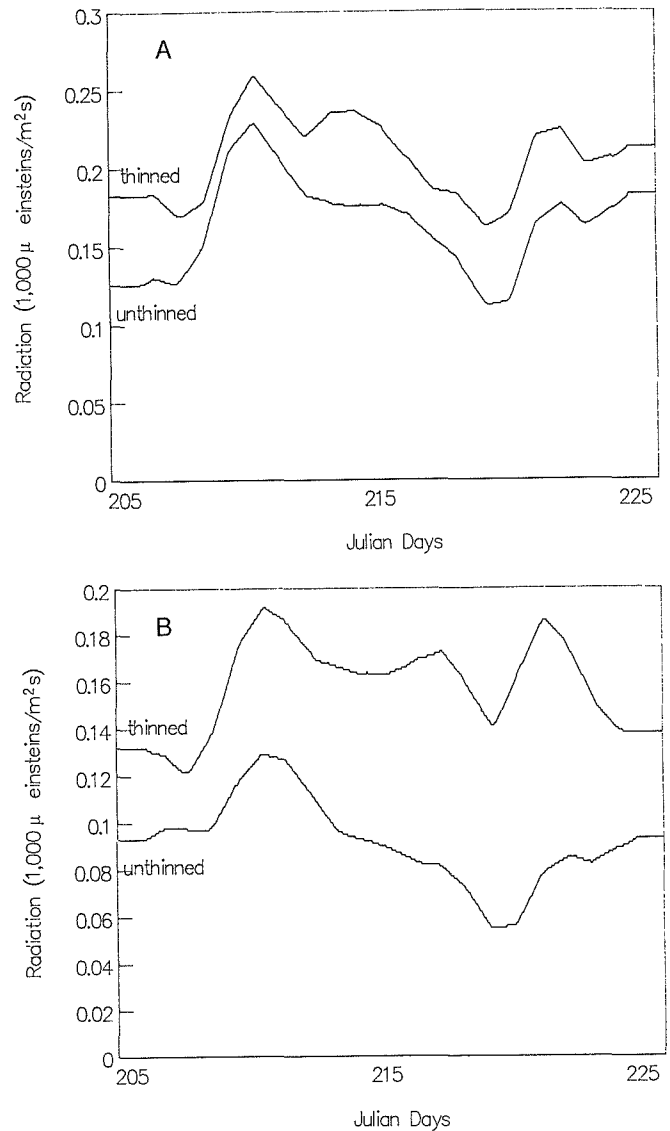


Figure 11--Smoothed curves for a 17-day time period in 1986 contrasting solar radiation (A) at instrument towers and (B) at d.b.h. on trees between thinned and unthinned lodgepole pine stands (from Bartos and Amman 1989).



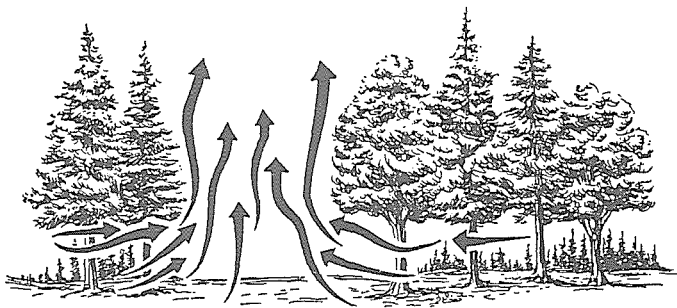


Figure 12--Openings in the canopy tend to act as chimneys when the soil and tree trunks are heated by solar radiation and light winds occur (from Schroeder and Buck 1970).

When MPB do infest a tree in a thinned stand of lodgepole pine, usually only the single tree--and occasionally a nearby tree, when spacing is not maintained--is infested. Geiszler and Gara (1978) emphasized the importance of tree spacing in switching of attacks from a tree under attack to a nearby tree. Trees spaced too far from a tree under attack will not be attacked. The openness of the stand probably causes convection currents created by solar insolation to transport the pheromone plume around infested trees vertically out of the stand rather than horizontally. Thus, the infestation of adjacent trees would be dependent on the degree of thinning. The reduced loss of trees to MPB in all partial cutting treatments in the Kootenai and Lolo studies (McGregor and others 1987) suggests that the density and spacing of natural stands do not have to be changed very much to have an effect on MPB response.

Bartos and Amman (1989) placed three pheromone-baited funnel traps 165 ft apart in both a thinned (67 ft<sup>2</sup> BA/a) and an unthinned stand (137 ft<sup>2</sup> BA/a) that had no currently infested trees. Traps between the two stands were located 330 ft apart. Of the 504 beetles caught, only 5.2 percent were caught in the thinned stands. Either beetles could not find the traps in thinned stands because of disruption of the pheromone plume, or beetles failed to respond because of microclimatic conditions of the stand. Shepherd (1966) showed in laboratory studies that MPB increased attempts to fly as light intensity and temperature increased. Thus, conditions encountered in thinned stands would have been conducive to beetle flight rather than arrestment.

These observations of growth and vigor response of lodgepole pine following partial cutting, MPB response to the partial cut stands, and microclimate changes as a result of partial cutting suggest that microclimate plays a major role in MPB behavior following partial cutting.

Infestation risk of managed lodgepole pine stands probably can be assessed by monitoring stand microclimate, specifically light, which may serve as an integrator of other important microclimatic factors. As tree diameter increases and crown closure begins to occur in partial cut or thinned stands, a favorable microclimate may occur and invite beetle attack, regardless of tree vigor. In addition, thinned stands that contain trees on which branches have not pruned well or that have tall shrub layers may be as subject to beetle infestation as unthinned stands. Additional studies are needed of MPB infestation in thinned and partial cut stands to determine microclimatic thresholds of MPB infestation and the association of thresholds with tree vigor levels, crown lengths, branch pruning, and understory tree and shrub layers.

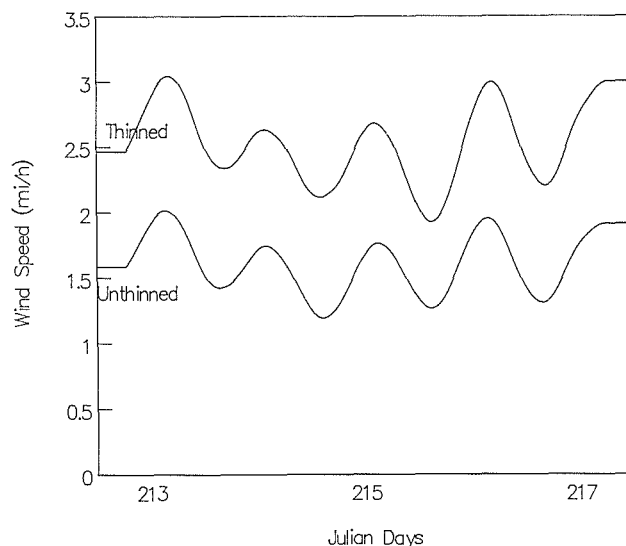


Figure 13--Smoothed curves for a 5-day time period in 1986 contrasting wind speed on instrument towers between a thinned and unthinned lodgepole pine stand (from Bartos and Amman 1989).

REFERENCES

- Afifi, A. A.; Clark, V. 1984. Computer-aided multivariate analysis. Belmont, CA: Lifetime Learning Publications. 458 p.
- Amman, G. D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *Journal of Economic Entomology*. 65: 138-140.
- Amman, G. D. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environmental Entomology*. 2: 541-547.
- Amman, G. D.; Lessard, G. D.; Rasmussen, L. A.; O'Neil, C. G. 1988a. Lodgepole pine vigor, regeneration, and infestation by mountain pine beetle following partial cutting on the Shoshone National Forest, Wyoming. Res. Pap. INT-396. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 8 p.
- Amman, G. D.; McGregor, M. D.; Cahill, D. B.; Klein, W. H. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. Gen. Tech. Rep. INT-36. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 19 p.
- Amman, G. D.; McGregor, M. D.; Schmitz, R. F.; Oakes, R. D. 1988b. Susceptibility of lodgepole pine to infestation by mountain pine beetles following partial cutting of stands. *Canadian Journal of Forest Research*. 18: 688-695.
- Anhold, J. A.; Jenkins, M. J. 1987. Potential mountain pine beetle (Coleoptera: Scolytidae) attack of lodgepole pine as described by stand density index. *Environmental Entomology*. 16: 738-742.
- Bartos, D. L.; Amman, G. D. 1989. Microclimate: an alternative to tree vigor as a basis for mountain pine beetle infestation. Res. Pap. INT-400. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 10 p.
- Berryman, A. A. 1978. A synoptic model of the lodgepole pine/mountain pine beetle interaction and its potential application in forest management. In: Berryman, A. A.; Amman, G. D.; Stark, R. W., eds. *Theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station: 98-105.*
- Cahill, D. B. 1978. Cutting strategies as control measures of the mountain pine beetle in lodgepole pine in Colorado. In: Berryman, A. A.; Amman, G. D.; Stark, R. W., eds. *Theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station: 182-186.*
- Chapman, J. A. 1967. Response behavior of scolytid beetles and odour meteorology. *Canadian Entomologist*. 99: 1132-1137.
- Cole, D. M. 1975. Culture of immature lodgepole pine stands for timber objectives. In: Baumgartner, D. A., ed. *Management of lodgepole pine ecosystems: symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University, Cooperative Extension Service: 536-555.*
- Cole, W. E.; Amman, G. D. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. Res. Note INT-95. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 7 p.
- Cole, W. E.; Cahill, D. B.; Lessard, G. D. 1983. Harvesting strategies for management of mountain pine beetle infestations in lodgepole pine: preliminary evaluation, East Long Creek Demonstration area, Shoshone National Forest, Wyoming. Res. Note INT-333. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 11 p.
- Cole, W. E.; McGregor, M. D. 1983. Estimating the rate and amount of tree loss from a mountain pine beetle infestation. Res. Pap. INT-318. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 22 p.
- Donner, B. L.; Running, S. W. 1986. Water stress response after thinning *Pinus contorta* stands in Montana. *Forest Science*. 32: 614-625.
- Fares, Y.; Sharpe, P. J. H.; Magnuson, C. E. 1980. Pheromone dispersion in forests. *Journal of Theoretical Biology*. 84: 335-359.
- Fritschen, L. J. 1984. Air circulation in forested areas. Effect on aerial application of materials. In: Garner, Willa Y.; Harvey, John, eds. *Chemical and biological controls in forestry: symposium proceedings; 1983 March 20-25; Seattle, WA. Washington, DC: American Chemical Society: 175-190.*
- Geiszler, D. R.; Gara, R. W. 1978. Mountain pine beetle attack dynamics in lodgepole pine. In: Berryman, A. A.; Amman, G. D.; Stark, R. W., eds. *Theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station: 182-186.*
- Graham, S. A.; Knight, F. B. 1965. *Principles of forest entomology*. New York: McGraw-Hill. 427 p.

- Gray, B.; Billings, R. F.; Gara, R. I.; Johnsey, R. L. 1972. On the emergence and initial flight behavior of the mountain pine beetle, Dendroctonus ponderosae, in eastern Washington. Zeitschrift angewandte Entomologie. 71: 250-259.
- Hamel, D. R. 1978. Results of harvesting strategies for management of mountain pine beetle infestation in lodgepole pine on the Gallatin National Forest, Montana. In: Berryman, A. A.; Amman, G. D.; Stark, R. W., eds. Theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station: 192-196.
- Hopping, G. R.; Beall, G. 1948. The relation of diameter of lodgepole pine to incidence of attack by the bark beetle (Dendroctonus monticolae Hopkins). Forestry Chronicle. 24: 141-145.
- Keen, F. P. 1958. Progress in bark-beetle control through silviculture in the United States. Tenth International Congress of Entomology Proceedings. 4(1956): 171-180.
- Mahoney, R. B. 1978. Lodgepole pine/mountain pine beetle risk classification methods and their application. In: Berryman, A. A.; Amman, G. D.; Stark, R. W., eds. Theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station: 106-113.
- Matson, P. A.; Hain, F. P.; Mawby, W. 1987. Indices of tree susceptibility to bark beetles vary with silvicultural treatment in a loblolly pine plantation. Forest Ecology and Management. 22: 107-118.
- McGregor, M. D.; Amman, G. D.; Schmitz, R. F.; Oakes, R. D. 1987. Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. Canadian Journal of Forest Research. 17: 1234-1239.
- Mitchell, R. G.; Martin, R. E.; Stuart, J. 1983a. Catfaces on lodgepole pine--fire scars or strip kills by the mountain pine beetle? Journal of Forestry. 81: 598-601, 613.
- Mitchell, R. G.; Waring, R. H.; Pitman, G. B. 1983b. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. Forest Science. 29: 204-211.
- Nebeker, T. E.; Hodges, J. D. 1983. Influence of forestry practices on host-susceptibility to bark beetles. Zeitschrift angewandte Entomologie. 96: 194-208.
- Patterson, J. E. 1930. Control of the mountain pine beetle in lodgepole pine by the use of solar heat. Tech. Bull. 195. Washington, DC: U.S. Department of Agriculture. 20 p.
- Peterman, R. L. 1977. An evaluation of the fungal inoculation method of determining the resistance of lodgepole pine to mountain pine beetle (Coleoptera: Scolytidae) attacks. Canadian Entomologist. 109: 443-448.
- Powell, J. M. 1967. A study of habitat temperatures of the bark beetle, Dendroctonus ponderosae Hopkins, in lodgepole pine. Agricultural Meteorology. 4: 189-201.
- Raffa, K. F.; Berryman, A. A. 1982. Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. Environmental Entomology. 11: 486-492.
- Rasmussen, L. A. 1974. Flight and attack behavior of mountain pine beetles in lodgepole pine of northern Utah and southern Idaho. Res. Note INT-180. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 7 p.
- Reid, R. W. 1963. Biology of the mountain pine beetle, Dendroctonus monticolae Hopkins, in the east Kootenay region of British Columbia. III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. Canadian Entomologist. 95: 225-238.
- Reid, R. W.; Whitney, H. S.; Watson, J. A. 1967. Reactions of lodgepole pine to attack by Dendroctonus ponderosae Hopkins and blue stain fungi. Canadian Journal of Botany. 45: 1115-1126.
- Reifsnyder, W. E.; Lull, H. W. 1965. Radiant energy in relation to forests. Tech. Bull. 1344. Washington, DC: U.S. Department of Agriculture. 111 p.
- Rosenberg, N. J.; Blad, B. L.; Verma, S. B. 1983. Microclimate. The biological environment. New York: John Wiley & Sons. 495 p.
- Safranyik, L. 1985. Effect of climatic factors on development, survival, and life cycle of the mountain pine beetle. In: Hall, P. M.; Maher, T. F., eds. Mountain pine beetle symposium proceedings; 1985 April 16-18; Smithers, BC. Pest Management Rep. 7. Victoria, BC: British Columbia Ministry of Forests: 14-24.
- Safranyik, L.; Jähren, R. 1970. Emergence patterns of the mountain pine beetle from lodgepole pine. Bi-monthly Res. Notes. 26: 11, 19. Victoria, BC: Canadian Department of Fisheries and Forests.
- Safranyik, L.; Shrimpton, D. M.; Whitney, H. S. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Tech. Rep. 1. Victoria, BC: Canadian Department of the Environment, Canadian Forestry Service, Pacific Forest Research Centre. 24 p.
- Schenk, J. S.; Mahoney, R. L.; Moore, J. A. 1980. A model for hazard rating lodgepole pine stands for mortality by mountain pine beetle. Forest Ecology Management. 3: 57-68.

- Schmitz, R. F. 1984. A passive aerial barrier trap suitable for sampling flying bark beetles. Res. Note INT-348. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 8 p.
- Schmitz, R. F.; McGregor, M. D.; Amman, G. D. 1980. Mountain pine beetle response to lodgepole pine stands of different characteristics. In: Berryman, A. A.; Safranyik, L., eds. Dispersal of forest insects: evaluation, theory and management implications: Proceedings of the second IUFRO conference; 1979 August 27-31; Sandpoint, ID. Pullman, WA: Washington State University, Cooperative Extension Service: 234-243.
- Schmitz, R. F.; McGregor, M. D.; Amman, G. D. [In Press]. Effect of partial cutting treatments of lodgepole pine on the abundance and behavior of flying mountain pine beetles. Canadian Journal of Forest Research.
- Schönherr, J. 1976. Mountain pine beetle: visual behavior related to integrated control. In: Proceedings of the XVI IUFRO world congress; 1976 June 20-July 2; Oslo, Norway. As, Norway: Norwegian IUFRO Congress Committee, Div. II: 449-452.
- Schroeder, M. J.; Buck, C. C. 1970. Fire weather-- a guide for application of meteorological information to forest fire control operations. Agriculture Handbook 360. Washington, DC: U.S. Department of Agriculture, Forest Service. 229 p.
- Shepherd, R. F. 1965. Distribution of attacks by Dendroctonus ponderosae Hopk. on Pinus contorta Dougl. var. latifolia Engelm. Canadian Entomologist. 97: 207-215.
- Shepherd, R. F. 1966. Factors influencing the orientation and rates of activity of Dendroctonus ponderosae Hopkins (Coleoptera: Scolytidae). Canadian Entomologist. 98: 507-518.
- Shrimpton, D. M. 1973. Age- and size-related response of lodgepole pine to inoculation with Euophium clavigerum. Canadian Journal of Botany. 51: 1155-1160.
- Somme, L. 1964. Effects of glycerol on cold-hardiness in insects. Canadian Journal of Zoology. 42: 87-101.
- Stuart, J. D. 1984. Hazard rating of lodgepole pine stands to mountain pine beetle outbreaks in southcentral Oregon. Canadian Journal of Forest Research. 14: 666-671.
- Waring, R. H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Advances in Ecological Research. 13: 327-354.
- Waring, R. H.; Pitman, G. B. 1980. A simple model of host resistance to bark beetles. Res. Note 65. Corvallis, OR: Oregon State University, School of Forestry, Forest Research Laboratory. 2 p.
- Yuill, J. S. 1941. Cold hardiness of two species of bark beetles in California forests. Journal of Economic Entomology. 34: 702-709.