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USDA FOREST SERVICE
RESEARCH PAPER INT-71
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THE MOUNTAIN PINE BEETLE IN LODGEPOLE PINE FORESTS

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ABSTRACT

The mountain pine beetle depletes Rocky Mountain lodgepole pine stands by removing periodically the largest, most vigorous trees. Some stands are replaced by succeeding species in 80 to 100 years.

Intensities of mountain pine beetle and dwarfmistletoe damage are influenced by forest associations and elevation. Dwarfmistletoe infection reduces phloem depth and probably results in lower mountain pine beetle brood production.

The probability of lodgepole pine surviving to 16 inches d.b.h. is about two out of three in the *Abies lasiocarpa/Vaccinium scoparium* association, but only one out of four in the *Abies lasiocarpa/Pachistima myrsinites* association. The latter association offers the greatest risk to lodgepole pine. More effective beetle control and alternatives such as type conversion, shorter rotations, mixing species, and developing better size and age class distribution must be considered.

CONTENTS

INTRODUCTION

Lodgepole pine (*Pinus contorta* Dougl.) forests provide an important cover type on more than 15 million acres in 11 states in the western United States. These forests serve many purposes such as cover and scenic backdrops for recreational areas; protective cover for watersheds; habitat for game animals; grazing for domestic livestock; and a storehouse of raw material for lumber, poles, posts, and pulpwood. But without protection and management these forests are transient pioneers giving way to natural forces such as insects, disease, and in the absence of wildfire, to succeeding vegetation. Maintenance of lodgepole pine forests requires both a greater understanding of the continuing biological processes and a high level of management.

Historically, the mountain pine beetle, *Dendroctonus ponderosae* Hopk. has infested extensive areas of lodgepole pine and probably has been active in the ecosystem as long as there have been lodgepole pine trees. Thorne (1935) uncovered evidence of several early outbreaks including one that was active in the Horse Creek territory in Utah over 180 years ago. He reported other outbreaks occurring in different areas between the years: 1870 and 1880; 1915 and 1917; 1924 and 1925; 1929 and 1932.

Flint (1924) reported an epidemic between 1914 and 1918 in lodgepole pine stands near Monture Ranger Station, Lolo National Forest, Montana.

Beginning in 1909, a small mountain pine beetle outbreak was reported on the Flathead National Forest in the northern Rockies.[1] During a succeeding period of 25 to 30 years, new infestations appeared in the Rocky Mountains and increased to epidemics on the National Forests and Parks and extended as far south as the Cache National Forest in Utah despite some direct control efforts along the way. Infestations were recorded on the Flathead, Lolo, Bitterroot, Beaverhead, Gallatin, Targhee, Teton, Bridger, Cache, and Caribou National Forests and Yellowstone and Teton National Parks. The infestation was considerably reduced, particularly on the northern forests, when extremely low temperatures in December 1932 and again in February 1933 caused high mortality in overwintering broods.

Another extensive beetle outbreak is currently in progress in a number of the Intermountain forests where many extensive stands have reached a high state of susceptibility to beetle attack. Direct control efforts to contain the beetle populations have met with variable success and extensive tree mortality has occurred.

One of the primary silvicultural problems is how to manage lodgepole pine in the face of constant beetle pressure and recurring tree mortality. The objective and scope of this paper is to explore the role of the mountain pine beetle as an ecological agent in lodgepole pine stands primarily in the Teton, Targhee, and Bridger National Forests and in the Yellowstone and Teton National Parks; also, the study points out some research needs and management alternatives.

ROLE OF THE MOUNTAIN PINE BEETLE

The mountain pine beetle, an indigenous organism in lodgepole pine ecosystems, exerts numerous and varied effects upon lodgepole pine stands. The phloem layer of the tree comprises the feeding and breeding habitat of the beetles; they spend a large portion of their life cycle in this layer. The adult beetle feeds upon and constructs an egg gallery in the phloem. The beetle larvae feeding at right angles to the egg gallery, in conjunction with blue stain fungi, girdle the tree and cause its death.

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[1]Evenden, James C. History of the mountain pine beetle infestation in the lodgepole pine stands of Montana. USDA Forest Insect Laboratory, Coeur d'Alene, Idaho, typewritten report, 25+ pp., illus. 1934.

TREE SELECTION

Not all lodgepole pine trees in infested stands are likely to be attacked and killed by the mountain pine beetle. The beetle first infests the larger diameter trees which usually have thick phloem and are a better food supply. The number of trees killed varies by environmental conditions as reflected in habitat types.

Diameter

Examination of three stands involved in the current epidemic show that the largest and most vigorous trees are attacked first. As the numbers of trees are reduced by mortality the beetles move into smaller trees until the epidemic subsides. Several studies support these conclusions.

Gibson[2] shows the intensity of beetle infestation by diameter classes observed in the Big Hole area of the Beaverhead National Forest from 1925 to 1940 (table 1). All the lodgepole pine trees 12 inches and larger in diameter were killed. But the percent of trees killed decreased rapidly in the smaller sizes below 12 inches in diameter. These data were collected from a lodgepole pine stand; the majority of this stand was in the Douglas-fir vegetational zone and was included in a severe outbreak that covered about 20,000 square miles.

Table 1.--Susceptibility of lodgepole pine trees to mountain pine and secondary bark beetle attacks by 2-inch diameter classes

Trees killed by	d.b.h. classes: 2	4	6	8	10	12+
	- - - -	- - - -	- - - -	-Percent-	- - - -	- - - -
Mountain pine beetle	0.1	6.5	27.5	56.5	87	100
Secondary beetles	1.5	5.0	9.0	5.5	1.5	None

Cole and Amman (1969) concluded from their studies of two stands in northwestern Wyoming that the beetles strongly favor the larger diameter trees in the stand in any given year as well as throughout the duration of the epidemic. Trees killed by the beetles ranged from 1 percent of the 4-inch trees to 87.5 percent of the trees 16 inches d.b.h. and larger. Furthermore, Cole and Amman pointed out that large infestations of the mountain pine beetle are dependent upon the presence of large diameter trees (14 inches d.b.h. and greater) within a lodgepole pine stand. They also speculated that this beetle is a food-limited insect within a given area because only trees 14 inches d.b.h. and larger contribute sufficient numbers of beetles to maintain or cause an increase in infestations.

Studies by Hopping and Beall (1948) near Banff, Canada, revealed about a 5-percent increase in infestation intensity for each inch increase in diameter; few trees under 6 inches d.b.h. were attacked. Our study shows an increase in percent of trees killed of about 8.8 percent for each 1-inch increase in diameter (figure 1). In the areas examined very few trees below 7 inches in diameter were killed.

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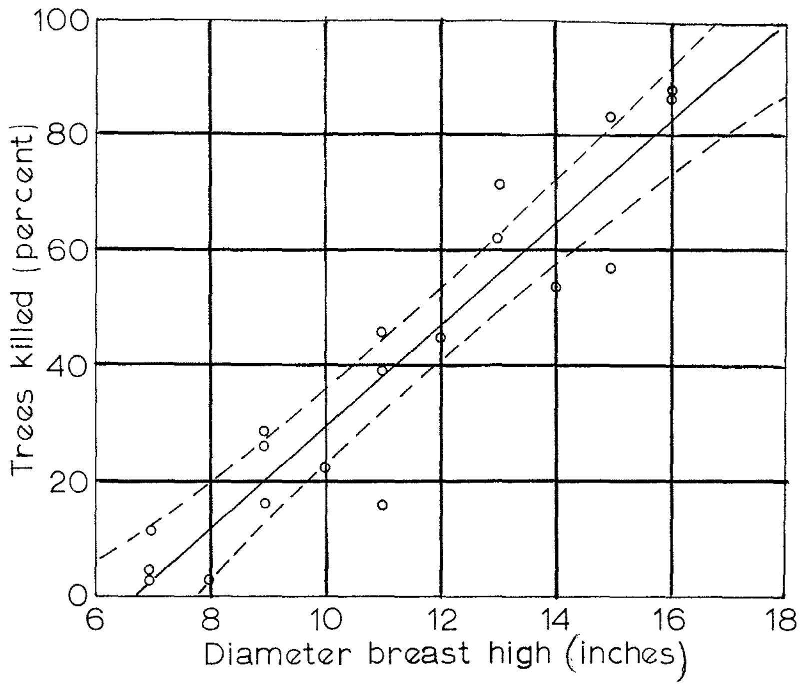
[2]Gibson, Archie L. Status and effect of a mountain pine beetle infestation on lodgepole pine stands. USDA Forest Insect Laboratory, Coeur d'Alene, Idaho, unpub. typewritten office report, 34 pp. 1943.

Figure 1.--Trees killed by mountain pine beetles as related to diameter of host trees. Confidence limits at the 95 percent probability level are shown by the dash lines.



Phloem Thickness

Considerable work is in progress to determine the effect of phloem thickness on beetle attack. Amman has shown in laboratory studies that successful brood development is correlated with phloem thickness. Trees having phloem less than about 0.12 inch thick do not produce enough brood per unit area of bark surface to sustain a successful infestation.

Phloem thickness among lodgepole pine trees is highly variable. However, we have observed that the beetles tend to attack and kill the trees having thicker phloem and pass up many trees of similar diameter that have thinner phloem. Observations show that the thickness of the phloem determines whether the insect can maintain or increase its numbers in the stand. During an epidemic Roe has observed beetles selecting trees in the stand possessing the thickest phloem; and sometimes beetles choose the portion of an individual tree having the thickest phloem. Hopefully, we will gain a greater understanding of the relationship between thickness of phloem and diameter of tree and this may help provide an index to tree susceptibility.

Habitat

Early work by Gibson[2] pointed to the differences in beetle infestation intensity that are related to elevation. He reported that the infestation appeared to be less intensive on the upper end of his sample strips than on the lower. In the Beaverhead National Forest data (table 2), the Elkhorn strip sample--located highest in elevation and in the subalpine fir-Engelmann spruce vegetational zone--showed the fewest beetle-killed trees. The Bitterroot Forest plot data in table 3 displayed the same trend except in the plot at the lowest elevation. Amman (1969) found that brood production in bark of a given thickness is inversely related to elevation. Differences in the rate of tree stocking do not seem to be great enough to explain the variation in infestation intensity in these studies.

Table 2.--Intensity of tree killing by the mountain pine beetle (Beaverhead National Forest 1923-1940)[1]

Location	Elevation	Vegetational zone	Trees per acre before infestation[2]: Lodgepole pine	Trees per acre before infestation[2]: Other	Trees per acre killed by the mountain pine beetle: Number	Trees per acre killed by the mountain pine beetle: Percent
	Feet		- - - - -Number- - - - -		Number	Percent
Battlefield	6,400-7,300	Douglas-fir	1,203	21	209	17.4
Wise River	6,400-7,300	Douglas-fir	533	180	46	8.6
Elkhorn	7,200-7,950	Subalpine fir-Engelmann spruce	1,044	12	24	2.3

[1]Compiled from data collected by Archie Gibson.
[2]Includes trees 3 inches d.b.h. and larger.

Table 3.--Intensity of tree killing by the mountain pine beetle (Bitterroot National Forest 1923-1940)[1]

Plot	Elevation	Vegetational zone	Trees per acre in spring 1923[2]: Lodgepole pine	Trees per acre in spring 1923[2]: Douglas-fir	Trees per acre in spring 1923[2]: Ponderosa pine	Trees per acre killed by the mountain pine beetle: Number	Trees per acre killed by the mountain pine beetle: Percent
	Feet		- - - - - - - - Number	- - - - - - - -		Number	Percent
A	5,400	Douglas-fir	320	32	--	272	85.0
B	5,400	Douglas-fir	32		136	LPP 32 PP 116	100.0 85.3
C	5,100	Douglas-fir	260	72	--	216	83.1
D	6,000	Douglas-fir	172	40	--	140	81.9
E	7,100	Subalpine fir-Engelmann spruce	172	--	--	112	65.1
F	4,750	Douglas-fir	256	--	--	112	43.8

[1]Compiled from data collected by Archie Gibson.
[2]Includes trees 3 inches d.b.h. and larger.

Habitat types reflect differences in environments (Daubenmire 1952, 1961; Daubenmire and Reed;[3] Roe 1967; Illingworth and Arlidge 1960). Therefore, it is plausible that beetle behavior and survival will differ in the various habitat types also. Reconnaissance of 42 stands in three of the most extensive types containing lodgepole pine disclosed some differences in the intensity of beetle activity. Each stand visited was classed in one of four categories as follows:

Intensity class	Criteria
1	No beetle-killed trees present.
2	Less than one-third of the susceptible trees killed.
3	One-third to two-thirds of the susceptible trees killed.
4	Over two-thirds of the susceptible trees killed.

Trees 6.6 inches d.b.h. and larger were regarded as susceptible to beetle attack. The three habitat types considered were as follows:

Habitat type	Elevation (feet)		Exposures
	Mean	Range	
Abies lasiocarpa/ vaccinium scoparium	7,470	6,550-8,450	All exposures
Abies lasiocarpa/ Pachistima myrsinites	7,183	6,700-7,800	Mostly northwest
Pseudotsuga menziesii/ Calamagrostis rubescens	6,474	6,000-7,750	All exposures and plateaus

In addition to beetle infestation, the intensity of dwarfmistletoe infection was also estimated in the same stands. Infected and noninfected dominant and codominant trees were counted and the proportion recorded in one of four categories as follows:

Intensity class	Criteria
1	All examined trees free of dwarfmistletoe.
2	Less than one-third of examined trees infected.
3	One-third to two-thirds of the examined trees infected.
4	More than two-thirds of the examined trees infected.

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[3]Daubenmire, R., and R. M. Reed. Progress report on a study of forest types in the Wind River Mountains, Wyoming. Ditto report on file, Intermountain Forest and Range Experiment Station, Ogden, Utah; limited distribution, 3 pp. 1968.

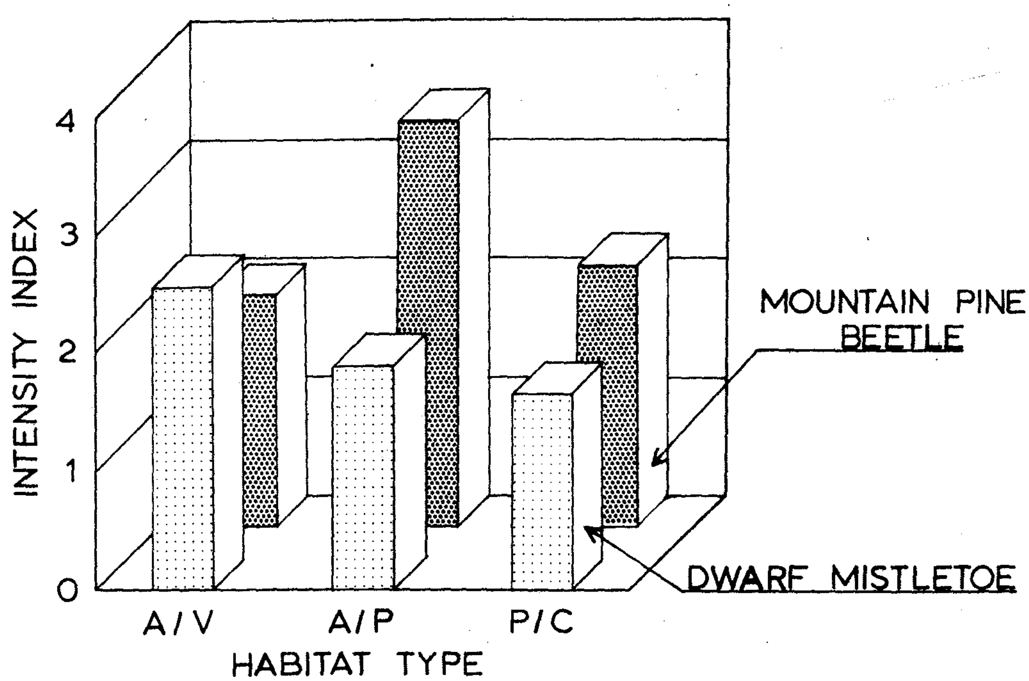


Figure 2.--Relative intensity of mountain pine beetle tree killing and dwarfmistletoe infection on three habitat types. A/V = Abies lasiocarpa/Vaccinium scoparium*; A/P =* Abies lasiocarpa/Pachistima myrsinites*; and P/C =* Pseudotsuga menziesii/Calamagrostis rubescens.

Intensity indexes for both beetle infestation and dwarfmistletoe infection were calculated as weighted indexes. The relative indexes derived simplify the comparisons by transforming the data to comparable units.

The higher elevation stands represented by the Abies lasiocarpa/Vaccinium scoparium habitat type show the lowest index of mountain pine beetle infestation as illustrated in figure 2. At the same time, these stands sustain the highest index of dwarfmistletoe infection. Whether or not this inverse relationship has biological meaning is largely unknown. However, the relationship is relevant if the ability of the mountain pine beetle to produce sufficient brood to sustain an infestation is related significantly to the thickness of the phloem layer. A small sample of 20 randomly selected trees taken in a lodgepole pine stand on the Moose Creek Plateau, Targhee National Forest, suggests that the thickness of the phloem in lodgepole pine trees is significantly reduced in trees moderately to heavily infected by dwarfmistletoe. The results are tabulated as follows:

Level of dwarfmistletoe infection	Radial thickness of phloem (Inches)	
No infection	0.170 ±0.0213	P = 0.95
Medium to heavy infection	0.112 ±0.0218	P = 0.95

A high proportion of the trees in the sampled area would not be suitable for sustaining an infestation if we assume that a radial phloem thickness of about 0.12 inch is needed.

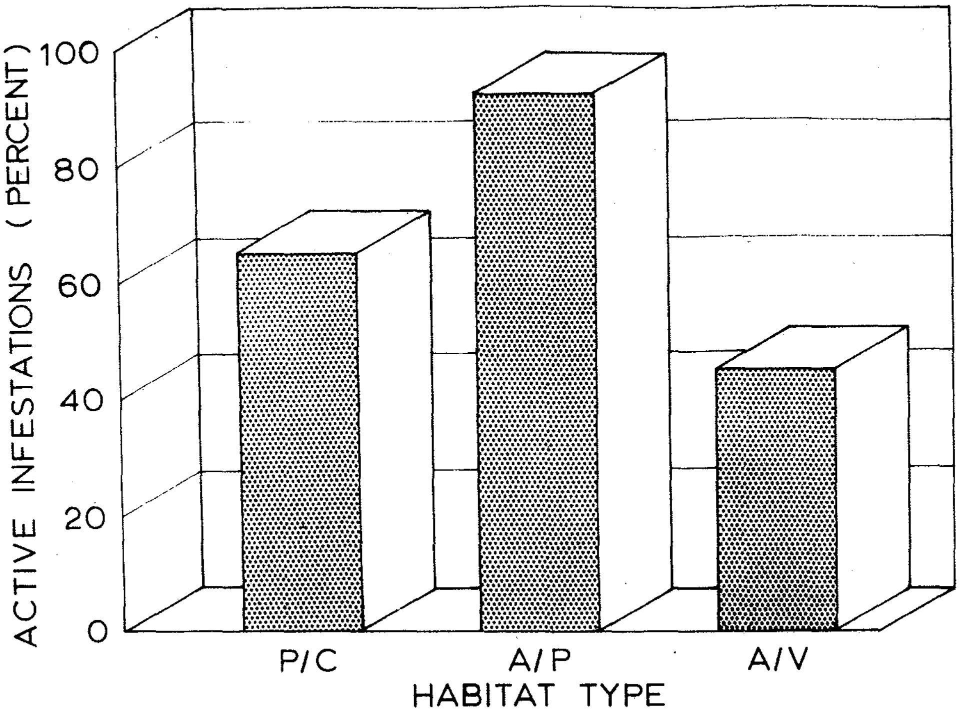


Figure 3.--The percent of stands showing active infestation within habitat types.

By far the most intense beetle activity was found in the Abies lasiocarpa/ Pachistima myrsinites habitat type which exists largely in the middle elevational zone. The high intensity index of 3.4 (figure 2) indicates that the bulk of the stands examined were classed in the medium to heavy categories of susceptible tree killing. The Dell Creek stand, which is described later in this report, exemplifies the state of advanced stand depletion, succeeded by subalpine fir growth commonly found in a large but undetermined portion of the Abies lasiocarpa/Pachistima myrsinites habitat type. The incidence of dwarfmistletoe infection ranked relatively low in this habitat type (see figure 2) with an intensity index of 1.9. There is no way of knowing how much past mortality was caused by dwarfmistletoe in these stands.

A large proportion of the stands examined in the Pseudotsuga menziesii/ Calamagrostis rubescens habitat type were in the light damage category resulting in a moderate intensity index of 2.2 (figure 2). This index places the type in an intermediate position among the three habitat types with respect to beetle activity. The lowest occurrence of dwarfmistletoe infection was found in the Pseudotsuga menziesii/Calamagrostis rubescens habitat type. The distribution of the disease was spotty with patches of heavy infection interspersed with extensive areas showing little or no infection.

A high proportion of the 42 stands examined sustained currently active mountain pine beetle infestations. The least activity, 44 percent of stands with active infestations, was found in the highest habitat type, Abies lasiocarpa/Vaccinium scoparium (figure 3). On the other hand, the Abies lasiocarpa/Pachistima myrsinites habitat type ranked first with active infestations in 92 percent of the stands examined. The pine grass type, Pseudotsuga menziesii/Calamagrostis rubescens, was midway with 64 percent of the stands sustaining active infestations.

Figure 4.--Lodgepole pine killed at Dell Creek (overall view).

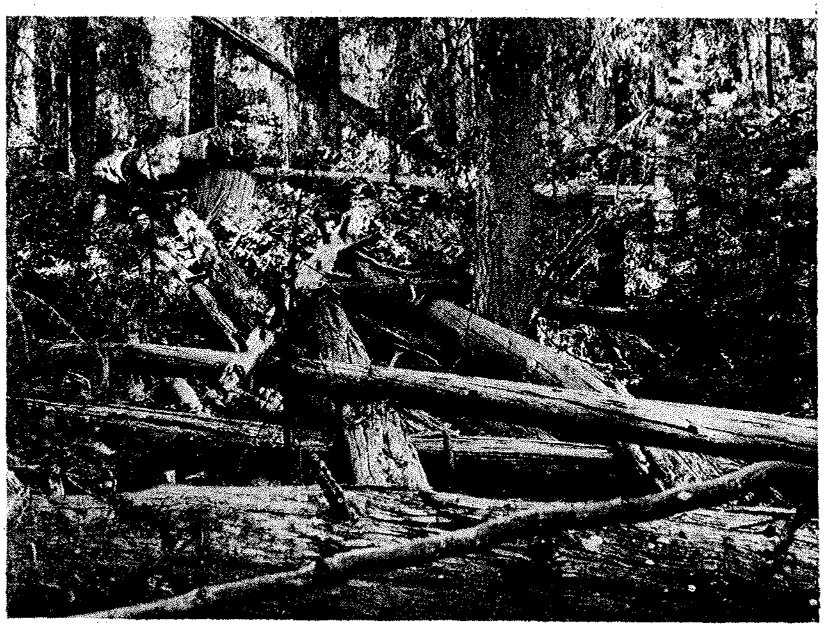


Figure 5.--Lodgepole pine killed at Dell Creek (beetle killed, fallen timber).

All three habitat types showed evidence of repeated infestations. Eighty-six percent of the stands on all the habitat types showed evidence of one or more infestations but 47 percent have survived both the earlier and the more recent infestations. The occurrence of repeated attacks was about the same in all three habitat types.

EFFECTS OF BEETLE INFESTATIONS

The effects of mountain pine beetle infestations are very important in the dynamics of lodgepole pine stands. These effects vary from the abrupt stand depletion of single infestations to the long range genetic selection caused by repeated infestations.

Stand Depletion and Replacement

Lodgepole pine stands depleted by mountain pine beetle infestations usually are replaced in one of two ways. The decimated stands may be succeeded by other species in the absence of fire or they may be replaced by lodgepole pine seedlings following a fire.

Succession

Studies on three stands of lodgepole pine in the Targhee and Teton National Forests have provided some information concerning the effect of mountain pine beetle infestations. Specifically, three facts of interest were developed: namely, (1) beetle infestations do in some instances occur at varying intervals within the same stand until the lodgepole pine is largely eliminated; (2) residual trees accelerate their growth when the beetle-infested trees die; and (3) growth of succeeding tree species is stimulated either by the release of existing reproduction or the establishment of new trees in the stand openings created by the death of beetle-infested trees. The stand data were collected on 1/10-acre plots systematically located within the stands. Sample trees on each plot were bored to determine age and past diameters.

Dell Creek.--The most interesting stand studied grows in Dell Creek on the Teton National Forest. Many large lodgepole pine windfalls attest to past beetle infestations. Lodgepole pine trees killed in the most recent infestation, with a few exceptions, still remain standing; but the trees on the ground were killed by beetles in earlier infestations (figures 4 and 5). Although we were unable to date the fallen trees, they obviously had been on the ground for various lengths of time. Some were decayed to such an extent that only remnants of recognizable material were left. Despite an advanced state of decay in some of the older windfalls, beetle engravings were visible on small sound remnants of the decayed boles.

Evidence obtained from the increment cores taken in this stand suggests that at least four mountain pine beetle infestations have occurred since 1892. The subalpine fir in the present stand developed from an understory that has been released by the periodic death of lodgepole pine overwood to become the dominant stand presently on the area (figure 6 and table 4). The sampling errors for the total values of Table 4 generally did not exceed 10 percent at the 95 percent probability level. Significant periods of release found in the subalpine fir are shown in the following tabulation:

Period	Percent of sample trees showing significant release
1892-1907	95
1919-1927	60
1937-1947	45
1956-1964	40

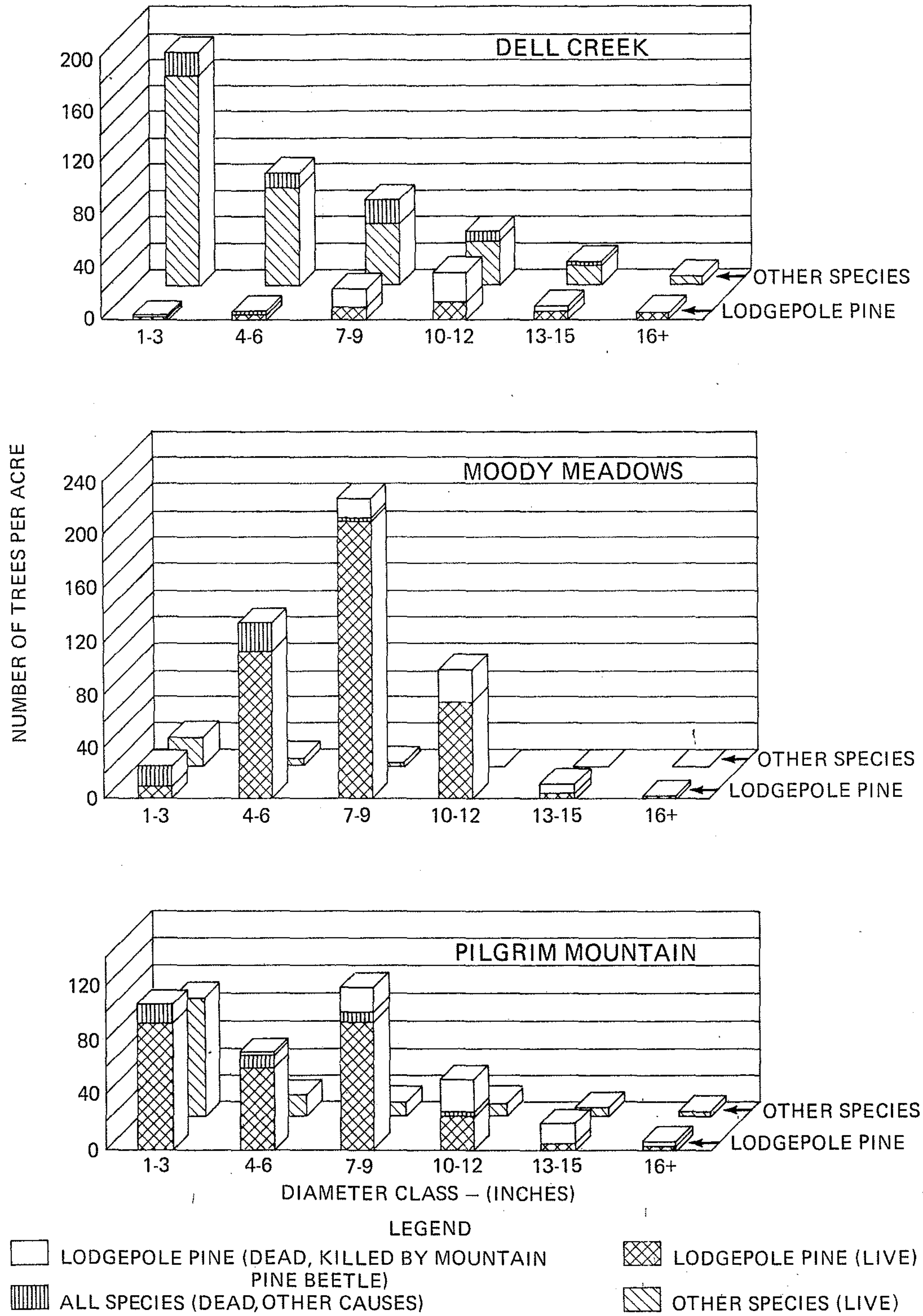
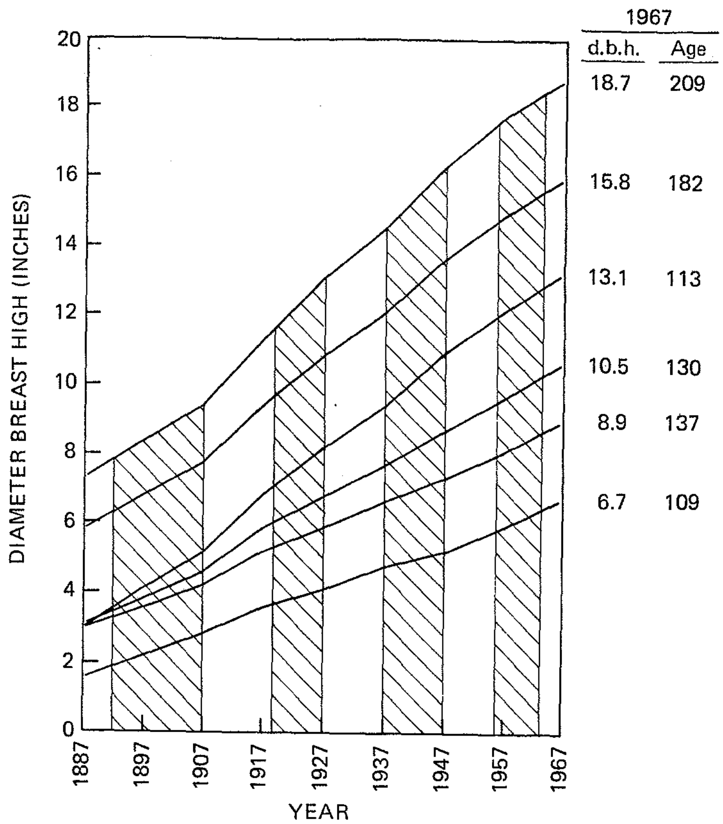


Figure 6.--The distribution of post-epidemic live and dead trees on Dell Creek and Pilgrim Mountain areas, Teton National Forest, and the Moody Meadows area, Targhee National Forest.

Figure 7.--Diameter trend curves of residual subalpine fir trees during four mountain pine beetle infestations in the lodgepole pine overwood, Dell Creek, Teton National Forest. The superimposed crosshatched bars show the periods of infestation.



Curves showing the trend of past diameters in the subalpine fir understory and the periods of beetle infestations superimposed over them are presented in figure 7. The changing upward trend in these curves reflects the release of the understory following the death of lodgepole pine in the overwood. For example, the rather abrupt upward change in the curves from 1907 to 1927 reflects an improvement in diameter increment during that period. It is noteworthy that all the trees in the stand did not show simultaneous release as would be expected from weather effects. Furthermore, the available weather records from the nearest but somewhat distant stations show generally below average precipitation between 1917 to 1937.

The greatest release of subalpine fir followed the first suspected infestation that occurred from 1892 to 1907. During that period 95 percent of the cores showed significant release and this is reflected in the upward trend of diameters following 1907. This trend continued for two decades into the middle of the moisture deficient period, 1917 to 1937, as well as through the second infestation. During the third infestation, 1937 to 1947, the diameter curves steepened again, probably reflecting the release during that period. While the larger trees showed the greatest release effect during the earliest infestation, the three smaller classes of trees displayed continued response following the later infestations. The earlier infestations apparently involved the death of greater numbers of lodgepole pine trees than the later ones; consequently, the earlier infestations had a greater release effect upon the subalpine fir stand. Furthermore, the larger subalpine fir trees had attained a more dominant position in the crown canopy by the time of the last infestation; therefore, they were not as subject to release as the smaller trees. The curves illustrate

Table 4.--Basal area summarized for three areas examined that have sustained one or more mountain pine beetle infestations

Tree condition	Dell Creek	Moody Meadows	Pilgrim Mountain
	Square feet		
		LODGEPOLE PINE	
Live	14.9	137.8	66.5
Dead[1]	27.5	28.8	46.8
Dead[2]	--	5.6	6.2
Total	42.4	172.1	119.5
		SUBALPINE FIR AND OTHER SPECIES	
Live	73.8	1.7	26.5
Dead[2]	17.0	--	--
Total	90.8	1.7	26.5
		ALL SPECIES	
Live	88.7	139.5	93.0
Dead[2]	44.5	34.3	53.0
Total	133.2	173.8	146.0

[1]Killed by mountain pine beetle.

[2]Other causes.

the development of the fir understory as the lodgepole pine overwood was reduced by repeated beetle infestations. Some mortality also occurred in the subalpine fir stand as reflected by the 17.0 square feet of basal area recorded under dead trees in table 4.

Moody Meadows.--Another lodgepole pine stand investigated by Roe near Moody Meadows on the Rexburg District of the Targhee National Forest has been infested twice. The first infestation occurred approximately 1937 to 1947. Some control effort, felling and spraying infested trees, was applied in the stand in 1946 (figure 8). This first infestation was light and was probably checked by the control effort or the beetles were unable to sustain themselves in the thin-barked trees in the stand. But now, 21 years later, the same stand is reinfested and the latter infestation is more intensive than the former--46.9 trees per acre killed in the current infestation as contrasted with 17.7 trees per acre in the first. The present infestation has killed trees in the 7- to 14-inch range amounting to 16.7 percent of the total basal area in the stand.

Trees in the residual stand with diameters 4 inches and larger range from 54 to 106 years in age with a mean age of 87 years. Some lodgepole pine trees up to 16 inches d.b.h. can be found in the stand. The Moody Meadows stand is stocked with 516 trees per acre, 1 inch d.b.h. and larger, and these are distributed among diameter classes as shown in figure 6.

Residual lodgepole pine trees in the Moody Meadows stand show definite release as illustrated by the upward trend in diameter following the 1937 to 1947 infestation (figure 9). The release effect appears to be most pronounced in the larger trees, particularly those that were located either in or near the margin of the openings

Figure 8.--View of a portion of the Moody Meadows stand on the Targhee National Forest, showing stumps and treated trees from the 1946 control effort. Note the denser clump of smaller trees in the background.

created in the earlier infestation. The released trees have continued to grow well to the present time, but trees in other parts of the stand showed signs of growth reduction for several years prior to 1967. Significant release has not yet become apparent from the thinning caused by the current infestation.

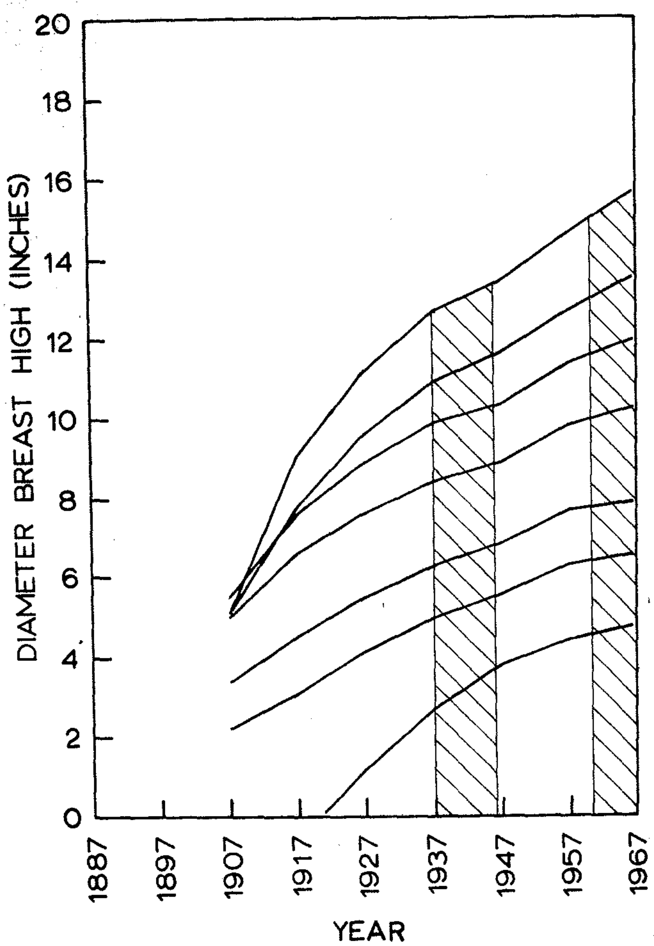
Losses to other causes are proportionately greater in the smaller trees as illustrated in figure 6. Few trees below about 6.5 inches were killed by the mountain pine beetle. This stand near Moody Meadows can still sustain a number of beetle infestations. Mortality has been light, probably because of the small size and thin bark of the trees. However, further growth of residual trees will provide suitable trees for future infestations.

A subalpine fir understory of about 29 trees per acre averages 2.62 inches in diameter and ranges from 1- to 7-inch trees. In addition, 1,115 subalpine fir seedlings 3 inches high to 1 inch d.b.h. per acre are growing in the stand which will fill the overwood openings as they are created by future beetle infestations (figure 10). The subalpine fir distribution by diameter classes simulates a J-shaped curve thereby demonstrating succession of lodgepole pine by subalpine fir.

Pilgrim Mountain.--This stand of lodgepole pine is in the northwestern part of the Teton National Forest bordering the Teton National Park. It is currently infested with its first known attack of mountain pine beetles. The stand contains 492 trees per acre that are 1 inch and larger in diameter. The age of the residual trees 4 inches d.b.h. and larger ranges from 33 years to 113 years with a mean age of 76 years. The distribution of trees by diameter groups is shown in figure 6 and stand basal areas are shown in table 4. The overwood includes trees up to 21 inches in diameter although all lodgepole pine trees 18 inches and larger have been killed in the current beetle infestation. Furthermore, trees down to and including 6.6 inches d.b.h. have been killed as shown in figure 4. Losses caused by factors other than the mountain pine beetle are proportionately greater in the smaller d.b.h. classes.

At present, no well defined release effect is evident in the diameter trends for the Pilgrim Mountain stand, and diameters show a steady increase through the life of the stand.

Figure 9.--Diameter trend curves of residual lodgepole pine trees in the Moody Meadows area, Targhee National Forest. The two periods of beetle infestation are shown by superimposed crosshatched bars.



The substantial understory consists mainly of subalpine fir and some Douglas-fir and comprises about 18.5 percent of the stand basal area shown in table 4. These trees average about 3.75 inches d.b.h. including trees from 1 to 15 inches in diameter. The distribution of these trees by diameter groups as illustrated in figure 4 resembles a J-shaped curve which is typical of succeeding species. A large number of seedlings (2,812 per acre) under 1 inch d.b.h. (mostly subalpine fir) provides a reservoir of trees not shown in figure 6. When released by the death of beetle infested lodgepole pines, these seedlings will grow to larger sizes and become more prominent in the stand.

One of the most obvious effects of tree killing by mountain pine beetles is the depletion of the lodgepole pine stand. This effect is rather dramatic and can be observed readily in the "red top" or faded trees that appear in the stand. The dead trees gradually fade from the conspicuous "red top" condition to a gray appearance in 2 to 3 years and begin to fall and accumulate on the ground within about 5 years after the infestation subsides (Flint 1924).

Individual trees live and grow in harmony with their environment which in turn is modified by the trees themselves. This modification results from processes such as shading the forest floor, intercepting snow and rain, reducing wind movement over the ground, utilizing soil moisture and nutrient materials, and adding organic matter to the soil as well as cycling minerals, and many others.

Figure 10.--Subalpine fir and Douglas-fir seedlings grow in stand openings created by mountain pine beetle infestations. Moody Meadows area, Targhee National Forest.

When a portion of the stand dies it causes changes in light, temperature, moisture accumulation, and soil moisture, among others, and thereby creates a new niche in the environment. This ecological niche is soon filled by the growth of newly established seedlings--chiefly more tolerant species--or the accelerated growth of existing trees or other vegetation. The Dell Creek data are a good example of a stand in which the displacement of lodgepole pine has progressed to an advanced stage. During the period of depletion the stand exists in varying degrees of mixtures of dead trees, green residuals, and succeeding species.

Stand structure in the Dell Creek stand, before stand depletion and accelerated understory growth changed it, probably compared well with the present stand structure in the younger Pilgrim Mountain stand (figure 6). Subalpine fir ranging from 6.7 to 18.7 inches in the present Dell Creek stand had a mean d.b.h. of 3.4 inches and a range of 1.6 to 7.3 inches in the stand 80 years ago. The subalpine fir contained in the present Pilgrim Mountain stand averages 3.8 inches d.b.h. and represents a range of 1 to 21 inches in diameter. We have been unable to reconstruct the depleted lodgepole pine stand in the Dell Creek area, but considering the volume of material on the ground it appears to have been a well stocked stand. If we assume the same rate of lodgepole pine depletion and subalpine fir understory growth on Pilgrim Mountain as occurred in Dell Creek, it is conceivable that the Pilgrim Mountain stand could arrive at nearly the same condition in about 80 years.

Regeneration

It is likely that many beetle-decimated lodgepole pine stands containing residual seed trees with serotinous cones have burned over in the past and reseeded promptly to establish new lodgepole pine stands. For example, the Sleeping Child Fire, touched off by a lightning strike in 1961, burned in excess of 25,000 acres of lodgepole pine and associated stands on the Bitterroot National Forest.[4] This fire burned lodgepole pine stands that had sustained heavy damage by a mountain pine beetle infestation from 1928 to 1932 when a large proportion of the dominant and codominant trees was destroyed. Following the fire, a large part of the burn (over 15,000 acres) restocked naturally

[4]Office report, Northern Region, U.S. Forest Service. Report on file at Intermountain Forest and Range Experiment Station, Ogden, Utah.

with lodgepole pine seedlings (figure 11). Four years after the burn, 10,000 acres were stocked so heavily with seedlings that thinning would be required to place the stand in good growing condition. In addition to providing conditions for area restocking, the fire cleaned up accumulated fuel that resulted from the beetle attack. Eighty to 90 years from now these newly established lodgepole pine trees will reach sizes attractive to the beetles; then these trees probably will be ready for another mountain pine beetle infestation.

All of the stands that originated during past years of high fire occurrence in the Rockies have reached simultaneously a stage of increased insect susceptibility. This means that the increased susceptibility is present over extensive areas. When these forests reached the proper stage of growth (i.e., diameter and phloem thickness) they provided the habitat in which the beetle populations could build up and sustain infestations. Furthermore, the outbreaks spread over wide areas because trees of susceptible diameter and age occurred extensively. However, repeated beetle infestations, dwarf-mistletoe infection, fire, and logging all have contributed to stand changes resulting in the variability of present lodgepole pine stands as well as conversion to other forest types. Tackle (1954) recognized at least six different stand types including both pure and mixed stands. He pointed out most of the above-mentioned factors in stand formation, but he failed to recognize insects, particularly the mountain pine beetle, among them. From our observations we conclude that the mountain pine beetle has exerted widespread, and in some instances rather dramatic, influence upon stand formation in Rocky Mountain forests.

The absence of fire in lodgepole pine stands, whether caused by organized fire protection or natural controls, combined with stand depletion by the mountain pine beetle, favors the displacement of lodgepole pine. The establishment and growth of succeeding trees, especially of Douglas-fir at the lower elevations and subalpine fir and spruce at the higher elevations, are encouraged by the environment in the beetle-decimated stands. Unless wildfire runs through these stands before repeated beetle infestations and other agents of mortality remove most of the residual seed-bearing lodgepole pine, the stand eventually will convert to climax species. The historical role of fire in stand formation and in the sustaining of lodgepole pine was stressed by Horton (1956) in Alberta. Fire or logging may intervene to reverse the successional trend and reestablish lodgepole pine as happened in the Sleeping Child fire.

Growth Potential

Mountain pine beetle infestations remove the most vigorous element of the stand because they prefer the largest trees, usually with the thickest phloem. The residual trees are usually of the intermediate and suppressed crown classes with some slow growing dominants and codominants. Occasionally the smaller residual trees are older than the larger trees in the stand. The stand structure becomes less favorable for rapid tree growth with each repeated infestation.

Even though the residual trees are released they rarely grow as large, within the same time, as those which had been killed by the mountain pine beetle. The limited number of residual lodgepole pines in heavily depleted stands is made up of old (sometimes nearly 300 years), extremely thin barked trees. These trees often grow extremely slowly with 10-year diameter increments of as little as 1/10 inch or less.

Genetic Selection

Genetic selection, a more subtle effect, probably is accomplished through the selective killing of lodgepole pine trees by the beetle. Because each beetle infestation removes the most vigorous element (i.e., the largest trees) of the stand, it is

Figure 11.--Extensive areas of the Sleeping Child Burn became stocked so heavily that thinning has been required to promote tree growth.

reasonable to speculate that the faster growing genotypes are being destroyed before the lodgepole pine trees can restock the area. Trees as young as 62 years have sustained beetle infestations so that selection sometimes begins early in the life of these stands. If wildfire strikes the stand before the selection process has progressed too far and seeds from serotinous cones are released to regenerate the stand, such selection may not be of much consequence. However, if fires or other stand-regeneration processes do not occur before the stand reaches an advanced stage of depletion the selection is likely to have more effect.

Some Secondary Effects

Populations of secondary beetles, such as Ips pini Say, build up in harmony with mountain pine beetle infestations (Gibson[2]). Emerging from trees either killed or weakened by mountain pine beetles, these secondary beetles may be present in sufficient numbers to kill trees. The secondaries attack principally smaller trees and therefore do not have the devastating effect on the stand that the mountain pine beetle does. In some instances, the tree killing by Ips beetles may amount to a thinning of the smaller residual trees.

Windthrown beetle-killed trees often cause destruction or damage to trees in the succeeding understory. The beetle-killed trees begin to topple within 5 years after an infestation has declined (Flint 1924) and such windthrow may continue for 10 or more years following the end of the infestation according to Gibson.[2] Gibson observed heavy damage among the trees in the very small diameter classes and even among seedlings.

Depending upon the amount of stocking present, this reduction in numbers may be somewhat beneficial to the stand; or, in sparsely stocked stands the removal of a few trees may seriously hamper natural restocking. Furthermore, the mechanical injury of these understory trees makes them more subject to heart rots and other fungus infections by providing the avenue of entrance in the scarred boles. This type of damage may be rather difficult to predict. The effect of damage and subsequent fungus attack may not manifest itself until many years after the epidemic.

Gibson also pointed out that direct windthrow of residual green trees in heavily attacked stands results when these trees lose the protection of trees killed by the beetles.

Increased fire hazard resulting from tree killing and windthrow has been pointed out by many writers including Flint (1924) and Gibson.[2] Flint estimated that the amount of labor necessary to control a fire in areas having large accumulations of beetle-killed trees may be doubled. There is no question but that the cost of fire suppression in beetle-decimated stands will be considerably higher for two reasons: (1) the physical job of removing the extra load of windfalls requires more labor and machine time for operations such as fireline construction; and (2) the large volume of dead material, either standing or on the ground, creates a much hotter fire than would normally occur resulting in a more difficult suppression job. The hotter burn also may have more far-reaching effects on soils than more normal cooler fires. More research is required to increase our knowledge of the effect of such hot fires on soils.

MANAGEMENT ALTERNATIVES

The nearly constant mountain pine beetle pressure being exerted in the Intermountain lodgepole pine forests poses perplexing management problems. Among them are such problems as successful beetle control, acceptable risk from stand decimating forces, and long term management goals and plans to cope with the beetle.

BEETLE CONTROL

Expensive stopgap measures such as direct control involving the spraying of standing or felled trees with penetrating toxic chemicals provide only a holding action until the potentially susceptible trees can be disposed of in some other way.[5] A great deal of mortality results despite any immediate success of the control measures. The unpredictability of these control measures and the relative certainty of reinfestation of the stand later on leaves the manager with relatively little choice of action. He must cut and regenerate the lodgepole pine stand as soon as possible if he wishes to avert further loss, or risk the loss of the stand to further depletion by beetle activity and ultimate displacement by other species which are sometimes considered less desirable.

One of the critical needs is to develop more effective and predictable beetle control measures, especially for use in combination with silvicultural practices.

Pheromones (chemicals produced and used for communication by insects) offer, at this time, some remote promise of control through population manipulation. The pheromones of several species of bark beetles have been identified (Renwick 1967; Silverstein et al. 1966a, 1966b, 1968). More recently, research sponsored by the

[5]Memorandum dated 10/11/68 from Floyd Iverson, Regional Forester, Region 4, to Chief of Forest Service, reporting on the R-4 field survey. Report on file at Intermountain Forest and Range Experiment Station, Ogden, Utah.

Montana-Northern Idaho Pest Action Council (Cox 1968) resulted in identification of a chemical attractive to the mountain pine beetle (Pitman et al. 1968). This research is directed toward manipulation of mountain pine beetle populations to reduce losses in the western white pine type.

Although tests have shown beetle response to pheromones, the practical field use of these chemicals has not been demonstrated. Atkins (1968) points out a number of obstacles to successful field use, particularly lack of understanding many of the basic physiological-behavioral aspects of bark beetle ecology.

LONG TERM MANAGEMENT GOALS AND PLANS

The management of lodgepole pine is handicapped by such factors as mountain pine beetle infestations, dwarfmistletoe infections, and lack of sufficient markets. Markets can and will develop with increased demands for timber and shortage of supplies in other areas. Dwarfmistletoe infections can be controlled through proper cutting methods and treatments applied to the cutover areas. However, in the absence of wholly effective control methods, the mountain pine beetle is apt to remain a threat to the lodgepole pine resource.

Acceptable Risk

Every forest management action assumes some calculated risk and growing lodgepole pine trees in the face of mountain pine beetle depredations is no exception. For example, as seen in figure 1, the probability of an 18-inch tree surviving a beetle epidemic is practically zero, whereas 12-inch trees have about a 50-50 chance of surviving and 10-inch trees show about a 70 percent chance of surviving.

Data presented from the reconnaissance of the 42 stands in the Targhee-Teton-Yellowstone area show that approximately 86 percent sustained one or more infestations. Therefore, the probability of a stand being infested in this area appears to be rather high. If we assume 86 percent probability of infestation in the stand and 50 percent probability that the 12-inch trees will be infested, then the product of these two (86 X 50 = 43 percent) would provide an empirical estimate of the probability of loss. On this basis there is about a 57 and 74 percent probability that 12-inch and 10-inch lodgepole pine trees, respectively, will not be killed by the mountain pine beetle. The utility of these probabilities is only to illustrate the point, but their applicability to other lodgepole areas is questionable. Much variability exists in the probabilities even locally, so widespread use of these values is not recommended.

Although the probability of attack by tree age is not known, nevertheless age and diameter are correlated so that probabilities by diameter classes do reflect age relationships.

As previously stated, the probability of infestation varies by habitat type. For example, in the *Abies lasiocarpa/Vaccinium scoparium* habitat type the probability of an infestation occurring is about 44 percent (figure 3). However, the probability of an active infestation in the *Abies lasiocarpa/Pachistima myrsinites* habitat type exceeds 90 percent. Therefore, habitat types must also be taken into account when considering risks to be assumed in management. For example, the risk of growing 16-inch trees on the *Abies lasiocarpa/Pachistima myrsinites* habitat type would be very high (92 X 82 = 75 percent probability of loss) where only 25 percent or less of the 16-inch trees could be expected to survive. On the other hand, a 44 percent probability in the *Abies lasiocarpa/Vaccinium scoparium* habitat type would present a brighter picture where (82 X 44 = 36 percent loss) 64 percent or nearly two-thirds of the 16-inch trees could be expected to survive.

When making the decision to grow lodgepole pine the forest manager will be faced with the choice of how much of a risk he is willing to accept. He may therefore decide that a 64 percent survival of 16-inch trees in the Abies lasiocarpa/Vaccinium scoparium habitat type is an acceptable risk, but the 25 percent expected survival in the Abies lasiocarpa/Pachistima myrsinites habitat type may be judged as an unacceptable risk. He could then consider other management alternatives for the Abies lasiocarpa/Pachistima myrsinites habitat type.

Management Practices

If the risk of lodgepole pine management is too high there are a number of management practices to be considered. Some of these are described below.

Type Conversion

Some objectives of management may be met as well with one forest type as another. For example, a subalpine fir-Engelmann spruce or a Douglas-fir stand could serve watershed management, recreation, range, wildlife, and in some instances timber objectives as well as a lodgepole pine stand. The type conversion can be accomplished naturally through culturing the understory or artificially by a cutting that is followed by planting or seeding.

Rotation

Another practice might be to select as an objective the smallest tree size that will fulfill product requirements and to select the shortest rotation to grow trees to this size. The size selection should be based upon the greatest beetle risk that the manager is willing to accept. Thus, he would probably select a small size objective of possibly 10, 12, or 14 inches and a short rotation for growing trees on the high risk Abies lasiocarpa/Pachistima myrsinites type and, at the same time, set a larger size objective with a longer rotation on the lower risk Abies lasiocarpa/Vaccinium scoparium type.

Species and Age Class Mixtures

A third practice could be to develop mixed stands including lodgepole pine. Presumably, beetles will infest the mixed lodgepole pine stands as readily as the pure stands (Flint 1924). However, some of the lodgepole pine will survive to 16-inch trees even in mixtures, and the other species will help to maintain a higher stocking rate than would be the case in pure decimated lodgepole pine stands. Overall production would probably be higher in mixed than in pure stands. Such mixed stands would meet the recreational, wildlife, and watershed objectives as well or better than pure lodgepole pine.

Achieving a desirable mix and juxtaposition of age classes provides yet another practice but this plan also entails some risk of loss. This would require long-range planning to avoid cuttings that would establish extensive areas of single age classes; also, this practice would require the use of the best known beetle control measures in reserved stands. Breaking up a stand into several age classes and separating similar age classes by interspersing others would probably do two things: (1) it would eventually place the minimum area in beetle-susceptible stands, making prompt removal of these stands, or the application of control measures more feasible when such stands become infested; and (2) it would limit the size of the areas and this separation of stands might help to hold the beetle population at lower levels. This is an objective which can only be met through long-range planning, good markets, adequate road systems, and the passage of time.

Preservation of Genotypes

The speculation that the faster growing genotypes may be diminishing under beetle pressure emphasizes the importance and urgency of preserving the best genotypes. Because this consideration is purely theoretical, studies of genetic variability in these beetle-infested stands are urgently needed to show the validity of the theory. If this is a valid theory then some attempt should be made soon to preserve the better genotypes. Great variation in tree growth does exist in lodgepole pine stands and a program to search out and propagate best phenotypes could be undertaken even before completion of the above studies.

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