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Role of the Mountain Pine Beetle in Lodgepole Pine Ecosystems : Impact on Succession

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The Role of Arthropods in Forest Ecosystems

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Chapter 1

The Role of the Mountain Pine Beetle in Lodgepole Pine Ecosystems: Impact on Succession

G. D. AMMAN

Introduction

The mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), is the most aggressive member of its genus in the western United States. Populations of the beetle periodically build up and kill most of the large dominant lodgepole pines, *Pinus contorta* var. *latifolia*, over vast acreages. The beetle is indigenous to North America and probably has been active in lodgepole pine ecosystems almost as long as lodgepole pine has existed. Frequency of infestations in a given area of forest appears to range from about 20 to 40 years, depending upon how rapidly some trees in the stand grow to large diameter and produce thick phloem, conditions conducive to buildup of beetle populations. In addition, trees must be at a latitude and elevation where temperatures are favorable for beetle development.

The Mountain Pine Beetle

The adult is stout, black to dark brown, cylindrical and about 6 mm long. The beetle usually completes one generation per year in lodgepole pine. However, two years may be required at high elevations and the cooler climates of northern latitudes. New adults emerge from the bark between late June and early September depending upon elevation, latitude, longitude, and weather conditions during the flight period. After a period of sparse, sporadic emergence, the majority of beetles emerge and make attacks in about a one-week period (Rasmussen, 1974). This rapid emergence by most of the population allows successful infestation of vigorous trees. If the attacking beetles are few in number, egg galleries may become impregnated with resin and all eggs and larvae are killed by resinosus (Reid et al., 1967). The tree may survive these light attacks.

The female initiates the attack, usually on the basal 2 m of the tree trunk, and produces an aggregating pheromone, *Trans* -verbenol (Pitman et al., 1968). This pheromone in conjunction with terpenes from the tree guides other beetles to the tree and serves as a signal for invasion of the host (Vité and Pitman, 1968). Beetles attack the tree en masse and kill it if their numbers are sufficient. To prevent overcrowding, attack density on individual trees is regulated by host condition (Renwick and Vité, 1970) and antiaggregative-rivalry pheromones that mask the aggregative pheromone (Rudinsky et al., 1974). The female usually mates early in gallery construction and lays eggs in irregularly alternating groups on the two sides of the vertical gallery. She lays about two eggs/cm of gallery; however, the number varies with size of female (Reid, 1962; McGhehey, 1971; Amman 1972a), with phloem thickness and temperature (Amman 1972a), and with freshness and moisture content of the bark (Reid, 1962). Eggs hatch in about two weeks and larvae feed individually in the inner bark (phloem). Larval galleries usually extend at right angles to the egg galleries, thereby girdling the tree.

Mature larvae excavate oval cells in the bark, lightly scouring the sapwood, where they pupate and later become adults. New adults feed within the bark prior to chewing exit holes through the outer bark and then emerge to attack healthy trees.

More females than males almost always survive. However, no single factor appears to be responsible for differential survival of the sexes. Differences have been attributed to crowding (W. E. Cole, 1973), length of cold storage (Watson, 1971; Safranyik, 1976), and phloem quality (Amman and Pace, 1976) in laboratory studies; and to drying in field studies (Amman and Rasmussen, 1974; Cole et al., 1976). The sexes survive about equally in large diameter trees where conditions appear most favorable to the beetle (Cole et al., 1976).

In addition to the girdling action of larvae, blue-stain fungi—*Ceratostomella montia* (Rumbold, 1941) and *Europhium clavigerum* (Robinson-Jeffrey and Davidson, 1968)—are introduced by adult beetles and have been considered the primary cause of tree death (Safranyik et al., 1974). Fungal spores which probably are picked up during maturation feeding by the new adult are carried in a maxillary mycangium (Whitney and Farris, 1970), indicating a true symbiotic relationship of fungus and beetle. The spores are introduced into the tree as the beetles construct egg galleries. The blue-stain fungi invade the phloem, and especially the sapwood of the xylem, where they interfere with conduction (Nelson, 1934). The principal benefit to the beetle appears to be regulation of moisture conditions in the tree during development. Trees having well developed blue stain dry out more rapidly than trees containing poorly developed blue stain following infestation, but remain more moist about 11 months following infestation when the beetle is completing development. Blue-stain fungi do not appear to be necessary to mountain pine beetle nutrition (Whitney, 1971).

E. clavigerum has been artificially inoculated into lodgepole pine to determine resistance to the fungus, and thus, an indicator of resistance to infestation by the beetle (Reid et al., 1967). The beetle killed more nonresistant than resistant trees rated according to response to fungal inoculation (Shrimpton and Reid, 1973). Trees rated potentially resistant had faster growth rates and thicker phloem than those rated nonresistant (Shrimpton, 1973).

Lodgepole Pine

Pinus contorta is one of the most widely distributed tree species in western North America, extending from the Yukon Territory to Baja California, and east to the Black Hills of South Dakota (Little, 1971). The lodgepole pine of concern here, *P. contorta* var. *latifolia*, is the inland variety found in mountainous areas from Colorado to the Yukon Territory.

Lodgepole pine grows rapidly where competition is limited, reaching a size of 24 m in height and 41 cm d.b.h. (diameter at breast height = 1.4 m above ground) in 50-60 years. Trees in unmanaged, even-aged stands on medium sites in Montana averaged 19 m in height and 21 cm d.b.h. at age 80 (Tackle, 1959). However, lodgepole pine on such sites is not mature until age 120, nor overmature until age 140 (Tackle, 1955).

Ecologically, lodgepole is typically described as seral, with low shade tolerance; possessing the ability to grow on almost any forest site;

having serotinous cones that require high temperatures to open and release seed; regenerating rapidly in large numbers that create stagnated stands; having rapid growth in young trees and slow growth in old trees; having high susceptibility to mistletoe infection and premature mortality from mountain pine beetle attack. Many of these characteristics contribute to large fuel buildups that lead to intense fires over large areas, thus renewing the cycle (Pfister and Daubenmire, 1975).

Pfister and Daubenmire (1975) recognized four basic successional roles for lodgepole pine:

1. Minor seral. Lodgepole pine is a minor component of young, even-aged, mixed species stands. It is rapidly replaced by shade-tolerant associates in 50-200 years; the more mesic the site, the sooner lodgepole pine is replaced.

2. Dominant seral. Lodgepole pine is the dominant cover type of even-aged stands with a vigorous understory of shade-tolerant species that will replace the lodgepole in 100-200 years. Succession occurs most rapidly where lodgepole pine and shade-tolerant associates become established simultaneously. Lodgepole pine gains dominance through rapid early growth, but shade-tolerant species persist and assume dominance as individual lodgepole pines die.

3. Persistent. Lodgepole pine forms the dominant cover type of even-aged stands with little evidence of replacement by shade-tolerant species. These species are present only as scattered individuals but apparently are too few and lack sufficient vigor to replace lodgepole pine. Lodgepole pine maintains its dominance because of inadequate seed sources for potential competitors, stand densities too great to allow regeneration of any other species, and light surface fires that remove seedlings without killing overstory lodgepole pine.

4. Climax. Lodgepole pine is the only species capable of growing on particular sites and is self-perpetuating. Some examples: In central Oregon, lodgepole pine forms an edaphic climax on poorly drained soils and a topoedaphic climax in frost pockets (Franklin and Dyrness, 1973). In Wyoming, lodgepole forms an edaphic climax on granitic soils in portions of the Bighorn Mountains (Despain, 1973) and on shallow, infertile soils of schist origin in portions of the Wind River mountains (Reed, 1976).

Mountain Pine Beetle-Lodgepole Pine Interactions

Many factors affecting beetle populations have been studied through life table sampling of populations using a method of bark removal outlined by Carlson and Cole (1965) and through systematic sampling of lodgepole pine stands described by Cole and Amman (1969). The four most important factors influencing beetle populations are structure of lodgepole pine stands, phloem thickness, moisture content of the tree during beetle development, and climate.

Infestations in Relation to Stand Structure

The mountain pine beetle infests and kills proportionately more large- than small-diameter trees. Hopping and Beall (1948) showed a 2% increase in mortality per cm increase in d.b.h. for stands in Alberta;

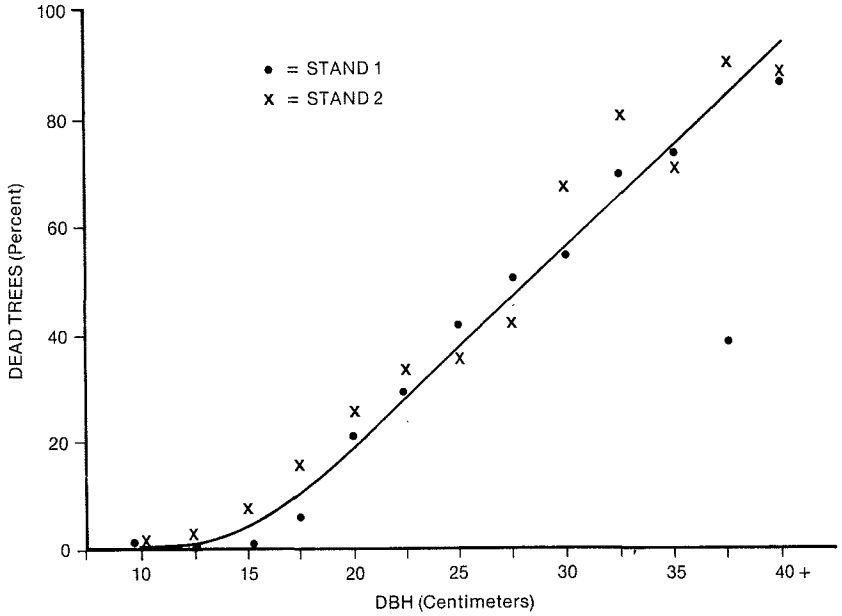

Fig. 1. Percent of lodgepole pine trees within each diameter class killed by the mountain pine beetle (Cole and Amman, 1969)

and Roe and Amman (1970) observed an increase of 3.5% in Wyoming and Idaho. Some of the greatest losses of lodgepole pine to the beetle occurred in the Big Hole Basin of Montana where 84% of the trees 23 cm and larger d.b.h. were killed (Evenden and Gibson, 1940). In two stands in northwestern Wyoming, mortality ranged from about 1% of trees 10 cm d.b.h. to 87% of those 41 cm and larger d.b.h. (Fig. 1) (Cole and Amman, 1969). Furthermore, the beetle attacks the trees of largest diameter each year of the infestation, until mostly small trees remain and the infestation then declines (Fig. 2) (Cole et al., 1976).

Shepherd (1966) studied behavior of the beetle in the laboratory and found that large dark objects against a light background were more attractive to beetles than small objects. His study indicates that the beetle uses visual stimuli, and selects trees to be attacked on the basis of size. Presently, this appears to be the most plausible explanation of the beetles' behavior. The evolutionary basis for this behavior is probably related to the much higher probability of encountering thick phloem (Fig. 3), the food supply of developing larvae (Amman, 1975).

Beetle Production in Relation to Phloem Thickness

Large diameter lodgepole pines, on the average, produce more mountain pine beetles per unit area of surface than do those of small diameter (Reid, 1963; Cole et al., 1976). The principal reason is the thicker phloem. Phloem thickness increases exponentially as diameter increases from 10 to 40 cm (Fig. 4). Furthermore, phloem thickness has been shown to be directly related to characteristics of good lodgepole pine vigor (D. M. Cole, 1973).

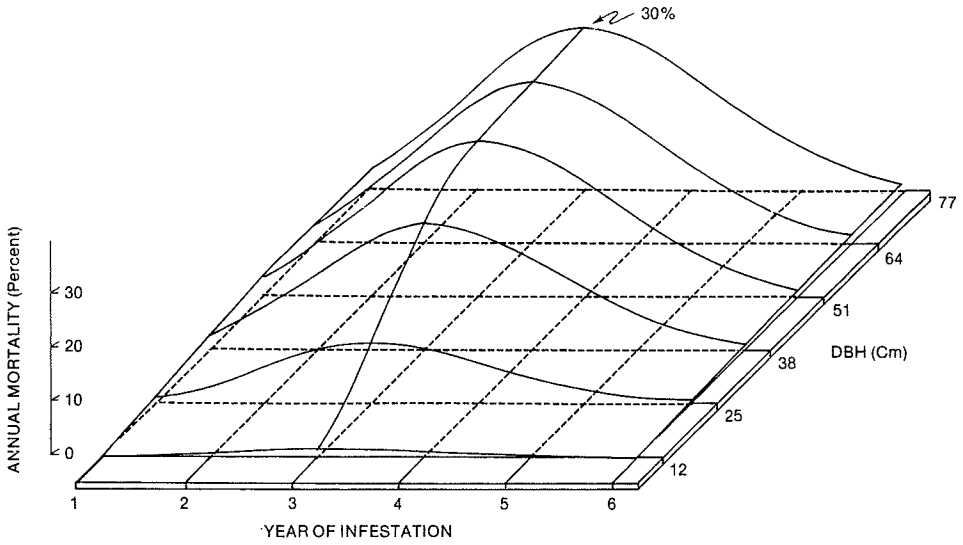

Fig. 2. Percent of lodgepole pine trees killed within each diameter class during each of the main years of a mountain pine beetle infestation (Cole et al., 1976)

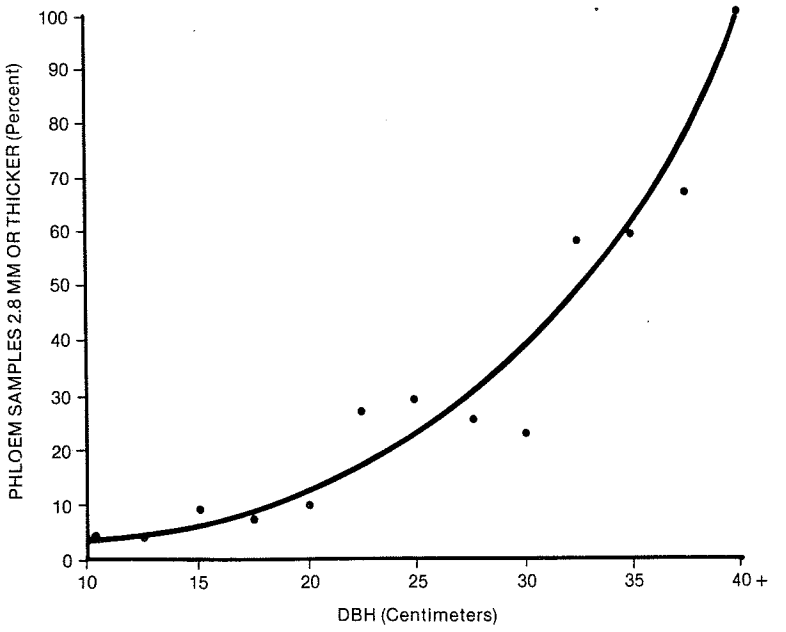

Fig. 3. Percent of phloem samples exceeding 2.8 mm by diameter class of lodgepole pine (Amman, 1975)

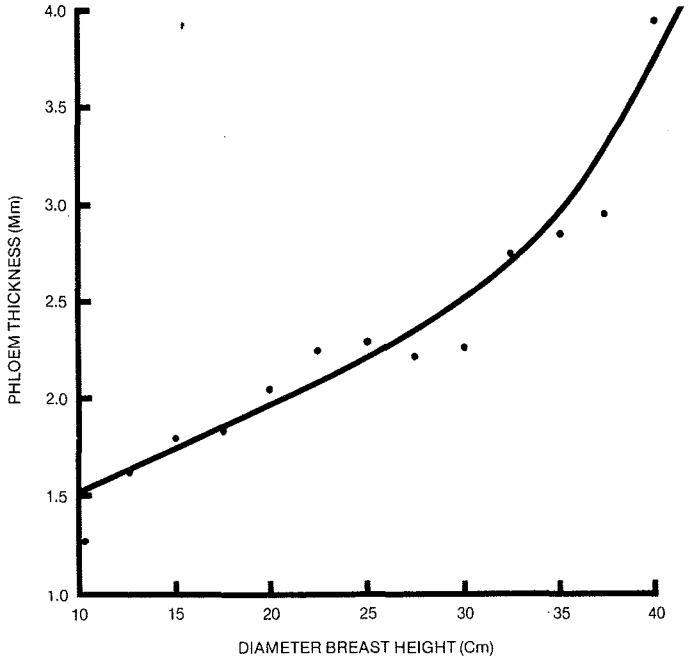

Fig. 4. Average phloem thickness for lodgepole pines of different diameters

Laboratory rearings of beetles in lodgepole pine billets show average production ranged from 3.0/dm^2 for phloem 2 mm thick to 8.7/dm^2 from phloem 6 mm thick (Amman, 1972b). Greater beetle production has been obtained with increased gallery densities. Production curves asymptote at 22.7 cm of gallery/dm^2 in thin phloem and 26.0 cm/dm^2 in thick phloem. These curves were maintained at higher gallery densities, indicating that above these levels a constant production of beetles could be expected in the laboratory (Amman and Pace, 1976). Laboratory studies so far have failed to demonstrate a clear qualitative difference between phloem of young and old trees and between phloem of small and large diameter trees. However, differences in sizes of beetles reared from thick and thin phloem suggest a qualitative difference (Amman and Pace, 1976).

Beetle Survival in Relation to Moisture Content of the Tree

Adequate moisture is essential throughout development of the mountain pine beetle. Drying usually is greater in small diameter than in large diameter trees infested by the beetle (Fig. 5), particularly in those trees that had a slow rate of growth. Differential drying probably accounts for some of the reduced beetle emergence (survival) observed between large and small trees having similar phloem thickness (Cole, 1974, 1975).

The role of blue-stain fungi in regulating moisture content of the tree is not completely clear. Reid (1961) observed that trees with abundant blue-stain fungi were drier in the fall after attack than were trees with poorly developed blue-stain fungi. I also observed this, but in

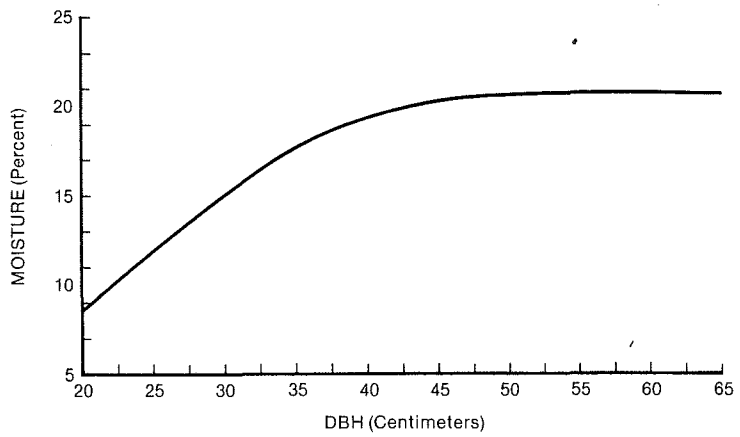

Fig. 5. Moisture content (percent of sample weight) of lodgepole pines 11 months after being infested and killed by the mountain pine beetle

addition found the opposite relation in early July, about 11 months following infestation. Trees having well-developed blue stain were more moist than trees in which blue stain was scarce. Beetle survival was low in trees with poorly developed blue stain. Blue-stain fungi appear to play a dual role—their presence results in increased drying in the fall and delayed drying in the spring. These conditions would be beneficial to both the fungus and the beetle.

Attack and gallery densities also influence rate of drying of the tree. Both increase over the several years of an infestation (Cole et al., 1976). Increased egg gallery density and increased numbers of feeding larvae in the phloem layer result in more rapid drying of the tree. The increase in attack and gallery densities has been attributed to a shift in the sex ratio of the beetle population toward more females (Cole et al., 1976). After most of the large diameter trees are killed and the beetles infest small diameter trees, drying is extensive and male survival declines. When these broods emerge and infest trees, probably not enough males are present to rapidly mate females and cause masking of the aggregative pheromone to limit the attacking population.

Beetle Infestations in Relation to Climate

Climate is a major limiting factor in the dynamics of the mountain pine beetle at extreme northern latitudes and at high elevations. Brood production by the beetle in bark of a given thickness is inversely related to elevation (Amman, 1969). With increased elevation, beetle development becomes so retarded that much of the beetle population enters the winter in stages particularly susceptible to being killed by cold temperatures—eggs and small larvae during the first winter, and prepupal larvae, pupae, and teneral adults during the second winter of the two-year life cycle at high elevations (Amman, 1973). Because of reduced brood survival, infestations are not as intense and fewer trees are killed as elevation increases (Fig. 6) (Amman and Baker, 1972; Amman et al., 1973).

Safranyik et al. (1974) outlined zones of infestation intensity for the mountain pine beetle in Canada, with the greatest intensity occurring at low elevations near the United States-Canada border. These zones

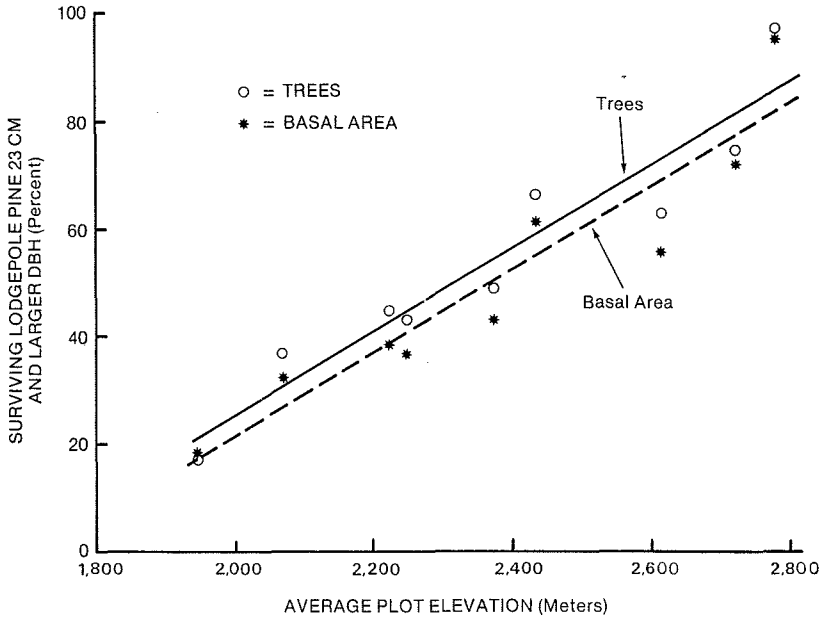

Fig. 6. Percent of lodgepole pine surviving at different elevations after a mountain pine beetle infestation had subsided (Amman, 1975)

represent changes in infestation intensity at different latitude-elevation combinations. Safranyik et al. (1975) have employed climatic factors in their model to predict probability of beetle infestation.

Beetle Infestations in Relation to Habitat Type

The intensity of beetle infestations and subsequent numbers of lodgepole pine trees killed differ by habitat type (Roe and Amman, 1970). A habitat type includes all sites with the potential of supporting the same climax plant association (Daubenmire and Daubenmire, 1968).

Beetle activity was compared on three habitat types within the lodgepole pine type on the Teton and Targhee National Forests in northwestern Wyoming and southeastern Idaho: (1) Subalpine fir/dwarf vaccinium (*Abies lasiocarpa/Vaccinium scoparium*), or A/V type, generally found at high elevations (range 1,997-2,576 m); (2) subalpine fir/mountain lover (*A. lasiocarpa/Pachistima myrsinites*), or A/P type, generally found at mid-elevations (range 2,042-2,377 m); and (3) Douglas-fir/pine grass (*Pseudotsuga menziesii/Calamagrostis rubescens*), or P/C type, generally found at low elevations (range 1,829-2,362 m) (Roe and Amman, 1970). Overlap in these elevational ranges indicates that habitat typing is a better way to classify stands than is a strictly elevational classification for investigating the ecology of the beetle. A classification based on habitat type considers environmental differences associated with slope, aspect, soil, latitude, and other factors.

The A/P type had the largest proportion of infested stands and suffered the greatest amount of loss (Fig. 7). The second highest infestation rate and tree losses were in stands on the P/C type, with the least

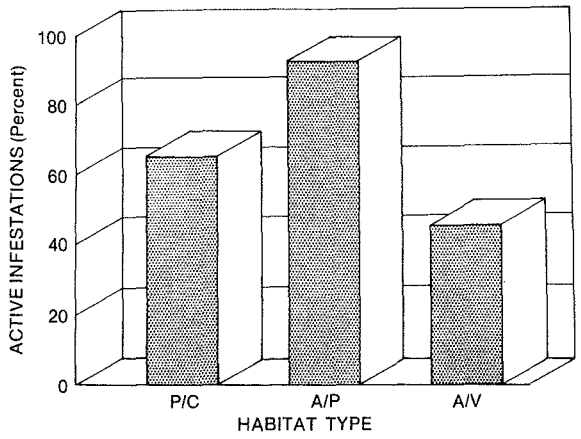

Fig. 7. Proportions of lodgepole pine stands in three habitat types that showed evidence of one or more mountain pine beetle infestations. *P/C:Pseudotsuga menziesii/Calamagrostis rubescens; A/P:Abies lasiocarpa/Pachistima myrsinites; A/V:Abies lasiocarpa/Vaccinium scoparium* (Roe and Amman, 1970)

infestation in the A/V type. Although temperature is important in differences among these habitat types, primarily because of differences in altitude, other factors enter in. For example, stands on more mesic sites will have trees that grow rapidly, and reach sizes and phloem thicknesses conducive to beetle population buildup more quickly than trees growing on more xeric sites. Consequently, beetle infestations will occur more frequently on sites providing for the best growth of lodgepole pine.

Role of the Mountain Pine Beetle in Lodgepole Pine Ecosystems

The role of the beetle differs in conjunction with the two basic ecological roles of lodgepole pine—where lodgepole pine is seral and where it is persistent or climax. The beetles' continued role in the seral stands will depend upon the presence of fire.

Role of Mountain Pine Beetle Where Lodgepole Pine Is Seral

Absence of Fire

Lodgepole pine stands depleted by the beetle and not subjected to fire are eventually succeeded by the more shade-tolerant species consisting primarily of Douglas-fir at the lower elevations and subalpine fir and Englemann spruce at the higher elevations throughout most of the Rocky Mountains (Fig. 8). Starting with a stand generated by fire, lodgepole pine grows at a rapid rate and occupies the dominant position in the stand. Fir and spruce seedlings also established in the stand grow more slowly than lodgepole pine.

With each infestation, the beetle kills most of the large, dominant lodgepole pines. After the infestation, both residual lodgepole pine

Fig. 8. Subalpine fir and Douglas-fir seedlings growing in openings created when mountain pine beetles killed some of the larger dominant lodgepole pines (trees on the ground)

and the shade-tolerant species increase their growth. When the lodgepole pines are of adequate size and phloem thickness, another beetle infestation occurs. This cycle is repeated at 20-40 year intervals depending upon growth of the trees, until lodgepole pine is eliminated from the stand.

Increment cores taken from subalpine fir trees growing within lodgepole pine stands in northwestern Wyoming show growth release at approximately 20-year intervals (Fig. 9). The more recent releases were correlated with periods of beetle activity, but there was no way of relating the older release periods to infestations. However, weather records from nearby stations indicated that the earlier release periods were not related to abundant moisture; in fact, several occurred when moisture was deficient. Consequently, increased growth was the result of stand disturbance, the most likely being an infestation of mountain pine beetle (Roe and Amman, 1970). Evidence of older beetle infestations consisting of the typical egg gallery etchings in the sapwood was found on fallen trees. These fallen trees could not be dated because of decay.

Subalpine fir succession in three lodgepole pine stands is shown in Figure 10 (Roe and Amman, 1970). The Moody Meadows stand is in the early stages of succession. The subalpine fir understory consists of only a few trees per hectare, most of which have small diameters. However, in this stand 2754 subalpine seedlings less than 2.5 cm d.b.h. per hectare were present. These will grow to fill overstory openings created by future beetle infestations.

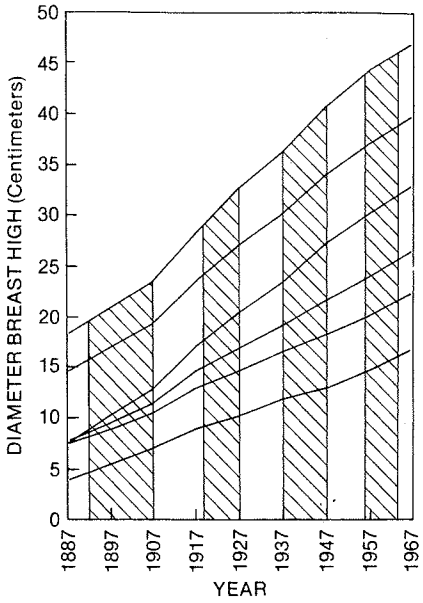

Fig. 9. Trends in diameter growth of subalpine fir trees in a stand of lodgepole pine that had been subjected to four mountain pine beetle infestations. Crosshatched bars were periods of beetle infestation (Roe and Amman, 1970)

The Pilgrim Mountain stand represents a more advanced stage of succession. Both subalpine fir, which was on the cool mesic sites, and Douglas-fir, which was on the warmer xeric sites, were present in this stand. A large reservoir of 6945 fir seedlings less than 2.5 cm d.b.h. per hectare was present, ready to assume a more prominent position in the stand as lodgepole pine trees are killed by the beetle.

In the Dell Creek stand, succession by subalpine fir is almost completed. In spite of the small number of large lodgepole pines remaining in this stand, the beetle was able to locate and infest them. Trends typical of succeeding species are very apparent in these data, with large numbers of small fir trees declining to a few large trees, some of which have reached 41 cm or larger d.b.h. Data from lodgepole pine stands located at lower elevations indicate a similar relationship with Douglas-fir.

The role played by the mountain pine beetle in stands where lodgepole pine is seral is to periodically remove the large, dominant pines. This provides growing space for subalpine fir and Douglas-fir, thus hastening succession by these species. The continued presence of the beetle in these mixed-species stands is as dependent upon fire as that of lodgepole pine, without it both are eliminated.

Presence of Fire

Where lodgepole pine is seral, forests are perpetuated through the effects of periodic fires (Tackle, 1964). Fires tend to eliminate competitive tree species such as Douglas-fir, the true firs, and spruces. Following fire, lodgepole pine usually seeds in abundantly. Serotinous cones attached to the limbs of the tree open because of the intense heat of the fire and release their seed (Clements, 1910; Lotan, 1975).

Large accumulations of dead material caused by periodic beetle infestations result in very hot fires when they do occur (Brown, 1975). Hot fires of this nature eliminate Douglas-fir, which otherwise is more

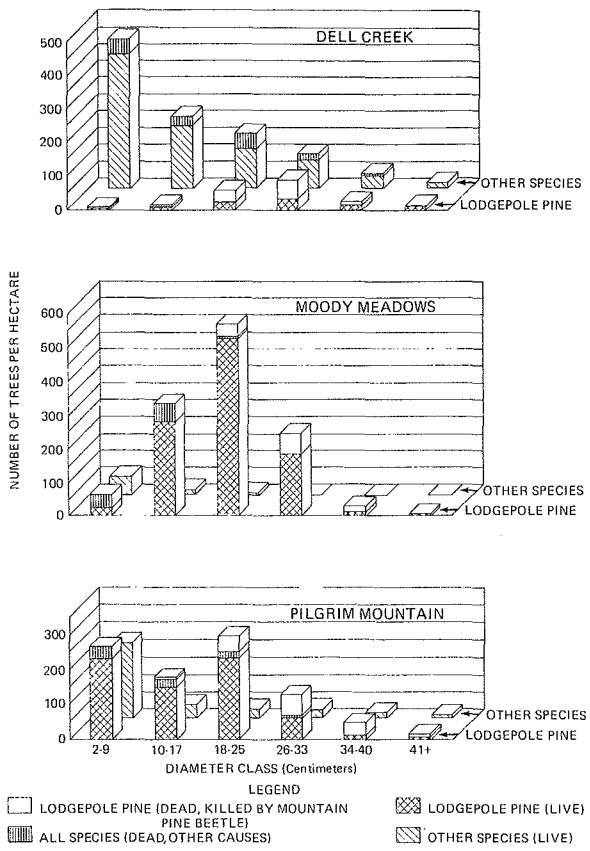

Fig. 10. Distribution of live and dead trees following the most recent infestation by the mountain pine beetle in three lodgepole pine stands in northwest Wyoming (Dell Creek and Pilgrim Mountain) and southeast Idaho (Moody Meadows) (Roe and Amman, 1970)

resistant to fire damage than lodgepole pine. The dominant shade-tolerant species are eliminated, resulting in a return to a pure lodgepole pine forest. On the other hand, light surface fires would not be adequate to kill large, thick-barked Douglas-fir and return lodgepole pine to a dominant position in the stand.

Following regeneration of lodgepole pine after fire, the mountain pine beetle-lodgepole interactions would be similar to those described in the absence of fire. A fire may interrupt the sere at any time, reverting the stand back to pure lodgepole pine. However, once succession is complete lodgepole pine seed will no longer be available to seed the burned areas except along edges where the spruce-fir climax joins persistent or climax lodgepole pine.

Role of Mountain Pine Beetle Where Lodgepole Pine Is Persistent or Climax

Lodgepole pine is persistent over large acreages and because of the number of shade-tolerant individuals of other species found in such

persistent stands, the successional status is unclear (Pfister and Daubenmire, 1975). In any case, lodgepole pine persists long enough for a number of beetle infestations to occur. In such cases and those of a more limited nature when lodgepole pine is climax because of special climatic or soil conditions, the forest consists of trees of different sizes and ages ranging from seedlings to a few overmature individuals. In these forests, the beetle infests and kills most of the lodgepole pines as they reach larger sizes. Openings created in the stand as a result of the larger trees being killed, are seeded by lodgepole pine. The cycle is then repeated as other lodgepole pines reach sizes and phloem thicknesses conducive to increases in beetle populations (Fig. 11).

The result is two- or three-story stands consisting of trees of different ages and sizes. A mosaic of small clumps of different ages and sizes may occur. The overall effect is likely to be more chronic infestations by the beetle because of the more constant source of food. Beetle infestations in such forests may result in death of fewer trees per hectare during each infestation than would occur in even-aged stands developed after fires and in those where lodgepole pine is seral.

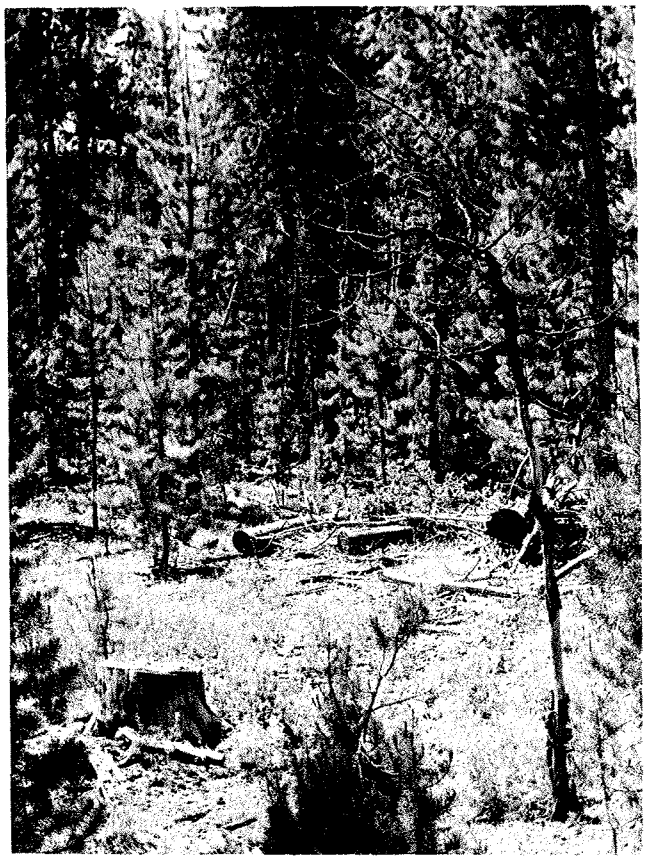

Fig. 11. Openings created when the mountain pine beetle kills large dominant trees in persistent and climax lodgepole pine stands are seeded by lodgepole pine. Stump is remnant of tree killed by mountain pine beetle about 12 years ago

Fires in persistent and climax lodgepole pine forests should not be as hot as those where large epidemics of beetles have occurred. Smaller, more continuous deposits of fuel are available on the forest floor. The lighter beetle infestations, and thus lighter accumulations of fuel, would result in fires that would eliminate some of the trees but probably would not cause total regeneration of the stand. This would be beneficial to the beetle because a more continuous supply of food would be maintained. Where large accumulations of fuel occur after large beetle epidemics, fire would completely eliminate the beetles' food supply from vast acreages for many years while the entire stand of trees grew from seedlings to sizes conducive to beetle infestation.

The mountain pine beetle's evolutionary strategies have been successful. It has exploited a niche that no other bark beetle has been able to exploit, that of harvesting lodgepole pine trees as they reach or slightly before they reach maturity. Such trees are at their peak as food for the beetle. Harvesting at this time in the age of the stand maintains the vigor of the stand, and keeps the stand at maximum productivity.

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