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CONTENT

MOUNTAIN PINE BEETLE DYNAMICS IN LODGEPOLE PINE FORESTS AND STRATEGIES FOR REDUCING TREE LOSSES

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ABSTRACT

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), periodically kills most of the trees of large diameter in a lodgepole pine stand, *Pinus contorta* var. *latifolia* Engelmann. Tree and stand factors conducive to infestations are large diameter trees having thick phloem and elevation of suitable climate for beetle development.

Forest management practices consisting of clear or partial cuttings are recommended for reducing losses in commercial forests. Particularly susceptible stands can be converted to other tree species, or harvest rotations can be shortened so that trees of small diameter that meet certain product requirements can be cut before the trees reach sizes and phloem thickness susceptible to beetle attack. Control strategies directed against the beetle are not recommended in recreational and noncommercial forests at this time. In these forests, lodgepole pine will be succeeded by spruce and firs. These species will fulfill requirements of recreation, watershed and other values as well as lodgepole pine. Chemical sprays applied to high value trees prior to beetle flight will protect these trees from attack.

INTRODUCTION

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, (Coleoptera: Scolytidae), is the most aggressive bark beetle in the United States. The beetle infests 13 species of pine that are native to North America (Wood 1963). Of this group of hosts, lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann, the tree of interest in this paper, is considered by many to be the favorite host of the mountain pine beetle. This assessment is based on the almost continued infestations in this host type and the large losses of trees that occur during these infestations. The close association of mountain pine beetle and lodgepole pine suggests that mountain pine beetle infestations are a necessity in order for both insect and host to survive (Amman 1977) and perhaps is responsible for the lack of a well-developed resistance response by lodgepole pine to beetle invasion. Based on studies of mountain pine beetle-lodgepole pine interactions, strategies to reduce losses of trees to the beetles have been proposed and some have been tested.

LODGEPOLE PINE

Lodgepole pine forests provide important cover on more than 13 million acres (5.2 million hectares) in western United States (Wellner 1975) and over 49.5 million acres (19.8 million ha) in western Canada (McDougal 1975). These forests serve many purposes, such as cover on scenic backdrops for recreational areas, protective cover on watersheds, habitat for game animals, grazing for domestic livestock and raw materials for lumber, poles, posts and pulp (Tackle 1954). Lodgepole pine has a wide geographic range extending from Alaska south to northern Baja California and east through Wyoming and Colorado. Elevationally, it can be found from sea level in Alaska to 11,500 feet (3,485 m) in Colorado.

Ecologically, lodgepole is typically described as seral, with low shade tolerance; possessing the ability to grow on almost any forest site; having both open and serotinous cones, serotinous cones requiring 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 (Pfister and Daubenmire 1975). Many of these characteristics contribute to creating large fuel buildups that lead to intense fires over large areas, thus renewing the lodgepole pine cycle (Brown 1975).

The occurrence of lodgepole as a seral type is largely due to fire, which eliminates competing climax vegetation, thus leaving the site open to colonization by lodgepole pine. Cones in many lodgepole stands are predominantly of the closed type, thus assuring a large supply of seed for colonization of the site after a fire (Lotan 1967). However, fire is not a requisite for seed release from closed cones; for cones can open when enough heat from insolation melts the resin that seals the scales.

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. 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. 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. Beetles attack the tree en masse and kill it if their numbers are sufficient. The female usually mates early in gallery construction and lays eggs in irregularly alternating groups within the phloem near the xylem on the two sides of the vertical gallery. Eggs hatch in about two weeks and larvae feed individually in the 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 scoring 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, except 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 are introduced by adult beetles and have been considered the primary cause of tree death (Shrimpton 1978). 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.

MOUNTAIN PINE BEETLE-LODGEPOLE PINE INTERACTIONS

Many factors affecting beetle populations have been studied through life table sampling of populations and through systematic sampling of lodgepole pine stands. 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. A method of hazard rating stands to beetle infestation has been developed based on some of these factors (Amman et al. 1977).

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 percent increase in mortality per cm increase in d.b.h. for stands in Alberta; and Roe and Amman (1970) observed an increase of 3.5 percent 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 percent 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 percent of trees 10 cm d.b.h. to 87 percent of those 41 cm and larger d.b.h. (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 (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 suggests 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, 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 (Cole and Amman 1969). The principal reason is the thicker phloem. Phloem thickness increases exponentially as diameter increases from 10 to 40 cm. Furthermore, phloem thickness has been shown to be directly related to characteristics of good lodgepole pine vigor (D. M. Cole 1973).

Laboratory rearings of beetles in lodgepole pine billets show average production ranged from $3.0/dm^2$ from phloem 2 mm thick to $8.7\ dm^2$ from phloem 6 mm thick (Amman 1972).

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, particularly in those trees that had a slow rate of growth (Amman 1976).

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. This relation was observed to reverse itself in early July, about 11 months following infestation (Amman 1976). 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.

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 (Amman and Baker 1972).

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 represent changes in infestation intensity at different latitude-elevation combinations.

MANAGEMENT STRATEGIES

The almost constant mountain pine beetle pressure being exerted on lodgepole pine forests poses perplexing management problems. Beetles disrupt sustained-yield forest regulation because of repeated depredations on mature forests. The repeated thinning from above, i.e., the large-diameter trees, has been described as a silvicultural catastrophe (Wellner 1978). Several management practices have been proposed and some are being tested for reducing tree losses (Amman et al. 1977; Cole 1978; Roe and Amman 1970).

Managing for timber values. Recognizing that the beetle concentrates heavily on trees of large diameter, continuous lodgepole pine forests can be broken up by using block clearcutting or small patch cuts, which will result in different age and size classes and thus reduce the area likely to be infested at any one time. Then, when a block or patch reaches high-risk conditions, all trees on the block or patch can be harvested immediately.

Partial cuts directed at the large diameter component of a stand can be used to preclude losses from impending epidemics of mountain pine beetle in special situations. Partial cutting is especially attractive in cases where clearcutting is unacceptable due to visual and environmental impacts; and, regardless of the beetle, may be the cutting method of choice in two- and three-story stands if they have vigorous understories, low dwarf mistletoe infection, and low risk of windthrow. Partial cuts effectively reduced tree losses to mountain pine beetle in Colorado (Cahill 1978) and Montana (Hamel 1978).

Harvesting trees before they reach sizes conducive to beetle outbreaks would be an effective method of preventing losses to the beetle where there are markets for material of small diameter. For example, in certain high-risk areas, the manager may elect to grow small trees that meet pole and mine timber requirements.

Another management alternative for stands that are particularly susceptible to beetle damage is to favor nonhost trees such as Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. In mixed species forests, the presence of nonhost trees will result in greater residual stocking, should an epidemic occur. However, the beetle infests lodgepole pine in mixed species forests just as readily as in pure forests (Amman and Baker 1972). In addition, the manager also must realize that if he elects to convert lodgepole pine forests to other species, he can expect losses by other insects--the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, if Douglas-fir is favored, and the large casebearer, *Coleophora laricella* (Hubner), if western larch, *Larix occidentalis* Nutt., is favored. However, entomologists generally agree that most insects would prove easier to cope with than the mountain pine beetle, particularly if blocks of nonhost species of trees are interspersed among blocks of lodgepole pine. Then, when any insect infestation occurs, less acreage of host type would be affected.

Managing for nontimber values. Forests that are committed to recreation, such as National and State Parks, Wilderness Areas, and other forested land not included in the timber-growing base, may not require action against the beetle. In seral lodgepole pine forests protected from fire, the proportion of other tree species can be expected to increase with each beetle infestation, until succession is complete and both lodgepole pine and the beetle are eliminated from the stand (Roe and Amman 1970). Conversion of noncommercial lodgepole pine forests to nonhost species of trees will eliminate the possibility of beetle populations building up and moving from noncommercial to adjacent commercial forested land. If fire occurs prior to completion of succession, some of these stands will revert to lodgepole pine and another cycle of mountain pine beetle infestations.

In stands where lodgepole pine is climax, periodical infestations of the beetle can be expected as trees in a portion of the stand develop large diameters and thick phloem, conditions needed by the beetle. Openings created in the forest when dominant and codominant trees are killed by beetles are seeded by lodgepole, thus forming an uneven-aged, multistoried forest.

Individual trees of high value. Ornamental trees and those in picnic areas, campgrounds, around visitor centers, and summer and permanent homesites have much higher value than trees in the forest situation. Chemical sprays offer promise for protection of such trees. A single application before flight and attack by beetles has prevented attacks for one year and, in some instances, through a second year (Smith et al. 1977). Managers of high-use recreation areas should also consider planting trees of different species where lodgepole pine trees have been killed. Thus, shade and esthetics will be preserved as other lodgepole pine die or are killed by beetles.

Although chemical treatment of high-value trees is justifiable, chemical control cannot be recommended on a forest basis. Previous efforts have shown this strategy to be only a holding action, at best, until potentially susceptible trees can be harvested. An assessment of chemical control efforts used during large beetle infestations revealed that tree survival following an infestation was the same in treated and untreated stands. Therefore, trees were not saved; however, in some cases, rate of tree loss was slowed and the infestation prolonged (Amman and Baker 1972).

These results and strategies to reduce losses are based on studies of epidemic beetle populations. Studies of endemic beetle populations are needed to determine if more effective means of dealing with mountain pine beetle populations can be devised.

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