

# Mountain Pine Beetle–Lodgepole Pine Interactions and Strategies for Reducing Tree Losses

Article

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The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), kills 70 to 90 percent of lodgepole pine, *Pinus contorta* Douglas var. *latifolia* Engelm., in many stands of the western United States and western Canada. Large beetle populations are dependent upon large-diameter lodgepole pine, in which conditions consisting of thick phloem, the food of developing larvae, and optimum moisture during beetle development occur. Killing of many lodgepole pines by the beetle just before maturation of the stand creates large amounts of fuel that, when ignited, result in intense fires that eliminate competing trees and their seed. The serotinous cones of lodgepole pine open and reseed the burned area to lodgepole, thus perpetuating lodgepole pine and providing a future food supply for mountain pine beetles. Control strategies that consider the dynamics of the mountain pine beetle–lodgepole pine system should emphasize creation of mosaics of lodgepole pine stands of different age and size classes and the harvesting of lodgepole pine prior to tree maturation or when beetle outbreaks occur.

## INTRODUCTION

The indigenous mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), kills from 70 to over 90 percent of lodgepole pines in many stands of the western United States and western Canada. The beetle infests 13 species of pine native to North America (1) as well as exotic pine species. Lodgepole pine, *Pinus contorta* Douglas var. *latifolia* Engelm., is considered the favorite host of mountain pine beetles because of the almost continual infestations in this host type and the extensive losses of lodgepole pine that occur during outbreaks. Mountain pine beetle populations periodically build up and kill most of the large dominant lodgepole pines over vast acreages. Initial infestations in lodgepole forests are related to fire history because most of these forests are established as a result of fire (2). These fire-generated mosaics of stands of similar age become susceptible at about the same time, making mountain pine beetle infestations continuous in the central and northern Rocky Mountains during the past 30 years. Immature trees that survived infestations during the 1950s and early 1960s have grown to sizes conducive to mountain pine beetle infestation and now are undergoing infestation.

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

close association of mountain pine beetle and lodgepole pine appears to favor survival of both insect and host (3) and is perhaps responsible for the lack of a highly developed resistance response by mature lodgepole pine to beetle invasion. Large losses of lodgepole pine affect timber management and recreation plans, increase water production during runoff, and limit wildlife and domestic livestock access. Strategies that exploit the beetle's preference for large-diameter trees are effective in minimizing tree losses. Strategies include partial cutting and clearcuts to create mosaics of lodgepole pine that increase age and size diversity in a forest.

## LODGEPOLE PINE

In North America, 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 3500 meters in Colorado (Figure 1). Lodgepole pine forests cover more than 5.2 million ha in the western United States (4) and over 19.8 million ha in western Canada (5).

Ecologically, lodgepole pine is seral (i.e. an early occupant of a disturbed site that will eventually be replaced by shade-tolerant climax species), with low shade tolerance; possesses the ability to grow on almost any forest site; has both open and serotinous cones that require high temperatures to open and release seed; regenerates rapidly in large numbers that create stagnated stands; has rapid growth in young trees and slow growth in old trees;

has high susceptibility to dwarf mistletoe infection, and premature mortality from mountain pine beetle attack (6). Many of these characteristics contribute to creating a large fuel buildup that leads to intense fires over large areas, thus renewing the lodgepole pine cycle (7).

The occurrence of lodgepole pine as a seral type is due largely to fire, which eliminates competing climax vegetation, thus leaving the site open to colonization by lodgepole pine. Cones in many lodgepole pine stands are predominately of the closed type, thus assuring a large supply of seed for colonization of the site after a fire (8). However, fire is not a prerequisite for seed release from closed cones, for cones can open when enough heat from insolation melts the resin that seals the scales.

Economically, lodgepole pine does not constitute a large portion of the annual timber harvest in the United States. For example, from national forests (predominate ownership of lodgepole), 3186 thousand m<sup>3</sup> of lodgepole sawtimber were harvested in 1985. This represented only 5.9 percent of total sawtimber sold from national forests in the United States. The value of lodgepole pine sold in 1985 was USD 9589 thousand, excluding pulpwood and miscellaneous products such as fenceposts, firewood, and rails (9). Two-thirds of the lodgepole pine was harvested in the Rocky Mountain states, where lodgepole pine accounts for 32 percent of sawtimber harvested from national forests. Thus, although not very important from the national point of view, lodgepole pine is important for local economies.

## MOUNTAIN PINE BEETLE

Mountain pine beetle can be found throughout the distribution areas of lodgepole pine, except for the extreme north (Figure 1). The adult mountain pine beetle is stout, black to dark brown, cylindrical, and about 5 mm long. The beetle usually completes one generation per year in lodgepole pine. However, two years may be required at high elevations and in 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 within about one to two weeks. This rapid emergence by most of

the population allows successful infestation of vigorous trees. When the attacking beetles are few in number, egg galleries may become impregnated with resin, and all eggs and larvae are killed by resinosis. Trees may survive these light attacks.

The female initiates the attack, usually on the basal two meters of the tree trunk, and produces an aggregating pheromone, trans-verbenol (10). This pheromone, in conjunction with terpenes from the tree, attracts other beetles to the tree, resulting in a mass attack that overcomes the host. The female usually mates early in gallery construction and following mating produces, as do the males, an anti-aggregative pheromone, verbenone, that maintains spacing of attacking beetles and, in sufficient concentrations, stops additional new attacks (11). Eggs are laid in irregularly alternating groups on the two sides of the vertical gallery within the phloem near the xylem. 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 phloem, lightly scoring the sapwood, where they pupate and later become adults (Figure 2). 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 usually survive, but when conditions are most favorable to the beetle, the ratio approaches 1:1 (12).

In addition to the girdling action of larvae, blue-stain fungi, *Ceratocystis montia* and *C. clavigera*, are introduced by adult beetles and have been considered the primary cause of tree death (13). Fungal spores, which probably are picked up during maturation feeding by the new adult, are carried in a maxillary mycangium (14), 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, especially the sapwood of the xylem, where they interfere with conduction. The principal benefit to the beetle appears to be regulation of moisture conditions in the tree during development (15, 16). Blue-stain fungi do not appear necessary to mountain pine beetle nutrition (17).

#### EPIDEMIC OR HIGH POPULATION LEVEL

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.

#### Infestations in Relation to Stand Structure

The mountain pine beetle infests and kills proportionately more large- than small-diameter trees (Figure 3). A 2 and 3.5 percent increase in mortality per centimeter increase in diameter at breast height (d.b.h.) occurred in stands in Alberta, Canada (18), and Wyoming and Idaho,

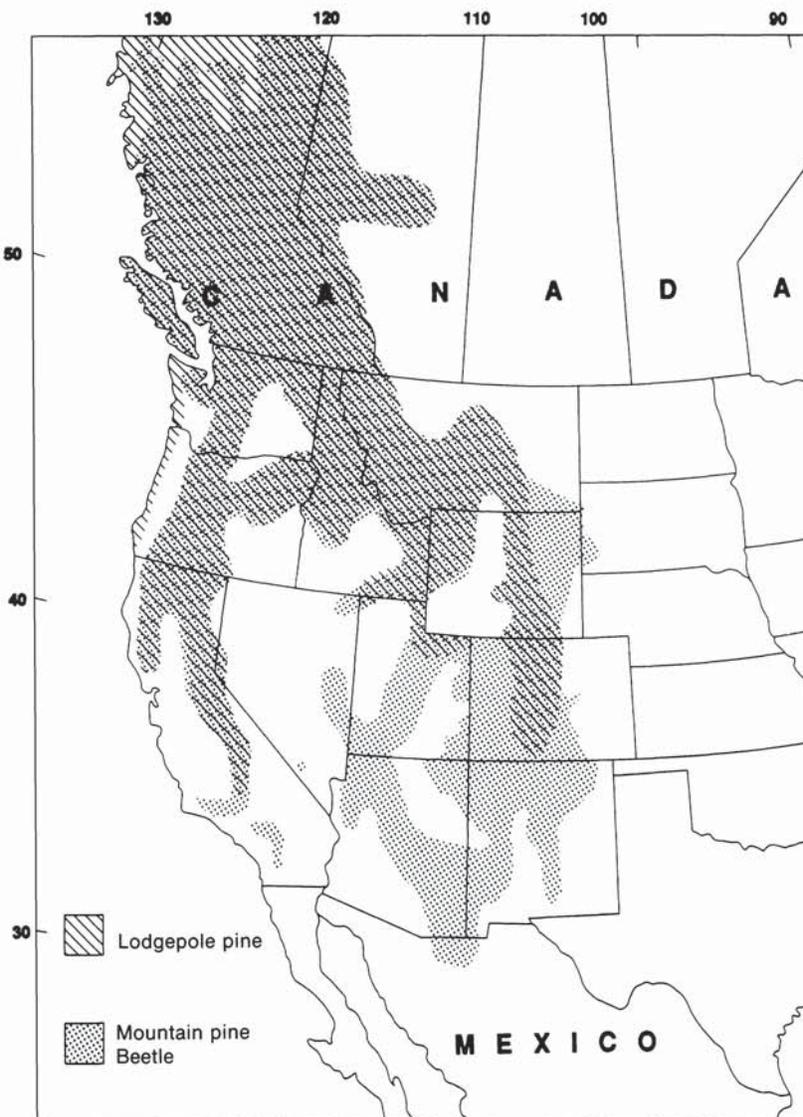


Figure 1. Distribution of lodgepole pine and mountain pine beetle in North America.

USA (19), respectively. Some of the greatest losses of lodgepole pine to the beetle occurred in western Montana, USA, where 94 percent of lodgepole 12.7 cm d.b.h. and larger were killed (20). When mostly small trees remain, in which phloem and moisture conditions for brood development are poor, the infestation declines (12).

Laboratory studies on host selection behavior revealed that more mountain pine beetles walked to large than small silhouettes (21), suggesting that mountain pine beetles use sight when selecting and attacking trees on the basis of size. However, flying beetles may also respond to odors from trees because terpene quantities increase with phloem thickness and size of tree (22).

#### Beetle Production in Relation to Phloem Thickness

On the average, mountain pine beetles produce more offspring per unit area of surface in large-diameter lodgepole pines than in small ones because of the thicker

phloem (23) (Figure 4). Phloem thickness increases as diameter increases (24) and is also related to lodgepole pine vigor (25).

#### Beetle Survival in Relation to Moisture Content of the Tree

Adequate moisture is essential throughout development of the brood. Drying usually is greater in small-diameter than in large-diameter trees infested by the beetle, particularly in those that had a slow rate of growth (16).

Blue-stain fungi appear to play a role in regulating moisture content of the mountain pine beetle-infested tree. Trees with abundant blue-stain fungi were drier in the fall after attack than were trees with poorly developed blue-stain fungi (16). This relationship reversed itself in early July, about 11 months following infestation (17). Trees with well-developed blue stain were more moist than trees in which blue stain was scarce or blue pigment had not yet manifested itself. Beetle survival was low in trees with poorly developed blue stain.

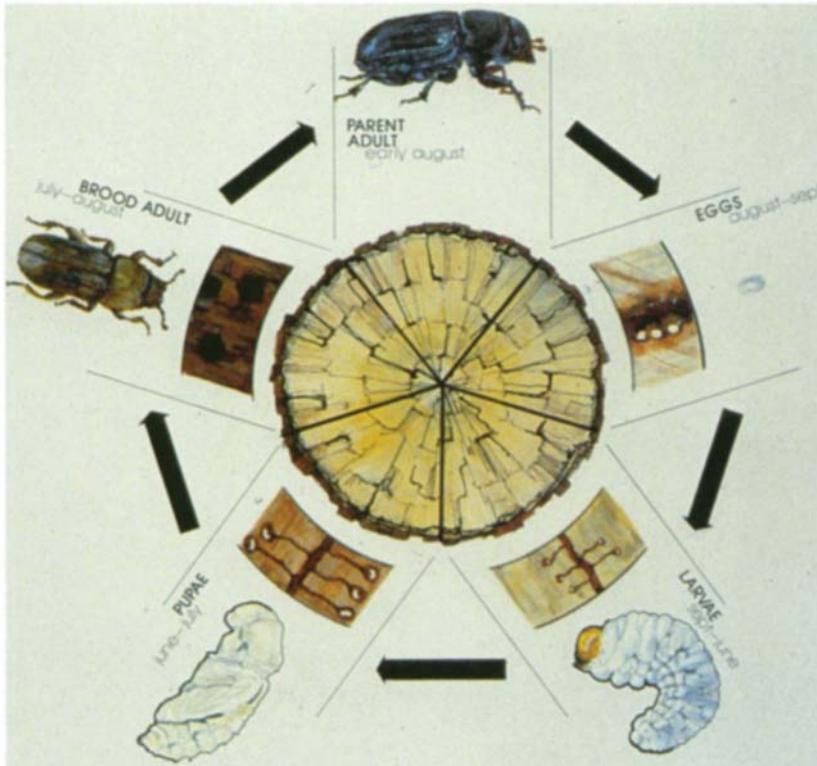


Figure 2. Generalized diagram of mountain pine beetle seasonal history.



Adult female mountain pine beetle, about 5 mm long, excavating vertical egg gallery in the inner bark. Eggs are laid in the phloem on alternate sides of the gallery. Photo: G. D. Amman.

Figure 3. Example of annual tree mortality (percentage) by diameter and year of infestation. The beetle infests a larger percentage of trees having large than small diameter each year of the infestation, until mostly small trees remain that have inadequate phloem thickness and moisture to support brood survival.

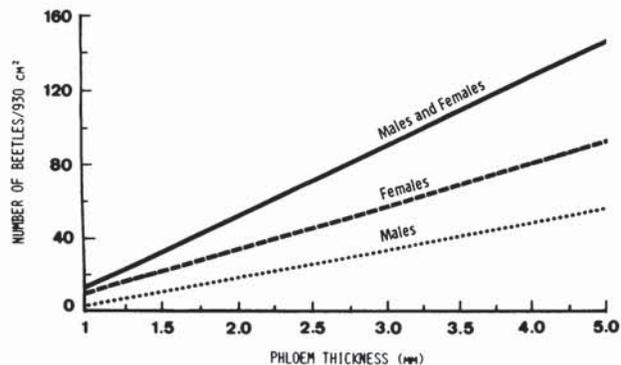
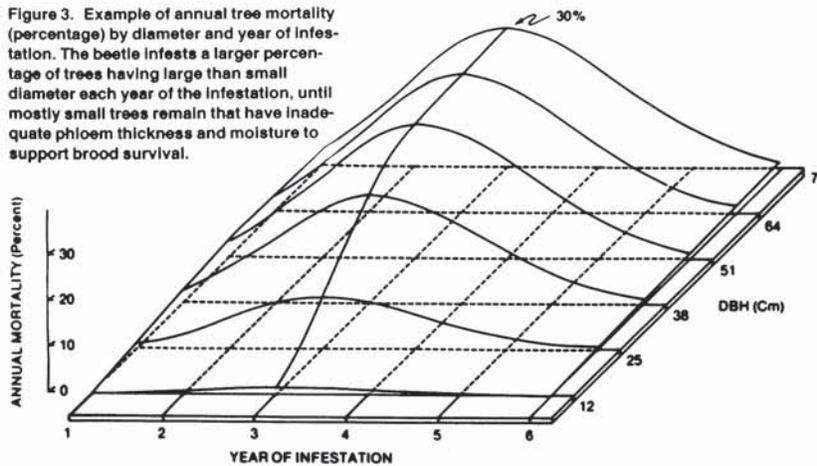


Figure 4. Number of mountain pine beetle offspring in relation to phloem thickness of lodgepole pine.

### Infestations in Relation to Climate

Cold climate in extreme northern latitudes and at high elevations slows beetle development and reduces survival. Brood production by the beetle in bark of a given thickness is inversely related to elevation (26). With increased elevation, beetle development becomes so retarded that much of the beetle population enters the winter period in developmental stages particularly susceptible to being killed by cold temperatures—eggs and small larvae during the first winter, and prepupal larvae, pupae, and new adults during the second winter of the two-year life cycle (27). Because of reduced brood survival, infestations are generally not as intense and fewer trees are killed as elevation increases (28). However, if infestations are intense or persist at lower elevations, a portion of these populations may continue to infest susceptible trees at higher elevations until many susceptible trees are killed. Climatic factors were used to outline zones of infestation intensity for mountain pine beetle in western Canada, with the greatest intensity occurring at low elevations near the United States-Canadian border (29).

### ENDEMIC OR LOW POPULATION LEVEL

The host selection behavior of the mountain pine beetle at low population levels (endemic) differs from that during the outbreak phase described above. During endemic periods, when mountain pine beetle population densities are such that less than one tree is infested per 10 ha, the beetle commonly selects trees previously infested by other bark beetles, particularly *Pityophthorus confertus* Swaine and *Ips pini* (Say). During the endemic phase, these associates generally infest suppressed sapling or pole-size trees that are well below average in growth, have thin phloem, and



During outbreaks of the severity depicted here, the mountain pine beetle kills all lodgepole pine trees larger than about 13 cm in diameter. Photo: G. D. Amman.

are often partially girdled by porcupines, while during an epidemic, the associates infest the tops or limbs of larger diameter trees killed by the mountain pine beetle the previous year. These species usually overwinter in the adult stage in litter of the forest floor. They emerge during spring and infest trees soon after the snow melts. In contrast, the mountain pine beetles emerge from late June to early September. At endemic levels, only a few beetles emerge on any one day. Unless the time required to locate suitable trees is minimized, a large proportion of such sparse populations is likely to succumb during dispersal. By utilizing trees already infested by other scolytids, such losses are reduced. Selection of these trees also suggests that the mountain pine beetle and these associates share a common component in their pheromone bouquets or are attracted to host volatiles released by attack of the associated scolytids and their accompanying fungi.

Trees infested with *Armillaria* root disease are frequently infested by the associated beetles. As a consequence, endemic mountain pine beetle populations in some locations are associated with *Armillaria* and comandra blister rust infested pines (30, 31). Mountain pine beetle selection of diseased trees infested by associated beetles provides a means of survival until the stand has the diameter structure that will support an outbreak. The associated scolytids attack earlier than mountain pine beetle and occupy most of the tree trunk. Therefore, only the lower 30 to 60 cm of the bole, a portion often avoided by the associated species, is infested by mountain pine beetle. This limited food supply prevents rapid population increase.

Selection of injured or weakened trees during the endemic period is a major factor regulating the dynamics of these scattered populations. Generally, when few beetles infest a tree, they are pitched out, or eggs laid during gallery construc-

tion and associated fungi carried by the beetles are killed by resin (32, 33). The type of host material selected by endemic populations lessens the likelihood that attacking beetles will be killed by resin exudation. Additionally, the thin phloem characteristic of these trees limits brood survival, ensuring that beetle populations remain at low levels until the stand matures, providing the conditions that will support the higher survival rates necessary for an outbreak.

Several hypotheses have been proposed for the start of bark beetle outbreaks. One theory is that sudden tree stress allows mountain pine beetles to infest recently vigorous trees that still have thick phloem, which results in greatly increased beetle production (34). In the case of southern pine beetle, *Dendroctonus frontalis* Zimmermann, lightning is suspected of triggering outbreaks, by injuring trees that then become the foci for beetle activity (35). Neither factor appears to be predominant

in triggering mountain pine beetle outbreaks in lodgepole pine.

Our observations suggest that an endemic infestation has the potential to build to outbreak status once subpopulations within scattered trees become sufficiently numerous to converge, attack, and overcome a common tree or group of trees. The phloem thickness in the trees attacked must be sufficient to ensure the emergent population substantially exceeds the attacking population.

### ROLE OF MOUNTAIN PINE BEETLE

Mountain pine beetle-lodgepole pine interactions appear to favor survival of both species. 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 (climax species are present in small numbers, but unable to increase and displace lodgepole pine) or climax. The beetles' continued role in the seral stands depends upon the presence of fire.

Lodgepole pine stands, depleted by the beetle and not subject to fire, are eventually succeeded by more shade-tolerant species consisting primarily of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, on warmer sites, and subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., and Engelmann spruce, *Picea engelmannii* Parry, on cooler sites throughout most of the Rocky Mountains.

Where lodgepole pine is seral, forests are perpetuated through the effects of periodic fires. The large buildup of fuel as a result of mountain pine beetle infestations sets the stage for a stand replacement fire that eliminates competitive tree species such as Douglas-fir, the true firs, and spruces. Following fire, lodgepole pine usually seeds-in abundantly. Mountain pine beetle outbreaks occur again close to the time when lodgepole pine matures, i.e. when adequate seed is available to regenerate the site to lodgepole, but before excessive amounts of seed are available that would cause an overstocked, stagnated stand (36).

A fire may interrupt succession at any time, reverting the stand to pure lodgepole pine. However, once succession is completed, lodgepole pine seed will no longer be available to seed-burned areas, except along edges where the spruce-fir or Douglas-fir climax joins persistent and climax lodgepole pine.

The role played by mountain pine beetle in persistent and climax lodgepole pine stands differs from sites where lodgepole pine is seral. Lodgepole pine is persistent over large acreages. In such cases, and those of a more limited nature where 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. Openings created in the stand, as a result of 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.

The result is two- and three-story stands



Fallen trees, mostly lodgepole pine, killed during several infestations by the mountain pine beetle, limit access and increase fuel loads. Photo: G. D. Amman.

consisting of trees of different ages and sizes, creating a mosaic. The overall effect is likely to be more chronic infestations by mountain pine beetles because of a 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.

Fires in persistent and climax lodgepole pine forests should not be as hot as those where large epidemics of beetles have occurred because the lighter beetle infestations result in smaller, more continuous deposits of fuel on the forest floor. This would be beneficial to the beetle because a more continuous supply of food would be maintained. Such a case was described in Oregon, which also includes the fungus *Poria asiatica* in the interactions with lodgepole pine, mountain pine beetle, and fire (37). Where large accumulations of fuel occur after large beetle outbreaks, fire would completely eliminate the beetles' food supply from vast acreages for many years until the stands mature.

### IMPACT OF MOUNTAIN PINE BEETLE

How the effects of mountain pine beetle infestations are viewed depends upon land managers' objectives. Although the effects of infestations are numerous they have not all been evaluated. Several that have are timber losses, water production, wildlife, understory vegetation, fuel loading, and recreation values.

#### Timber Loss

Where timber production is primary, mountain pine beetle infestations are a disaster because the large-diameter trees are killed, the very ones most valuable to the manager. Stand volume is frequently reduced below the level of economic operability, thus increasing the cost of regenerating a stand when not enough

timber remains to bear the cost of timber harvest and regeneration of a stand. It has been suggested that mountain pine beetle selection of large trees will adversely affect the lodgepole pine gene pool (19). However, seed from serotinous cones of all dead trees help seed space previously dominated by these trees, ensuring that fast-growing genotypes will remain in the gene pool.

#### Water

Death of trees results in reduced interception and use of water, thus increasing runoff within a drainage. Streamflow data before and after a mountain pine beetle infestation that killed 35 percent of the timber in a drainage showed a 15-percent increase in annual water yield, a two-week to three-week advance in the annual hydrograph, and a 10-percent increase in low flow rates, but little increase in peak runoff (38). This may not be detrimental. However, when coupled with timber-harvesting activities that may already be reaching hydrologic limitations, the additional runoff could increase erosion and sedimentation beyond acceptable levels. Such increases can be especially detrimental to fisheries.

#### Wildlife

Most species of wildlife occupying a drainage will be affected by a beetle outbreak. For example, mountain pine beetle infestations alter the arrangement and abundance of food and cover for large mammals such as elk and deer (39). Hiding and thermal cover may be greatly reduced. The additional light and moisture in the stand may improve forage, but access by large mammals may be limited once dead trees start falling. Birds such as chickadees and kinglets that belong to the foliage-gleaning guild, as well as nuthatches and brown creepers belonging to the bark-gleaning guild, decrease in number with an increase in beetle-killed trees. In contrast, wood-



Heavy fuel loads resulting from trees killed by the mountain pine beetle commonly result in high intensity stand-replacement fires. Photo: G. D. Amman.

peckers increase with the number of dead trees (40) and increased insect fauna under the bark of dead trees.

#### Understory Vegetation

Where forage production is important for wildlife and domestic livestock, tree losses to mountain pine beetle may be beneficial. The death of overstory trees results in additional sunlight and moisture for understory vegetation, increasing grass, sedge, and forb production in ponderosa pine forests (41, 42). Similar changes probably occur in lodgepole pine forests, although specific studies have not been completed. Even though forage production increases, access by livestock may be inhibited by large numbers of fallen trees.

#### Fuel Loading

The amounts of dead fuel resulting from mountain pine beetle infestations can be large and make fire suppression difficult. For example, death of over 1000 lodgepole pine,  $\geq 12.7$  cm d.b.h., per ha in some western Montana stands provides tremendous amounts of fuel, which sets the stage for a stand replacement fire.

#### Recreational Values

Losses of trees to mountain pine beetle infestation within national parks, wilderness areas, and unregulated forests are viewed as part of nature and are not necessarily detrimental. Such tree losses, however, increase maintenance costs associated with campgrounds, picnic areas, administrative sites, fences, and trails. Dead trees must be removed to prevent them snapping off or blowing over on users of camp and picnic sites. Trees fall across roads, trails, and fences and must be removed. In general, a site that sustains a severe mountain pine beetle infestation becomes a dangerous place to recreate. Recreationists in southeastern Idaho discriminated against some sites where mountain pine beetle had killed large numbers

of trees, preferring campgrounds with less tree mortality. Reduced campsite occupancy could have significant economic impact (43). Large fuel buildups in national parks may result in fires that are difficult to keep within a reasonable size, making park objectives of maintaining species and size mosaics of vegetation difficult to achieve.

#### WHAT CAN BE DONE?

Several management strategies have been tested against the mountain pine beetle. However, features of the lodgepole pine-mountain pine beetle system must be considered before using various strategies to prevent or minimize losses. It seems unlikely that large, mature trees in susceptible zones of elevation and latitude can be kept from mountain pine beetle infestation even though growing well. Growth efficiency of lodgepole pine (that is, the ability to produce wood per unit of foliage) has been considered a measure of tree susceptibility to infestation by mountain pine beetles, with susceptibility decreasing as efficiency increases (44, 45). A test of this hypothesis in natural and thinned stands shows that mountain pine beetle selection of trees to infest is more strongly related to diameter of the trees than to growth efficiency (46, 47). Trees in growth efficiency classes were infested proportional to their occurrence in the stands.

#### 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 and small patch cuts that create a mosaic of age and size classes and thus reduce the area likely to be infested at any one time. When a block or patch reaches high-risk conditions (large diameter in highly susceptible climatic zone), all trees on the block or patch can be harvested simultaneously.

Partial cuts directed at the large-diameter component of a stand can be used to preclude losses from impending outbreaks of mountain pine beetle in special situations. Partial cutting is especially attractive in cases where clearcutting is unacceptable due to visual and environmental impacts. Regardless of the beetle, this 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 (48). Partial-cutting stands effectively reduced tree losses to mountain pine beetle in Colorado and Montana (49, 50, 20). Mountain pine beetle infestation declined immediately following partial cutting, but remaining trees did not increase in growth until the second or third year. Therefore, changes in stand microclimate as a result of partial cutting are believed to have affected beetle behavior and hence reduced beetle infestation (47).

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 managers may elect to grow small trees that meet pole and mine timber requirements.

In mixed species forests, another management alternative for susceptible stands is to favor nonhost trees such as Douglas-fir. The presence of nonhost trees will result in greater residual stocking, should a beetle outbreak occur. However, the beetle infests lodgepole pine in mixed species forests just as readily as in pure forests (28).

#### Managing for Nontimber Values

Forests committed to recreation, such as national and state parks, wilderness areas, and other forested land not considered for timber products, 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 (19). 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.

#### Individual Trees of High Value

Ornamental trees and those in picnic areas, campgrounds, administrative sites, and summer and permanent homesites have much higher value than trees in forests. Such trees can be protected with chemical sprays. A single application before flight and attack by beetles has prevented attacks for one year and in some instances through a second year (51, 52). Trees of different species can be planted in high-use recreation areas 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-wide basis. Previous efforts show this strategy to be only a holding action at best, until timely harvest of potentially susceptible trees.

If harvest is delayed too long, even when chemical control is used, losses reduce residual stands below the level of economic operability (28).

These results and strategies to reduce losses are based primarily on studies of

large beetle populations. Studies are needed to determine whether more effective strategies can be applied while mountain pine beetle populations are still small.

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