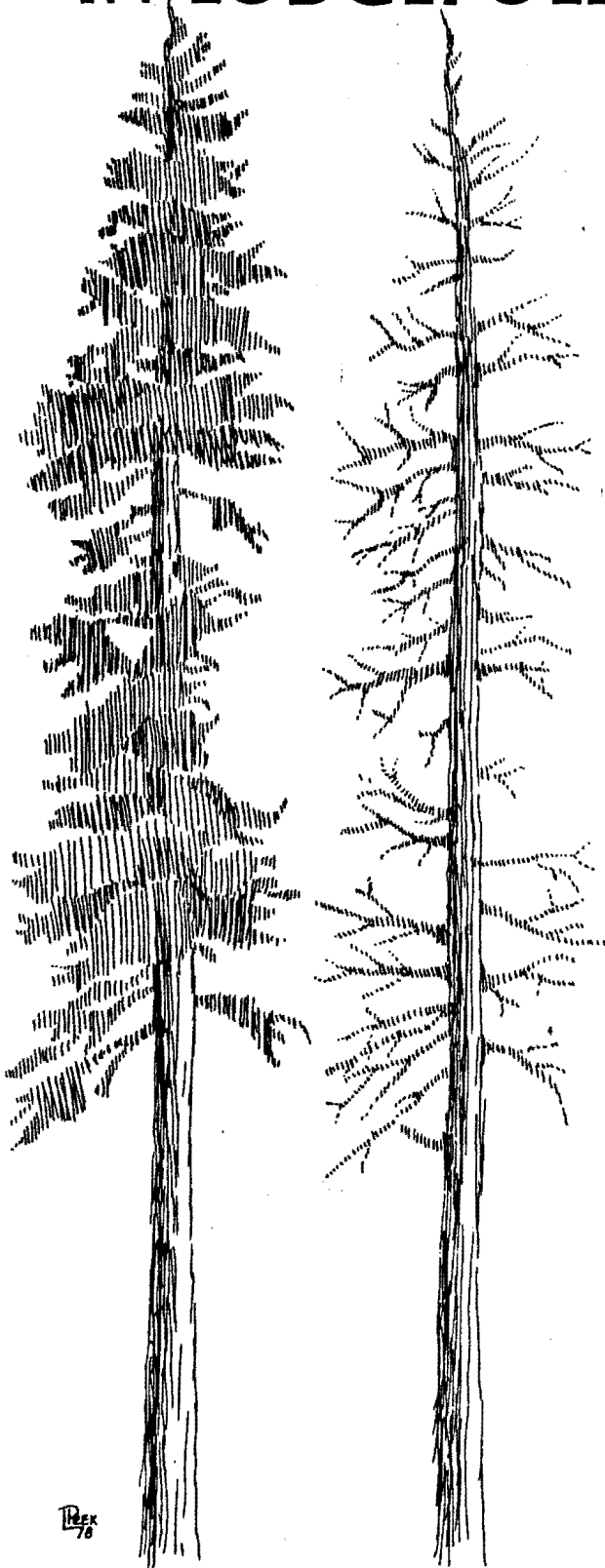
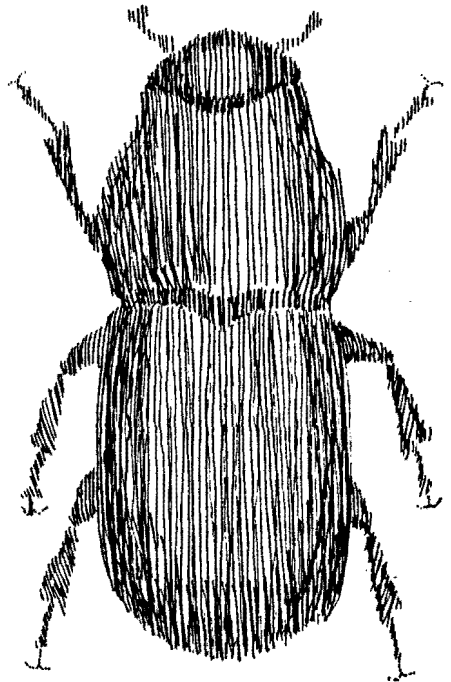


THEORY AND PRACTICE OF MOUNTAIN PINE BEETLE MANAGEMENT IN LODGEPOLE PINE FORESTS



SYMPOSIUM PROCEEDINGS

DECEMBER 1978



Reprinted from

THEORY AND PRACTICE OF MOUNTAIN PINE BEETLE MANAGEMENT IN LODGEPOLE PINE FORESTS

**Symposium Co-sponsored by: National Science Foundation
Washington State University
University of Idaho
USDA Forest Service**

**Held at Washington State University
Pullman, Washington
April 25-27, 1978**

**Edited by Darline L. Kibbee
Alan A. Berryman
Gene D. Amman
Ronald W. Stark**

**Proceedings Published by the Forest, Wildlife and Range Experiment Station,
University of Idaho, Moscow, in collaboration with:
USDA Forest Service, Forest Insect and Disease Research, Washington, D.C.,
and the Intermountain Forest and Range Experiment Station, Ogden, Utah.**

December 1978

Biology, Ecology, and Causes of Outbreaks of the Mountain Pine Beetle in Lodgepole Pine Forests

Gene D. Amman

ABSTRACT

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) typically produces one generation per year. The year begins with adults infesting trees and introducing blue-stain fungi into them in July and early August. Eggs are laid singly in niches on alternate sides of the vertical egg galleries. Larvae hatch and feed in the phloem, usually at right angles to the egg gallery. Larvae overwinter, then complete development in the spring. Pupation occurs in chambers made in the bark and outer sapwood. During endemic periods, beetles infest weakened and injured trees and those infested by other species of bark beetles. Epidemics appear to start when enough such trees are in proximity and emerging brood adults converge and infest a common tree or group of trees of medium to large diameter and medium to thick phloem. The beetle shows a strong preference for such trees, and its survival usually is best in them. Tree stress is not necessary for the start of epidemics. Stand characteristics associated with epidemics are 1) trees more than 80 years old, 2) average tree diameter more than 20 cm (8 inches), 3) a substantial number of trees in the stand with diameter at breast height of 30 cm (12 inches) or more and phloem 0.25 cm (0.10 inch) thick or more, and 4) stand site at an elevation where temperatures are optimum for brood development.

INTRODUCTION

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is the most important insect infesting lodgepole pine, *Pinus contorta* Douglas var. *latifolia* Engelman. During endemic periods, only an occasional tree is infested by the beetle. Then, within a period of 6 to 10 years, from 25 to 50 percent of the stand 10 cm (4 inches) diameter at breast height (dbh) and larger will be killed by a beetle epidemic.

The epidemiology of the beetle from the start of the population build-up through the epidemic has been studied and described in considerable detail. This is the period primarily covered by this symposium. The endemic period is yet to be studied in depth. Factors that keep the beetle population low could lead to development of methods for preventing losses to the mountain pine beetle. The endemic period, particularly the endemic-epidemic interface, is the next research area to be emphasized by the Population Dynamics of Primary Bark Beetle research work unit of the Intermountain Forest and Range Experiment Station in Ogden, Utah.

Abundance of suitable breeding material is of prime importance if bark beetle outbreaks are to occur (Rudinsky 1962). The way in which this material becomes available to the beetles differs according to species of beetle and of host tree. Two main theories have to do with the causes of beetle infestations: 1) the classical theory holds that some stress factor, such as drought or pathogen, weakens the trees, making possible successful infestation by the beetles and associated fungi; and 2) the alternative theory proposes that physiological maturity of the trees (regardless of stress) is required for build-up of beetle populations. The purpose of my paper is to present an overview of the biology and the ecology of the mountain pine beetle and to explore the causes of epidemics.

BIOLOGY AND ECOLOGY

Distribution and Host Trees

The mountain pine beetle can be found throughout the range of lodgepole pine up to about 56° north latitude and about 1220 m (4000 ft) elevation in British Columbia (Safarynik et al. 1974). Although infestations occur to higher elevations farther south (to about 3354 m in Colorado), these are usually light, resulting in low tree mortality (Amman and

Baker 1972, Amman et al. 1973, Amman et al. 1977). The most important hosts of the mountain pine beetle on the basis of commercial value and intensity of beetle epidemics are lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann), ponderosa pine (*P. ponderosa* Lawson), western white pine (*P. monticola* Douglas), and sugar pine (*P. lambertiana* Douglas). In addition, whitebark pine (*P. albicaulis* Engelmann), limber pine (*P. flexilis* James), pinyon pine (*P. edulis* Engelmann), bristlecone pine (*P. aristata* Engelmann), and foxtail pine (*P. balfouriana* Greville & Balfour) may be infested (McCambridge and Trostle 1972). Some infestations, at high elevations where whitebark pine is commonly found, have caused heavy losses in whitebark stands during weather favorable for the beetle. Occasionally, native non-host trees such as Engelmann spruce (*Picea engelmannii* Parry), grand fir (*Abies grandis* (Douglas) Lindley), and incense cedar (*Libocedrus decurrens* Torrey) are infested, but no brood is produced (Evenden et al. 1943), although a small brood was produced in Norway spruce (*Picea abies* (Linnaeus) Karsten) in a University of Idaho arboretum (Furniss and Schenk 1969).

Life Cycle

The mountain pine beetle usually completes a single generation per year. Beetles mature in July. Adults average about 0.5 cm (0.2 inch) in length and are dark brown to black in color. Prior to emergence, the new adults feed within the bark to complete maturation. During this feeding period, flight muscles increase in size (McCambridge and Mata 1969, Reid 1958) and about 2 percent of the new brood mate (McCambridge 1970). Feeding adults obtain and store fungus and yeast spores and probably bacteria in a special structure for transporting spores, the maxillary mycangium (Whitney and Farris 1970). When the density of brood adults is high, their feeding chambers may coalesce. Then, when one beetle chews an exit hole through the bark, all beetles within the common chamber emerge through the single hole (Amman 1969, Reid 1963).

Emergence and flight of new adults usually begin after several days of relatively high temperatures and abundant sunshine (Rasmussen 1974, Reid 1962). Beetles emerge only during the warm part of the day, starting when temperatures reach about 19°C (66°F) and ceasing in the afternoon when temperatures drop to about the same level (Rasmussen 1974, Reid 1962). Maximum flight activity generally occurs from 4:00 p.m. to 6:00 p.m. (mountain daylight time) in the mountains of Arizona, Colorado, Idaho and Utah in both lodgepole and ponderosa pine forests (Blackman 1931, McCambridge 1971, Rasmussen 1974). Farther north in Washington and British Columbia, maximum flight activity takes place from 11:00 a.m. to 4:00 p.m. in both ponderosa and lodgepole pine forests (Gray et al. 1972, Reid 1962). Data presented by Powell (1967) suggest that the threshold temperature for flight probably occurs earlier in the day in Washington and British Columbia.

Although emergence may continue for a month or more, usually about 80 percent of the beetles emerge within 1 week. In southeastern Idaho and northern Utah, most emergence and

attacks occurred during 7 days in 1970, 9 days in 1971 and 7 days in 1972. Light thunderstorms may have caused the slightly longer period of peak emergence in 1971; beetles remain in the trees during such weather (Rasmussen 1974).

Emerging adults select and infest living trees. The beetles are strongly oriented to trees of large diameter, and vision is believed to play a strong role in final tree selection (Schonherr 1976, Shepherd 1966). Once the female starts boring into a tree, she produces a pheromone that attracts other beetles to the tree (Pitman et al. 1968). When attacks reach a certain density, an antiaggregative pheromone signals the newly arriving beetles not to attack the tree; so they infest another (Rudinsky et al. 1974). Attacks on successfully infested trees are usually completed within 48 hours (Rasmussen 1974). Differences in attack density observed among trees suggest that the beetles are able to adjust density to the vigor of the tree, generally, with greatest attack density occurring on the largest, most vigorous trees (Cole et al. 1976). Others have related attack density to bark texture (Safranyik and Vithayasai 1971, Shepherd 1965). There is some evidence that the sex ratio of the attacking population may affect attack density toward the end of an epidemic; density appears to increase with the proportion of females in the population (Cole et al. 1976). Changes in sex ratio would affect pheromone production and hence the rate at which attacks would stop.

Evidence of beetle infestation usually consists of pitch tubes where beetles have entered the tree and boring dust in cracks and at the base of the tree. In dry years like 1977, few pitch tubes may be present. Beetle entries that leave no pitch tubes are called "blind attacks" and may be difficult to detect. Although pitch tubes may be absent, orangish-brown boring dust around the base of the tree is a sure sign that the tree has been killed.

Adult beetles bore through the outer bark into the phloem/cambium layer, constructing vertical egg galleries. The late July attack period corresponds well with the beginning of a seasonal decline in tree resistance as determined by tree response to inoculations of blue-stain fungi (Reid and Shrimpton 1971). The greatest resistance, however, occurred in the lowest part of the stem (Reid and Shrimpton 1971), the portion of the tree first infested by the beetles (Rasmussen 1974).

Fungus and yeast spores and bacteria carried by the beetle commence growth in the living phloem and xylem tissues soon after the beetle starts its gallery. Although the role of many of these is unknown, the blue-stain fungi help to kill the tree by interrupting water conduction and causing a rapid reduction in moisture of the sapwood (Amman 1977, Reid 1961). The zone of drying is larger than could be expected from the beetle alone, because of the action of the blue-stain fungi (Reid et al. 1967). This initial reduction in moisture the autumn immediately following attack probably benefits larval survival during the winter. Blue-stain fungi have also been considered to be nutritionally beneficial to the beetle larvae; however, Whitney (1971) found beetles to be in contact with

blue-stain fungi only during the first instar and again after pupation, so the nutritional relationship is not well supported.

Eggs are laid singly in niches along the sides of the gallery. They hatch within a week or so, and the larvae feed in the phloem, usually at right angles to the gallery. Most larvae overwinter in the second or third instar. A few reach the fourth instar before the cold weather of late October and November when they become dormant for the winter. Large larvae survive the winter better than small larvae (Amman 1973). The survivors begin to feed again in April, completing development in June after four instars. Larvae pupate within cells excavated in the bark and the sapwood. Pupae transform into adults from late June to mid-July.

The usual 1-year life cycle can have exceptions that are primarily dependent upon weather and climate. Parent beetles can produce two broods in some years (Reid 1962). After infesting one tree, adults emerge and attack a second. This phenomenon is relatively uncommon in lodgepole pine forests south of Montana. However, in Montana, for example, trees along Hellroaring Creek in the Gallatin Canyon showed a high rate of parent reemergence in 1973. Reemerging parents then attacked and killed additional trees, thus causing a spectacular increase in damage. It is doubtful that the second attacks produced much brood, because they came so late in the fall that few eggs hatched. Heat units are insufficient for all eggs to hatch when beetles infest trees in late August (Reid and Gates 1970). All eggs and many small larvae are killed by cold winter temperatures (Amman 1973).

Two years may be required for the beetle to complete a generation at high elevations in eastern Montana and central Idaho (Evenden et al. 1943, Gibson 1943) and in northwest Wyoming at elevations above about 2438 m (8000 ft) (Amman 1973). Cool temperatures delay development and emergence of beetles (McCambridge 1974). Reid (1962) found that the beetle required 2 years to complete a generation in Banff National Park, Alberta, in 1956, although previously he had noted that a generation was completed in a single year in the Park. Thus, the life cycle of the beetle will vary because of weather differences from year to year and place to place, because of elevation and latitude.

Infested trees can be detected by aerial surveys after the foliage has dried and changed color (Klein 1973). As the foliage dries it turns from green to pale green in the spring, then to light orange, and finally to a bright orange by July. Emergence holes in late summer signify that the brood has left the tree to infest green trees.

Factors Affecting Brood Survival

Factors affecting beetle survival within trees have been studied in many infestations. Some individual causes of beetle mortality have been studied in considerable depth. For example, DeLeon (1935a, 1935b) studied the small wasp,

Coeloides dendroctoni Cushman, and the fly, *Medetera aldrichii* Wheeler, respectively the most important insect parasite and insect predator of the mountain pine beetle. DeLeon concluded that *Coeloides* was the mountain pine beetle's most important natural enemy because it parasitizes larvae that are almost mature and ready to pupate. These larvae have a high probability of becoming adults, emerging and attacking other trees if they are not parasitized by *Coeloides*. On the other hand, *Medetera* consumes most beetle larvae in the fall. Many of these larvae would be killed by other causes, such as cold winter temperatures and drying, even if *Medetera* did not kill them.

Reid (1963) reported a comprehensive study of the beetle and its mortality factors in south-central British Columbia. He concluded that beetle survival was more closely correlated with tree diameter than with any other factor he studied. Reid (1963) also found a low degree of association between beetle survival and other factors, including predators, parasites, resinosis, egg gallery density and moisture content of the tree. Factors limiting outbreaks in the study area were thought to be the high resistance of most trees and their generally small size (Reid 1963).

Amman (1969) related beetle production to bark thickness and later to phloem thickness (Amman 1972, Amman and Pace 1976). Phloem is generally thicker in trees of large diameter (Amman 1969, 1975) and is more closely related to diameter growth than to any other factor (Cole 1973). The generally thinner phloem in trees of small diameter, coupled with excessive drying, results in low brood survival in such trees (Cole et al. 1976). The greater amount of drying in trees of small diameter is probably related to the thinner sapwood in small mature trees (Fig. 1).

Berryman (1976) evaluated the effects of phloem thickness, cortical resin canals, predation by woodpeckers, intraspecific competition, parasitism and resinosis in the egg gallery on brood survival. His study corroborated the importance of phloem thickness to beetle survival and showed the negative effect of phloem resin canals on brood production. In the laboratory, larvae avoided areas in the phloem that had many pitch pockets (Amman 1972).

Cole (1974, 1975) evaluated the effects of the following mortality factors on a beetle population in southeast Idaho: crowding, temperature, drying, pitch, pathogens, woodpeckers, parasites and predators. He concluded that none of these mortality factors offered regulatory influence on the beetle population. Cole (1975) found that a beetle has a better chance to survive in trees of large diameter, even when phloem is thin, than in trees of small diameter. Greater survival in large trees with thin phloem is probably related to the slower rate of drying in such trees.

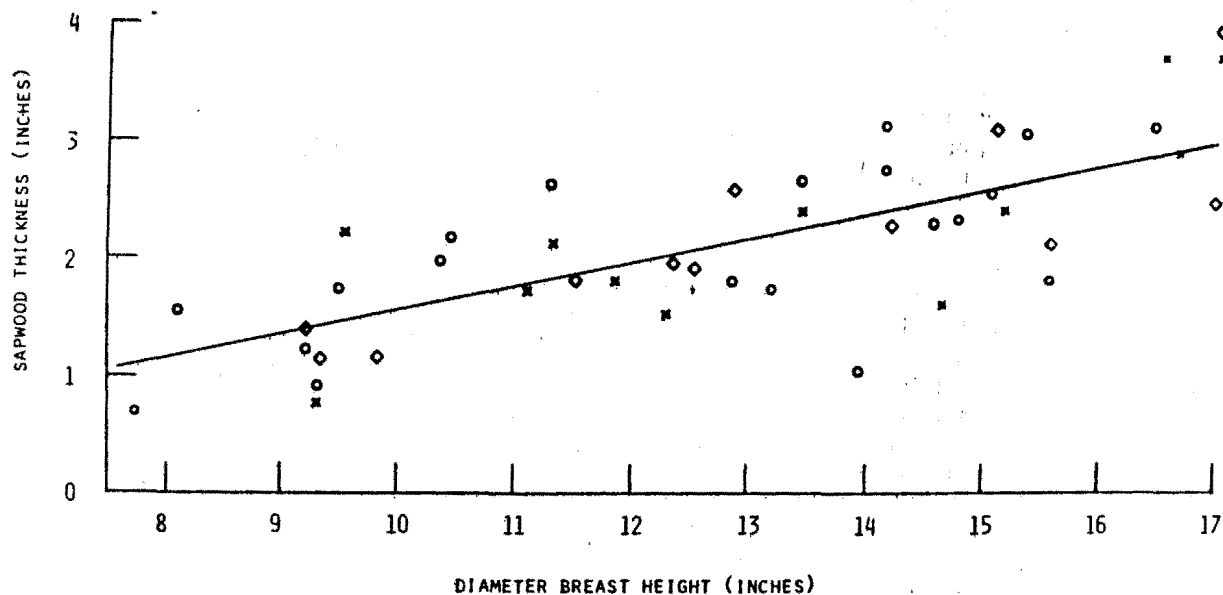


Fig. 1. Sapwood thickness (1 inch = 2.54 cm) at breast height for lodgepole pine trees killed by mountain pine beetles in 1971 (◇), 1972 (x), and 1973 (O), Bear River, Wasatch National Forest, Utah.

CAUSES OF BEETLE OUTBREAKS

Behavior of the mountain pine beetle differs between endemic and epidemic population levels. Hopkins (1909) stated that the mountain pine beetle prefers to attack injured and felled trees. We know from our observations and those of others that he was referring primarily to endemic beetle populations attacking injured trees and that infestation of felled trees is rare in lodgepole pine. Within the same paragraph, Hopkins also wrote, "As a rule, the largest and best trees are attacked first . . ." Again, from many observations, we know that this statement applies to epidemic populations. Craighead et al. (1931) stated that the mountain pine beetle is usually found in lodgepole pines that have been weakened by fire, by lightning or by other causes during endemic periods. However, during epidemics "... it is the larger, thick-barked trees that are first attacked . . ."

During endemic periods, we have found the mountain pine beetle associated with *Pityophthorus* and *Ips* spp. in trees that clearly were infested first by the last two bark beetle species. These trees were usually well below average in growth, had thin phloem and produced few beetles. In addition, we found mountain pine beetles attacking trees severely injured by porcupines.

The undersides of trees blown over but still attached by some roots are occasionally infested. In one case, a few beetles were found in bark on the underside of a log—the tree had been cut during powerline construction. Because they occasionally observed mountain pine beetles in logs or windthrown trees, entomologists thought this behavior could be exploited by using trap trees to attract the beetles. Trap trees have been successful in dealing with the spruce beetle, *Dendroctonus rufipennis* (Kirby) (Nagel et al. 1957); however, attempts to attract the mountain pine beetle in lodgepole pine have failed in the Rocky Mountains.

Shrimpton and Reid (1973), who used inoculation of blue-stain fungus as a measure of tree resistance to mountain pine beetle infestation, suggested that endemic populations maintain themselves by infesting trees that are least resistant.

During endemic periods, the behavior of infesting injured or weakened trees or those of low resistance apparently enables the beetles to maintain their populations at low levels while the stand is growing into conditions that will support an epidemic.

The change from endemic to epidemic beetle infestation is a period of prime importance. Generally, when few beetles

infest a vigorous tree, they are pitched out or eggs laid during gallery construction and fungi introduced by the beetles are killed by resin (Reid and Gates 1970, Reid et al. 1967). We believe that the change from endemic to epidemic populations occurs when subpopulations within scattered trees are close enough to converge on a common tree or group of trees of medium to large diameter and moderate to thick phloem. In such trees, beetle production is greatly increased. The epidemic can start then. If weather conditions are unfavorable, however, the population may decline, in which case, several years may again be required before an epidemic gets under way.

Berryman (1976) theorized that sudden tree stress would allow beetles to infest recently vigorous trees that still have thick phloem for greatly increased beetle production. A long-term decline in tree vigor, such as might occur because of tree disease, would result in a reduction in growth and in phloem thickness. Such trees would produce small numbers of beetles (Amman 1972).

Under epidemic conditions, the beetles most certainly are dependent upon the best trees in the stands for population build-up. As a result, tree losses are usually intensive and extensive. It is therefore essential that we understand the behavior and the dynamics of the beetle under both endemic and epidemic conditions, particularly at the interface of the two.

Theory Based on Weakened or Stressed Trees

Factors that could contribute to bark beetle outbreaks, such as tree injuries or stress, were reviewed by Rudinsky (1962). The classical theory for bark beetle outbreaks emphasizes some form of tree stress or decline in vigor. Stress factors that have been mentioned as possible causes for mountain pine beetle epidemics are insect defoliation, tree disease and drought. Because of the importance of phloem thickness to epidemics of mountain pine beetle (Amman 1972) and the direct relation of phloem thickness to radial growth of lodgepole pine (Cole 1973), Berryman (1976) suggested that the effects of stress may not be immediately apparent in phloem thickness because the tree retains an accumulation of several years of phloem growth (Cabrera these proc.). However, an examination of xylem for recent stress would be easier and just as reliable.

Insect Defoliation/Mountain Pine Beetle Associations

Defoliation would provide one of the most rapid stresses to which a tree could be subjected. Lodgepole pines in Yosemite National Park defoliated by the lodgepole pine needle miner (*Coleotechnites milleri* Busch) were later killed by the mountain pine beetle (Patterson 1921). However, Patterson also reported beetle infestations in that area before defoliations by needle miners. According to Stark and Cook (1957), an outbreak of a needle miner (*C. starki* (Freeman)) in southeastern British Columbia severely weakened and killed some lodgepole pines, but did not result in increased bark beetle activity; however,

there was little bark beetle activity anywhere in that region at that time (R.W. Stark, pers. comm.,¹ 2 June 1978).

Mountain pine beetle infestations occurred in lodgepole pine defoliated by the pandora moth (*Coloradia pandora* Blake) in Utah; however, it was believed that these were extensions of an older beetle infestation adjacent to the defoliated area and were not specifically related to defoliation (Carolin and Knopf 1968). Nor were infestations of pandora moth in Colorado and Wyoming followed by bark beetle outbreaks.

Tree Disease/Mountain Pine Beetle Associations

Partridge and Miller (1972) examined root rot/beetle associations in several species of conifers in Idaho, including lodgepole, ponderosa and western white pines. Among the pines, they found a significant association between only *Armillaria mellea* (Vahl ex Franco) Kummer and beetles in ponderosa pine. Of a total of 32 trees, 3 contained both beetles and fungi, 2 had beetles only and 2 had fungi only. The authors did not mention the species of bark beetles found.

Another almost ubiquitous disease of lodgepole pine, dwarf mistletoe (*Arceuthobium americanum* Nuttall ex Engelman), has been suspected of contributing to the large infestations of mountain pine beetle within the Intermountain area. Parker and Stipe (1974) attempted to evaluate the association of mountain pine beetle and mistletoe in lodgepole pine. They concluded that the beetle shows more preference for the trees most heavily infected with mistletoe. Few trees with a dbh of less than 25 cm (10 inches), even though heavily infected by mistletoe, were attacked by the mountain pine beetle in the stands examined by Parker and Stipe (1974). The beetle's strong preference for trees of large diameter makes it difficult to separate the influence of mistletoe from that of diameter. McGregor (these proc.), however, was able to achieve a separation of these effects. He observed that the proportion of trees killed in heavily mistletoed stands was less than in stands that had little or no mistletoe.

During early dwarf mistletoe infection of lodgepole pine, growth is stimulated at the site of infection and results in localized thick phloem. Our observations show that when beetles infest trees that have infection sites of mistletoe on the main bole these sites produce significantly more beetles per unit area than the remainder of the tree. In trees with medium to heavy mistletoe infections in the crown, however, phloem is significantly thinner than in uninfected trees (Roe and Amman 1970).

If the mountain pine beetle infested heavily diseased trees in which tree growth was drastically affected, it is doubtful that a surplus of brood adults would be produced. A surplus is the number over and above the number of parents that

¹ R.W. Stark is currently at the College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, ID 83843.

attacked and killed the tree. Consequently, the population of beetles would be expected to decline.

Drought/Mountain Pine Beetle Associations

Drought has long been considered a major contributing factor to outbreaks of the mountain pine beetle.

Hopping and Mathers (1945) reported that two outbreaks (Kootenay and Banff, Canada) of the mountain pine beetle in lodgepole pine occurred during a period of deficient moisture. Although Powell (1969) found no strong relation between weather and beetle infestations in western Canada for a 60-year period, infestations were more likely to occur when spring and summer temperatures were above normal and precipitation was below average during the growing season.

Growth data from lodgepole pine in the Bear River drainage on the north slope of the Uinta Mountains in Utah showed that the present infestation increased sharply about 1969, during moist years, and continued to spread under average to better-than-average precipitation. The few trees that were infested in 1968 were widely distributed in the stands. These trees had shown increased growth starting about 1959 (Fig. 2). Non-infested trees in the stand showed a 28 percent

increase in growth in 1969, and trees infested that year (average dbh 27.5 cm) showed an average emergence of 0.03 beetles/cm² (28 beetles/ft²) of bark surface. Moisture content of infested trees averaged 16 percent (range 0 to 26%) as determined by an electrical resistance meter about 3 weeks before beetle emergence. Beetle production during this period of favorable moisture conditions was compared with beetle production that occurred during the dry 1976-1977 generation year. Trees that were infested in 1976 (average dbh 25 cm) showed the same growth as in 1975, the result of precipitation coming as snow the winter of 1975-1976 and rainfall early in the summer of 1976. However, lack of precipitation during late summer, fall and winter of 1976-1977 resulted in excessive drying of infested trees. Average moisture content was 11 percent (range 7 to 18%) on a fresh oven-dry weight basis about 3 weeks before beetle emergence in 1977. These trees yielded an average of only 0.0015 beetles/cm² (1.4 beetles/ft²). Tree mortality declined following this drastic reduction in the beetle population.

Our observations in lodgepole pine are in general agreement with those of Blackman (1931) in ponderosa pine in northern Arizona. He suggested that an increase in the moisture available to the tree during average or better-than-average precipitation results in increased brood survival of the beetle.

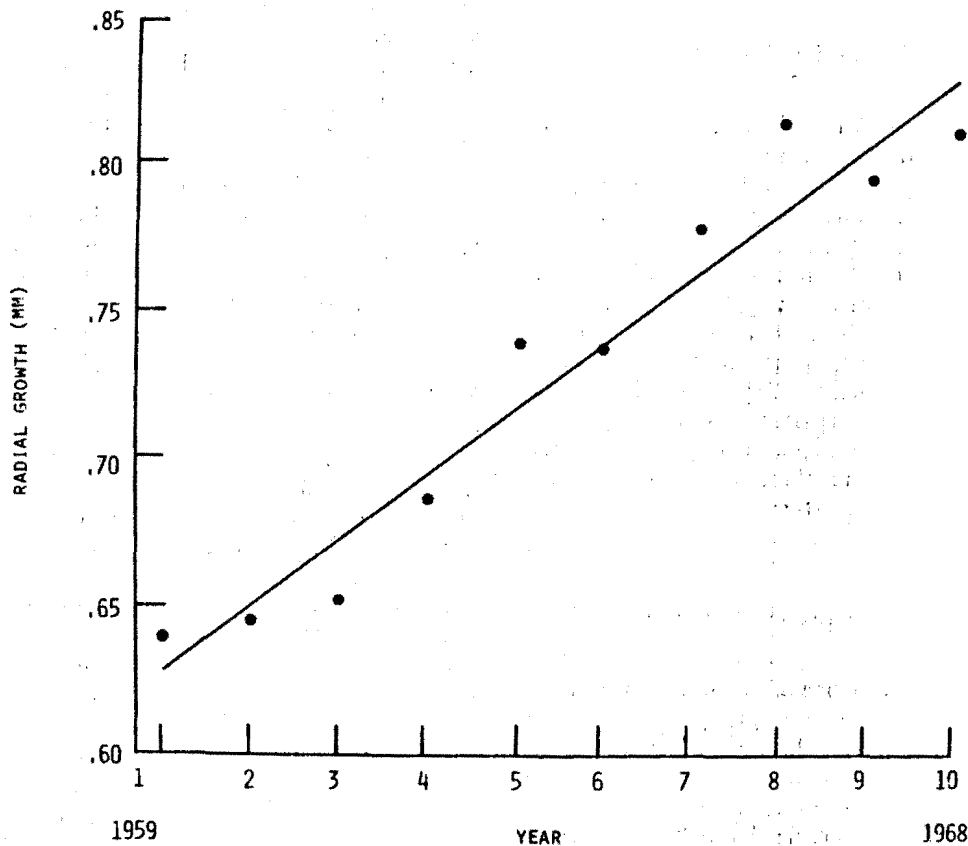


Fig. 2. Average growth of lodgepole pine trees (N = 45) before infestation by mountain pine beetle in 1968. Level of infestation was about 1 tree per 39 ha (100 acres); average diameter breast height of infested trees was 33 cm (13 inches). Bear River, Wasatch National Forest, Utah.

A marked deficiency in available moisture associated with drought results in decreased brood survival.

From this examination of tree stress/mountain pine beetle associations, it can be seen that none of the factors has been studied in depth. Specific studies are needed to establish conclusively the significance of stress factors in mountain pine beetle epidemiology.

Theory Based on Maturation of Lodgepole Pine Trees

I propose that the cause of mountain pine beetle infestations is based on physiological changes of the tree associated with good vigor, not stress. There are four main conditions that must be met for epidemics of the beetle to occur. These are 1) sufficient numbers of trees of large diameter, 2) thick phloem in many large trees, 3) optimal age of trees, and 4) optimal temperature for beetle development.

Effect of Tree Diameter

The mountain pine beetle usually selects the largest trees in the stand to infest, at least during a major epidemic and the few years that precede it (Cole and Amman 1969, Evenden and Gibson 1940, Hopping and Beall 1948). These are the most vigorous trees in the stand (Roe and Amman 1970).

The preference of the beetle for trees of large diameter is apparent when the proportional loss for each diameter class is calculated for an entire infestation. Trees killed by the beetles ranged from 1 percent of the trees with a dbh of 10 cm (4 inches) to 87 percent of the trees with a dbh of 41 cm (16 inches) and larger in two stands in northwest Wyoming (Cole and Amman 1969). Losses reported by other authors (Evenden and Gibson 1940, Hopping and Beall 1948, Parker 1973, Reid 1963, Roe and Amman 1970, Safranyik et al. 1974) show a similar relation of mortality to tree diameter. In addition, the preference of the beetle for large-diameter trees is apparent each year of a major infestation (Cole and Amman 1969).

Safranyik et al. (1975) showed tree mortality to be proportional to the basal area that the diameter class represented in the stand, and suggested that the beetles attack trees according to the surface area that each diameter class represents. Burnell (1977) then presented a dispersal/aggregation model for the beetle in lodgepole pine stands based on a random attack pattern and surface area relations of the trees.

Washburn and Knopf (1959) reported that 3 years of aerial surveys showed the beetle's preference for large open-grown or edge trees during the early stages of infestation to be similar for all epidemic centers. They stated, "Invariably, the epidemics have gotten their start in full-crowned trees, but not necessarily the oldest or biggest, usually located on the outer edge of the timber bordering open rangeland, or lake and stream shores." In the more open portions of stands (Fig. 3), the proportional losses of lodgepole pine are much greater.

Effect of Phloem Thickness

Trees on edges or in the more open stands are usually growing faster than those within stands, and consequently have thicker phloem. The evolutionary basis for the beetle's behavior of selecting trees of large diameter and in more open stands is probably related to the high probability of encountering thick phloem (Amman 1975) that results in high beetle production (Amman 1972, Amman and Pace 1976). Estimates of beetle production from trees in northwest Wyoming ranged from 300 for trees 20 to 23 cm (8 to 9 inches) in diameter to over 15,000 for trees 46 cm (18 inches) in diameter (Cole and Amman 1969). Klein et al.² sampled emergence holes over the entire bole of infested trees and obtained results of even greater magnitude. They reported a range of emergence holes from 152 for a 20-cm (8-inch) tree to over 18,000 for a 46-cm (18-inch) tree. On the average, the number of beetles produced in small trees is less than the number of parent beetles that killed the tree. In contrast, a large surplus of beetles is usually produced in large trees. When the evolutionary strategy of the beetle is viewed over many generations of lodgepole pine, the killing of the largest trees as they become mature or slightly before they reach maturity in persistent and climax lodgepole pine stands provides a continuous supply of food, helps maintain the vigor of the stand, and keeps the stand at maximum productivity (Amman 1977).

Phloem thickness usually increases as diameter increases, yielding coefficients of determination ranging from 0.69 to 0.95 for stands in Montana, Idaho and Utah (Table 1). Although this relation exists for all stands we have measured, the phloem thickness for any given diameter will differ among stands because of differences in stocking level and site quality. For example, Cole and Cahill (1976) predicted that beetles in a stand in Colorado would not build up and cause heavy losses because the stand contained few trees having either large diameter or thick phloem. That prediction has held to date (Cahill, pers. comm.,³ 3 April 1978). Conversely, on good sites, phloem for any given diameter is generally thick—for example, the findings of McGregor et al. (1975) in the Lazier-Meadow Creek area of western Montana. Losses in these stands now have exceeded 750 trees per hectare (300 trees per acre) and are some of the heaviest ever attributed to the mountain pine beetle (McGregor et al. 1977).

The effect of stand density on beetle production was noted by Amman (1969) and is probably related to phloem thickness, which declines with increased stand density (Amman et al. 1977). Brood production (measured as emergence holes) from trees having thick bark in the least dense stands was 0.13 per cm² (125 per ft²) of bark surface, over 4 times

² Klein, W.H., D.L. Parker and C.E. Jensen. (In preparation). Attack, emergence and stand depletion trends of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, during an epidemic (Coleoptera: Scolytidae).

³ D.B. Cahill is currently at Forest Insect and Disease Management Division, USDA Forest Service, Lakewood, CO.

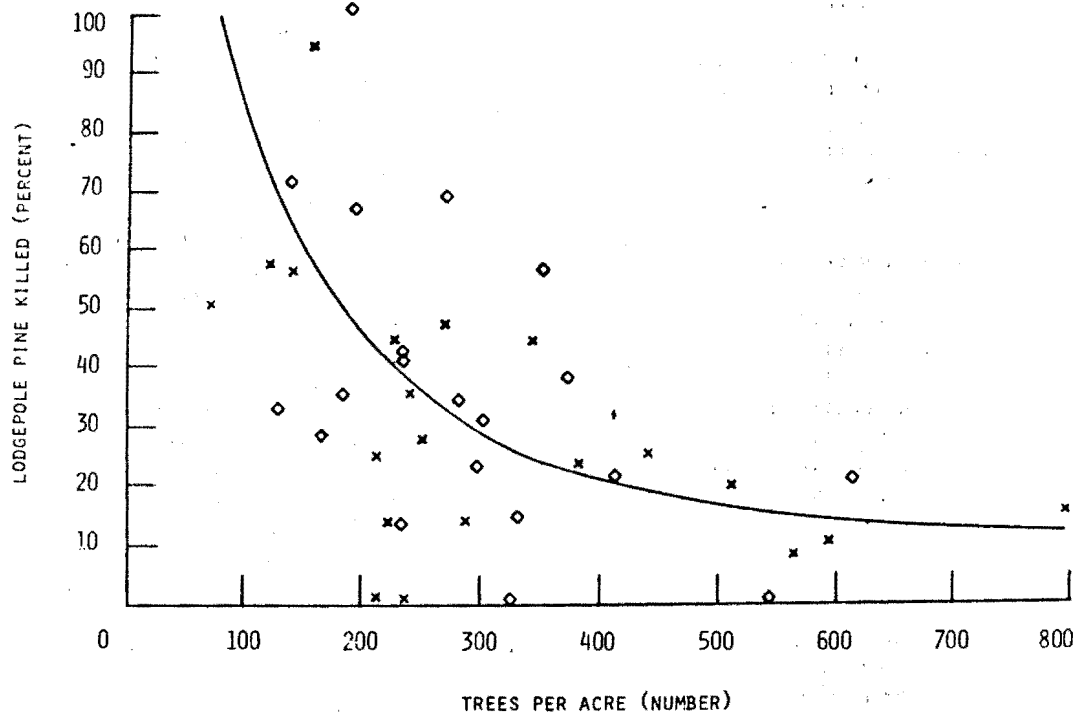


Fig. 3. Percent of lodgepole pine trees killed in relation to tree density of all species 10 cm (4 inches) diameter breast height and larger on Pilgrim Mountain, Grand Teton National Park, Wyoming (◇) and Pacific Creek, Teton National Forest, Wyoming (x). Multiply numbers of trees/acre by 2.5 to obtain approximate numbers/hectare.

greater than in the most dense stands, which had 0.03 per cm^2 (30 per ft^2).

Tree losses also have been related to 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) and reflects a difference in environment from other habitat types. Both lodgepole pine and the mountain pine beetle react to a given environment in certain ways, as evidenced by differences in growth and phloem thickness of lodgepole pine (Cole 1973) and in intensity of infestations by the mountain pine beetle (Roe and Amman 1970, McGregor these proc.).

After radial growth, habitat type was the second most important variable explaining variance in phloem thickness in all higher ranking regressions of from two to six independent variables (Cole 1973). Consequently, infestations of mountain pine beetle probably can be expected more frequently on sites providing for the best growth of lodgepole pine.

Effect of Age

Age of host trees is a commonly considered variable in mountain pine beetle infestations. Infestations seldom occur in

lodgepole pine stands less than 60 years of age and there is only moderate probability of infestation in stands 60 to 80 years of age (Safranyik et al. 1974). The age of host trees points clearly to the necessity of a change from juvenile to mature tree for successful brood production by the beetle.

Although part of this age difference may be associated with the generally smaller diameters of trees less than 60 years old, other elements also are involved. Phloem in young trees tends to be more spongy and resinous. Shrimpton (1973) found that blue-stain fungi artificially inoculated into such trees did not establish well because of the greater resinous response of young trees. Tree resistance was found to be highest in the 41- to 60-year age class, where about 90 percent of the trees showed resistance to inoculations. After that age, resistance to blue stain dropped rapidly, with only 30 percent of the trees 111 to 140 years old showing resistance to blue-stain infection. Occasionally, we have found young trees that have been infested and killed, but such trees tend to dry rapidly and few if any brood complete development. Shrimpton and Reid (1973) found fungal inoculation useful in categorizing trees that were resistant and those that were non-resistant to beetle infestation. Peterman (1977), however, obtained poor results when he used the method.

Table 1. Relation of phloem thickness to diameter at breast height of lodgepole pine trees.

Plot location	Coefficient of determination (r^2)	Y intercept	Regression coefficient
Camas Creek, Glacier National Park, MT ¹	.69	.036	.0031
Lazier Creek, Lolo National Forest, MT	.86	.023	.0067
Calyx Creek, Kootenai National Forest, MT	.81	.034	.0038
Solo Joe, Kootenai National Forest, MT	.88	.012	.0052
West Yellowstone, Gallatin National Forest, MT	.95	.043	.0050
Pineview, Targhee National Forest, ID	.77	.057	.0033
Warm River, Targhee National Forest, ID	.88	.027	.0066
Signal Mountain, Grand Teton National Park, WY	.91	.038	.0059
Black Rock Creek, Teton National Forest, WY	.77	.028	.0058
Bear River, Wasatch National Forest, UT	.70	.060	.0042

¹ Mark D. McGregor, Entomologist, Forest Service, Forest Insect and Disease Management, Missoula, MT, kindly furnished data from Camas, Lazier, Calyx and Solo Joe areas.

Shrimpton (1973) reported that resistant trees generally had faster radial growth and thicker phloem than non-resistant trees. When these resistant trees are successfully infested, they usually yield large numbers of beetles and are therefore important to epidemics.

Observations by Roe and Amman (1970) revealed that, in two stands in the Teton and Targhee National Forests that were undergoing beetle infestations, the ages of live trees ranged from 54 to 106 years (average 87) and from 33 to 113 years (average 76) respectively, for trees 10 to 41 cm (4 to 16 inches) dbh. In a third stand in northern Utah where an infestation had started to change from endemic to epidemic, ages ranged from 39 to 220 years (average 97) for trees 15 to 51 cm (6 to 20 inches) dbh. Of the 124 trees measured in this stand, 85 percent would be classed as immature (40 to 120 years) and only 6 percent as overmature, according to silvicultural ages specified by Tackle (1955). Within the stand, the average tree age was 104 years and the average tree size was 33 cm (13 inches) dbh for trees infested by the mountain pine beetle. This apparent age requirement for beetle epidemics points to silviculture as a means of reducing losses to the beetle. Trees probably can be grown to fairly large size under intensive management and be harvested at about 80 years of age without significant loss to the mountain pine beetle.

Effect of Climate

Although diameter and phloem thickness are major items involved in the dynamics of mountain pine beetle populations, epidemics can develop only in stands where temperatures are optimum for beetle development (Amman 1973, Safranyik et al. 1975). Climate becomes an overriding factor at extreme northern latitudes and at high elevations. At these extremes, beetle development is out of phase with winter conditions. Consequently, stages of the beetle that are particularly vulnerable to cold temperatures enter the winter and are killed.

Because of reduced brood survival, infestations are not as intense and fewer trees are killed as elevation and latitude increase (Amman and Baker 1972; Amman et al. 1973, 1977; Safranyik et al. 1974). Tree mortality is low even though an ample food supply (trees of large diameter with thick phloem) exists (Amman et al. 1973).

CONCLUSIONS

Lack of in-depth studies and conflicting evidence that proposes that tree stress contributes to mountain pine beetle epidemics make a clear-cut judgment impossible. Tree weakening occurring over several years will slow growth and result in thin phloem and, subsequently, in low beetle production. However, rapid decline in stand vigor may contribute to the start of an epidemic, as proposed by Berryman (1976), provided enough beetles are present in a stand to take advantage of sudden stress.

On the other hand, evidence that mountain pine beetle epidemics are related to physiological maturity of the trees, irrespective of stress, has considerable support. Epidemics are associated with 1) trees of large diameter, 2) thick phloem that is less spongy and resinous than that found in young trees, and 3) trees about 80 years old, at which age the resinous response is not as great as in younger trees.

The philosophy to which one subscribes will dictate the treatment to be used to reduce tree losses. If stress is considered the primary factor, then one would ignore age. Maintenance of good growth would be the treatment of choice and cutting would take place whenever the stand reaches the desired size. On the other hand, if maturity (as related to tree size, phloem thickness and consistency, and tree age) is considered to be the primary factor, then an upper limit is placed on how long trees can be grown before harvest, regardless of treatment. Emphasis must be placed on intensive management and harvesting of trees at about 80 years of age.

QUESTIONS AND ANSWERS

- * circulate to
P-pine S/H
Nations group
- Q. Is there any intrinsic relationship between tree age and outbreak occurrence, or is age merely confounded with tree size?
- A. Age and diameter are related to some extent. There seems to be a maturing of the phloem with age, however, which is important to brood survival of the beetle and probably determines the earliest age that an infestation can occur in a stand. Young trees of large diameter have phloem that is spongy and contains many pitch pockets that phloem of older trees of similar diameter does not have. However, following an epidemic many smaller trees usually survive, frequently of the same age as those killed. These trees must grow to sizes and phloem thicknesses conducive to beetle build-up before the next infestation can occur. These later infestations would not be age dependent.
- Q. If temperature is critical for beetle survival, why did the population in West Yellowstone and Yellowstone Park survive?
- A. Winter temperatures that occur in these areas are not consistently cold enough to kill most mountain pine beetle brood. The other temperature relation, associated with high elevations, does not seem to apply to most of the stands in these areas. Elevations are low enough for the beetle to complete a generation in a single year, emerge and attack trees early enough that the new brood gets a good start before fall temperatures stop beetle development. At high elevations, however, the beetles may require 2 years to complete a generation, or may complete development but be prevented from emerging by cold fall temperatures. The advanced brood then is killed by winter temperatures.
- Q. Is it suspected that drought years affect the blue stain's ability to spread and thus indirectly affect the beetle, or is it a direct effect of drought on the beetle?
- A. We don't know enough about the role of blue-stain fungi, except that they appear initially to dry the bark and wood rapidly, but may possibly affect moisture retention in the long run. In the latter case, if the tree dried rapidly before blue stain penetrated most of the sapwood, the beetle would be affected indirectly. Whether this is the case or whether the beetle-infested tree dries only as a direct result of drought, excessive drying of the tree reduces brood survival.
- Q. You mentioned that beetles are oriented toward the larger trees in an epidemic. Is this a visual orientation or a matter of greater surface area of larger trees in the stand? Is there a primary attractant or a random selection of the target trees?
- A. Evidence is fairly strong that a visual response, but not a strict response to surface area, is involved in final tree selection by the beetle. When the surface area of all trees in the stands 10 cm dbh and larger is considered, the beetle attacks proportionately less surface area in diameters 22.5 cm (9 inches) dbh and less than their representation in the stand. The mountain pine beetle attacks proportionately greater amounts of surface area in diameters 25 cm (10 inches) dbh and larger than their representation in the stand. Consequently, the tree-attack pattern of the beetle cannot be random. Primary attraction involving quantitative differences in terpenes or other host constituents has not been demonstrated.
- Q. If phloem thickness is a measure of food for the beetles, then I presume that the nutritional quality of the phloem will be at least as important as phloem thickness per se. One could imagine thick phloem that is nutritionally poor and thin phloem that is nutritionally rich. Apart from the obvious implications of such factors as defoliators and/or leaf and root diseases—all of which would affect the nutritional value of the phloem—what effect do you think the associated blue-stain fungi and particularly yeasts may have on beetle productivity (that is, the course of outbreaks) in thin- and thick-phloemed trees?
- A. Most of our work with phloem thickness and beetle production shows a direct relationship between the two, but some of the variance could be caused by differences in phloem quality, and in turn might influence some of the microorganisms. Our work (Amman and Pace 1976) showed that beetles reared from thin phloem were smaller than those from thick phloem, and the sex ratio of beetles from thin phloem was more in favor of females than that of beetles from thick phloem. There seems to have been little work done on yeasts in relation to mountain pine beetle that would answer your question. However, I see no reason to think that quality of the microorganisms associated with the beetle would not change depending upon phloem quality and available moisture. It seems very likely that the quality of microorganisms could receive a big boost when beetles start invading the larger trees. The improved quality of microorganisms when inoculated into small-diameter trees may enable beetles to produce more brood when they eventually must infest small-diameter trees after most large ones are killed. The benefit probably would be short lived, however—one or two generations at best.
- Q. How far will beetles travel during flight period (average)?
- A. I know of no study that has researched this question. However, I suspect that they fly no farther than is necessary to find a tree that meets their specifications—during early years of epidemics this probably would be no farther than 0.4 to 0.8 km (¼ to ½ mile). However, as most desirable trees are killed the beetle would need to fly farther in search of suitable host trees. During

endemic periods, flight may be no farther than to find a tree that has been severely injured or infested by other species of bark beetles. What we see so far would suggest that beetles from the larger trees having thick phloem on the average are larger, and would be able to fly farther because of greater fat content. Studies on Douglas-fir beetles indicate that beetles can fly over 48 km (not continuously). Collections of beetles from snow fields suggest that beetles are often caught in updrafts and deposited many miles away.

Q. How big were the trees in the British Columbia needle miner outbreak? Could the reason that the beetles did not come into the stand be related to food supply?

A. Not knowing more about the stands, I cannot answer your question. Several possibilities exist in addition to food supply—weather conditions, no beetles in immediate area, or simply that they did not respond to the defoliated trees.

Q. Based on your theory, how do you explain the existence of thick-phloemed, large-diameter stands of 120 years plus at low elevations in Montana and Idaho?

A. Over the past 20 years we have seen most such stands infested and the large-diameter component killed by the beetles. Some stands have not been infested (yet), but, except for those at high elevations, history would indicate that it is going to happen. Factors that might account for the stands' escape up to now are adverse weather conditions such as cold drainages and no beetles in or near the stands.

Q. If phloem thickness is one key to brood development and phloem thickness is correlated with dbh, how do we account for the high mortality in eastern Oregon?

A. I have not seen the infestations in eastern Oregon, but my colleagues have told me that phloem is thicker for any given diameter than what we have seen in the drier Rockies. Even in the Oregon stands, beetle production in these small-diameter trees probably is not great enough to produce surpluses (numbers in excess of those attacking the tree and those lost during flight). The population increase comes from production in the large trees.

Q. At the time of death, most mountain pine beetle-killed trees show decreased growth and are very slow growing—i.e., 8 to 12 rings per cm (20 to 30 rings to the inch). How can you define these trees as fast-growing and vigorous? If this isn't considered as a stress period, what is it?

A. Most measurements of growth are taken at breast height, and then usually only the width of the ring is measured. I don't think radial increment at breast height is necessarily a good measure of current vigor. Most of these trees, certainly the dominants and co-dominants in which beetle production is high, have only 3 to 4 rings per cm (8 to 10 rings to the inch) in the tops. Vigor should be based on volume of growth to account for the much greater surface area of the older, larger trees.

I have seen beetle infestations increase and do very well during periods of increasing tree growth; therefore, I don't believe that stress is a necessary ingredient for epidemics to start or to continue.

Q. If stress on individual trees is necessary to sustain endemic populations, would not stress on stands create epidemics?

A. During endemic periods, beetle numbers are low, and therefore they would be unable to kill vigorous trees. Consequently, they infest injured trees or those attacked by other species of beetles. When mountain pine beetle from a number of such trees are in close proximity, they have the capability of infesting and killing the most vigorous trees in the stand. My position with respect to tree stress is that it is not necessary for beetle epidemics to occur. I have arrived at this position by seeing infestations develop during periods of good tree growth.

Q. Do you believe that physiological maturity is in fact stress due to limitations of various vital elements necessary for continued vigorous growth?

A. No, I don't think a shortage is involved. I believe that changes occur in the phloem, such as those indicated in Cabrera's examination of phloem—a greater compression of phloem and a reduction in resin canals in the phloem. The trees are still growing well, and certainly if the beetle is oriented to poor-vigor trees, it would have taken those left in the stand rather than the dominant and co-dominant trees that it infested and killed.

Q. Why do you consider stress and age as mutually exclusive explanations—can't both be operative?

A. Age per se cannot be a stress factor as long as the tree is growing well. Stress can occur at any age of the tree's life, and is not limited to one time period such as when it reaches maturity. Maturity and thickness of phloem are the essential items. Consequently, epidemics can occur with or without stress.

Q. How do you define maturity? Is your term "physiological maturity" not surely synonymous to undefined stress?

A. I find it difficult to compare my definition of physiological maturity as stated above to something that is undefined. I suspect that many items that people like to toss in the "stress basket" really are not stress at all—for example, age. The problem with the stress theory is that it has been taken for granted and never examined critically, especially in view of new information on the mountain pine beetle/lodgepole pine interaction. To have credibility, any stress theory is going to need consistency with observed beetle epidemics rather than a long listing of possible stresses without hard data to back them up.

Q. Relief of stress by thinning has been successful in preventing beetle epidemics in young ponderosa pine. Has this been tested in young lodgepole, and if not, do you think it will work?

A. We suspect that thinning changes the microclimate in thinned ponderosa pine stands, and that success may not be solely due to relief from stress. The change in beetle response is usually so dramatic that one could not associate it with a change in tree vigor alone.

Mountain pine beetle is not usually much of a problem in lodgepole pine under 80 years of age. Thinning stands when they are approaching this age, or even well before, may make a difference. It needs to be tested. However, lodgepole pine grows in cooler climates and the beetle may not avoid these stands as it does in ponderosa pine. The beetle shows a preference for the more open lodgepole pine stands throughout most of the type. Just the opposite appears to be the case in ponderosa pine, where the beetles show a preference for the dense stands over much of the type.

Q. Do you speculate that there is any advantage in prescribing a mixed species stand (Douglas-fir and lodgepole pine) for beetle control in lodgepole pine? If yes, what percent of the stand would you prescribe to be lodgepole pine at stand age 60 years?

A. The advantage of a mixed species stand is that when a beetle epidemic occurs, considerable volume will remain after most of the lodgepole pine are killed. The beetle appears to kill proportionately as much lodgepole pine in mixed species stands as in pure lodgepole stands. Whether or not an epidemic is as likely to start in mixed species stands is yet to be determined.

Q. What general similarities or differences exist between ponderosa pine and lodgepole pine as regards mountain pine beetle attraction (infestation)?

A. Behavior of the mountain pine beetle in ponderosa pine seems to be more variable over the range of ponderosa. For example, the beetle seems to prefer the small-

diameter trees in dense clumps in eastern Oregon and in parts of Idaho, Montana and South Dakota. In Colorado, the beetle shows a preference for a greater range in diameters. In southern Utah and northern Arizona the beetle appears to prefer the large-diameter trees. No work has explained these differences in beetle behavior.

In lodgepole pine, the beetle shows a strong preference for large-diameter trees over the entire range, but kills trees even in the small-diameter classes, particularly toward the end of an epidemic (for example, in eastern Oregon and parts of western Montana). In these stands the phloem was thicker for any given diameter class than in stands south of Montana. In general, for population build-up to occur, the beetle must infest the large-diameter lodgepole pines where food (phloem) and moisture (throughout beetle development) are more abundant than in small trees.

Q. To what extent can land managers expect the mountain pine beetle to affect ponderosa pine in areas of associated lodgepole pine?

A. I have not worked in areas where these two species were associated, but I have been told that beetles produced in lodgepole pine are now infesting ponderosa pine in eastern Oregon. At low to moderate population levels of mountain pine beetle, Hopkins' host selection principle (beetles infest the species of plant on which they developed) appears to be operative. We have seen this in white bark pine/lodgepole pine associations. Losses in one host type did not result in corresponding losses in the adjacent host type. However, when epidemics occur, the host selection principle does not appear to hold.

Q. What stand densities would you prescribe for a stand 60 years of age on a habitat type that has a potential growth capacity of 60 cu ft per year?

A. Thinning to basal area of 16.5 m²/ha (80 ft²/acre) probably would result in substantial growth over the next 20 to 40 years. However, keep in mind that the risk of loss to the mountain pine beetle increases considerably with each year after tree age 80.

Q. This morning we saw a picture of an area near a campground where one lodgepole apparently was not hit by bark beetles. Would you speculate on why this has occurred?

A. The tree was located on one end of the group. Therefore, I suspect wind direction, hence direction of beetle flight when the other trees were infested, may have been involved; or there may have been only enough beetles to kill all the trees except that one. I have seen similar occurrences, only to have the beetles return in a year or so to kill the remaining large-diameter trees.

REFERENCES

- Amman, G.D. 1969. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. USDA Forest Serv. Res. Note INT-96. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- _____. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *J. Econ. Entomol.* 65:138-140.
- _____. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environ. Entomol.* 2:541-547.
- _____. 1975. Insects affecting lodgepole pine productivity. Pages 310-341 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- _____. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: impact on succession. Pages 3-18 in W.J. Mattson (ed.). Arthropods in forest ecosystems, Proc. in the Life Sciences. Springer-Verlag, New York.
- Amman, G.D., and Bruce H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. *J. Forest.* 70:204-209.
- Amman, G.D., and V.E. Pace. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. USDA Forest Serv. Res. Note INT-209. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- Amman, G.D., B.H. Baker and L.E. Stlpe. 1973. Lodgepole pine losses to mountain pine beetle related to elevation. USDA Forest Serv. Res. Note INT-171. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp.
- Amman, G.D. M.D. McGregor, D.B. Cahill and W.H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.
- Berryman, A.A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environ. Entomol.* 5:1225-1233.
- Blackman, M.W. 1931. The Black Hills beetle (*Dendroctonus ponderosae* Hopkins). New York State College Forest. Tech. Publ. 36, Vol. 4. Syracuse. 97 pp.
- Burnell, D.G. 1977. A dispersal-aggregation model for mountain pine beetle in lodgepole pine stands. *Res. Popul. Ecol.* 19:99-106.
- Carolin, V.M., Jr., and J.A.E. Knopf. 1968. The pandora moth. USDA Forest Serv. Pest Leaflet. 114. Washington, D.C. 7 pp.
- Cole, D.M. 1973. Estimation of phloem thickness in lodgepole pine. USDA Forest Serv. Res. Pap. INT-148. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 10 pp.
- Cole, W.E. 1974. Competing risks analysis in mountain pine beetle dynamics. *Res. Popul. Ecol.* 15:183-192.
- _____. 1975. Interpreting some mortality factor interactions within mountain pine beetle broods. *Environ. Entomol.* 4:97-102.
- Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA Forest Serv. Res. Note INT-95. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Cole, W.E., G.D. Amman and C.E. Jensen. 1976. Mathematical models for the mountain pine beetle-lodgepole pine interaction. *Environ. Entomol.* 5:11-19.
- Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. *J. Forest.* 74:294-297.
- Craighead, F.C., J.M. Miller, J.C. Evenden and F.P. Keen. 1931. Control work against bark beetles in western forests and an appraisal of its results. *J. Forest.* 29:1001-1018.
- Daubenmire, R., and J.B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agr. Exp. Sta. Tech. Bull. 60. Pullman. 104 pp.
- DeLeon, D. 1935a. The biology of *Coeloides dendroctoni* Cushman (Hymenoptera-Braconidae) an important parasite of the mountain pine beetle (*Dendroctonus monticolae* Hopkins) Ann. Entomol. Soc. Amer. 28:411-424.
- _____. 1935b. A study of *Medetera aldrichii* Wh. (Diptera-Dolichopodidae), a predator of the mountain pine beetle (*Dendroctonus monticolae* Hopkins, Coleoptera: Scolytidae). *Entomol. Amer.* 15:59-91.
- Evenden, J.C., and A.L. Gibson. 1940. A destructive infestation in lodgepole pine stands by the mountain pine beetle. *J. Forest.* 38:271-275.
- Evenden, J.C., W.D. Bedard and G.R. Struble. 1943. The mountain pine beetle, an important enemy of western pines. U.S. Dept. Agr. Circ. 664. Washington, D.C. 25 pp.
- Furniss, M.M., and J.A. Schenk. 1969. Sustained natural infestation by the mountain pine beetle in seven new *Pinus* and *Picea* hosts. *J. Econ. Entomol.* 62:518,519.
- Gibson, A.L. 1943. Penetrating sprays to control the mountain pine beetle. *J. Econ. Entomol.* 36:396-398.
- Gray, B., R.F. Billings, R.I. Gara and R.J. Johnsey. 1972. On the emergence and initial flight behaviour of the mountain pine beetle, *Dendroctonus ponderosae*, in eastern Washington. *Z. ang. Entomol.* 71:250-259.
- Hopkins, A.D. 1909. Contributions toward a monograph of the scolytid beetles. I. The genus *Dendroctonus*. U.S. Bureau of Entomology Tech. Ser. 17. Washington, D.C. 164 pp.
- Hopping, G.R., and G. Beall. 1948. The relation of diameter of lodgepole pine to incidence of attack by the bark beetle (*Dendroctonus monticolae* Hopkins). *Forest. Chron.* 24:141-145.
- Hopping, G.R., and W.G. Mathers. 1945. Observations on outbreaks and control of the mountain pine beetle in the lodgepole pine stands of western Canada. *Forest. Chron.* 21:98-108.
- Klein, W.H. 1973. Beetle-killed pine estimates. *Photogramm. Eng.* 39:385-388.
- McCambridge, W.F. 1970. Spermatozoa in unemerged female mountain pine beetles, *Dendroctonus ponderosae* Hopkins. *Ann. Entomol. Soc. Ontario* 100:168-170.
- _____. 1971. Temperature limits of flight of the mountain pine beetle, *Dendroctonus ponderosae*. *Ann. Entomol. Soc. Amer.* 64:534-535.
- _____. 1974. Influence of low temperatures on attack, oviposition and larval development of mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Can. Entomol.* 106:979-984.

- McCambridge, W.F., and S.A. Mata, Jr. 1969. Flight muscle changes in Black Hills beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), during emergence and egg laying. *Can. Entomol.* 101:507-512.
- McCambridge, W.F., and G.C. Trostle. 1972. The mountain pine beetle. USDA Forest Serv. Pest Leaflet 2. Washington, D.C. 6 pp.
- McGregor, M.D., D.R. Hamel and R.D. Oakes. 1977. Evaluation of mountain pine beetle infestations, Thompson River Drainage, Plains District, Lolo National Forest, Montana, 1976. USDA Forest Serv., Northern Region Rep. 77-5. Missoula, MT. 8 pp.
- McGregor, M.D., D.R. Hamel, R.C. Lood, H.E. Meyer and S. Kohler. 1975. Evaluation of mountain pine beetle infestations, Lazier and Meadow Creek drainages, Plains District, Lolo National Forest, Montana. USDA Forest Serv., Northern Region Rep. 75-17. Missoula, MT. 11 pp.
- Nagel, R.H., D. McComb and F.B. Knight. 1957. Trap tree method for controlling the Engelmann spruce beetle in Colorado. *J. Forest.* 55:894-898.
- Parker, D.L. 1973. Trend of a mountain pine beetle outbreak. *J. Forest.* 71:698-700.
- Parker, D.L., and L.E. Stipe. 1974. Does the mountain pine beetle select and kill dwarf mistletoe-infected lodgepole pine? USDA Forest Serv. Insect and Disease Contr., State and Private Forest. Region 4. 5 pp. + append. (unpublished).
- Partridge, A.D., and D.L. Miller. 1972. Bark beetles and root rots related in Idaho conifers. USDA Plant Disease Rep. 56:498-500.
- Patterson, J.E. 1921. Life history of *Recurvaria*, the lodgepole pine needle miner in Yosemite National Park, California. *J. Agr. Res.* 21:127-143.
- Peterman, R.M. 1977. An evaluation of the fungal inoculation method of determining the resistance of lodgepole pine to mountain pine beetle (Coleoptera: Scolytidae) attacks. *Can. Entomol.* 109: 443-448.
- Pitman, G.B., J.P. Vité, G.W. Kinzer and A.F. Fentiman, Jr. 1968. Bark beetle attractants: *trans*-verbenol isolated from *Dendroctonus*. *Nature* 218:168-169.
- Powell, J.M. 1967. A study of habitat temperatures of the bark beetle *Dendroctonus ponderosae* Hopkins in lodgepole pine. *Agr. Meteorol.* 4:189-201.
- _____. 1969. Historical study of the relation of major mountain pine beetle outbreaks in western Canada to seasonal weather. Forest. Res. Lab., Info. Rep. A-X-23. Calgary, Alberta. 11 pp.
- Rasmussen, L.A. 1974. Flight and attack behavior of mountain pine beetles in lodgepole pine of northern Utah and southern Idaho. USDA Forest Serv. Res. Note INT-180. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 7 pp.
- Reid, R.W. 1958. Internal changes in the female mountain pine beetle, *Dendroctonus monticolae* Hopkins, associated with egg laying and flight. *Can. Entomol.* 110:464-468.
- _____. 1961. Moisture changes in lodgepole pine before and after attack by the mountain pine beetle. *Forest. Chron.* 37:368-375.
- _____. 1962. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of British Columbia. I. Life cycle, brood development, and flight periods. *Can. Entomol.* 94:531-538.
- _____. 1963. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of British Columbia. III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. *Can. Entomol.* 95:225-238.
- Reid, R.W., and H. Gates. 1970. Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*). *Can. Entomol.* 102:617-622.
- Reid, R.W., and D.M. Shrimpton. 1971. Resistant response of lodgepole pine to inoculation with *Europhium clavigerum* in different months and at different heights on stem. *Can. J. Bot.* 49:349-351.
- Reid, R.W., H.S. Whitney and J.A. Watson. 1967. Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue-stain fungi. *Can. J. Bot.* 45:1115-1126.
- Roe, A.L., and G.D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA Forest Serv. Res. Pap. INT-71. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 23 pp.
- Rudinsky, J.A. 1962. Ecology of Scolytidae. *Annu. Rev. Entomol.* 7:327-348.
- Rudinsky, J.A., M.E. Morgan, L.M. Libbey and T.B. Putnam. 1974. Antiaggregative rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. *Environ. Entomol.* 3:90-98.
- Safranyik, L., and C. Vithayasal. 1971. Some characteristics of the spatial arrangement of attacks by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), on lodgepole pine. *Can. Entomol.* 103:1607-1625.
- Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. *Can. Dept. Environ., Forest Serv., Pac. Forest Res. Cent. Tech. Rep. 1.* Victoria, B.C. 24 pp.
- _____. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue-stain fungi in western Canada. Pages 406-428 in D.M. Baumgartner (ed.). Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman.
- Schonherr, J. 1976. Mountain pine beetle: visual behavior related to integrated control. Pages 449-452 in Proc. XVIIth IUFRO World Congr., Div. II. Oslo, Norway.
- Shepherd, R.F. 1965. Distribution of attacks by *Dendroctonus ponderosae* Hopkins on *Pinus contorta* Douglas var. *latifolia* Engelmann. *Can. Entomol.* 97:207-215.
- _____. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Can. Entomol.* 98:507-518.
- Shrimpton, D.M. 1973. Age- and size-related response of lodgepole pine to inoculation with *Europhium clavigerum*. *Can. J. Bot.* 51:1155-1160.
- Shrimpton, D.M., and R.W. Reid. 1973. Change in resistance of lodgepole pine to mountain pine beetle between 1965 and 1972. *Can. J. Forest. Res.* 3:430-432.
- Stark, R.W., and J.A. Cook. 1957. The effects of defoliation by the lodgepole needle miner. *Forest Sci.* 3:376-396.
- Tackle, D. 1955. A preliminary stand classification for lodgepole pine in the Intermountain Region. *J. Forest.* 53:566-569.

Washburn, R.L., and J.A.E. Knopf. 1959. Mountain pine beetle conditions in the lodgepole pine stands of Forest Service Region 4. USDA Forest Serv., Div. Forest. Insect Res., Intermtn. Forest and Range Exp. Sta., Ogden, UT. 8 pp. + 9 maps (unpublished).

Whitney, H.S. 1971. Association of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) with blue-stain fungi and yeasts during brood development in lodgepole pine. Can. Entomol. 103:1495-1503.

Whitney, H.S., and S.H. Farris. 1970. Maxillary mycangium in the mountain pine beetle. Science 167:54-55.