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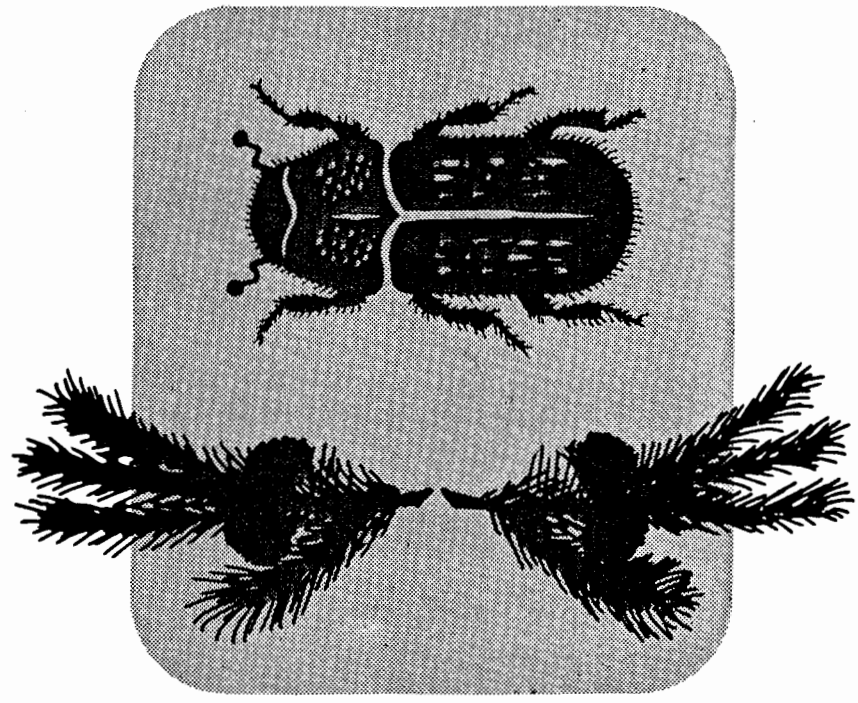


Ministry of
Forests

Honourable J.H. Heinrich
Minister

MOUNTAIN PINE BEETLE SYMPOSIUM PROCEEDINGS

Smithers, B.C., 1985



654848

PEST MANAGEMENT REPORT NUMBER 7

DYNAMICS OF 1-YEAR AND 2-YEAR LIFE CYCLE POPULATIONS
OF MOUNTAIN PINE BEETLE AND RELATED TREE LOSSES

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Introduction

The dynamics of mountain pine beetle (MPB) populations are closely tied to variations in their life cycle. Generally, beetle populations that have a 1-year life cycle are regulated by their food supply - - that is, lodgepole pine with large diameter and thick phloem. But beetle populations that have a 2-year life cycle, and those having both 1-year and 2-year cycles, are regulated by weather.

Life Cycles

Variations in the length of the life cycle set the stage for dynamics of MPB populations. Three situations exist:

1. Day-degree (a day-degree is 1 degree of temperature sustained for 1 day above the threshold temperature of development) accumulation is adequate for development to be completed consistently by late July and early August (1-year cycle).
2. Day-degree accumulation is inadequate for development to be completed in 1 year. The cycle usually is completed in late July and August of the second year (2-year cycle).
3. The transition zone between situations 1 and 2 (both 1-year and 2-year cycles).

Situation 1. Typically, at low elevations, the life cycle begins the last week of July and first week of August when new adult beetles emerge and attack green trees, constructing their galleries and laying eggs. Most of these eggs will hatch before the cold temperatures in late October and early November prevent additional egg hatch and larval development. Conditions are usually best for MPB when attacks by parent beetles occur in late July and early August and galleries average about 25 cm long. Under these conditions, most eggs will hatch and many larvae will reach second and third stages before cold temperatures set in and prevent further development. The larger the larvae - - that is, the later stages - - the less likely they will be killed by sub-

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freezing temperatures during the winter (Amman 1973; Reid 1962; Safranyik 1978). The estimated minimum day degrees needed for MPB to complete its life cycle in a single year is 833 (Safranyik 1978).

In areas where the 1-year cycle prevails, foliage of trees is bright orange within 1 year after trees are killed by MPB.

Situation 2. In Situation 2, weather usually is too cool for MPB to complete a generation in 1 year. This usually occurs at high elevations; the elevational level gets progressively lower as latitude increases (Safranyik et al. 1975). Adult beetles emerge and infest trees about the same time as those undergoing a 1-year life cycle, that is, late July and early August. However, cooler temperatures in these areas slow gallery construction and oviposition. Eggs take considerably longer to hatch. Eggs hatch after 10 days at a constant 20°C, compared to 37 days at a constant 10° C.

First and second stage larvae can feed and develop at temperatures as low as 2.2°C (McCmabridge 1974). However, by the times the eggs hatch, not enough day degrees above the developmental threshold temperature remain before winter for development to proceed to third and fourth stage larvae, which are most resistant to freezing. Higher threshold temperatures are required for development to proceed to later stages. For example, fourth stage larvae require temperatures higher than 10°C in order to pupate.

In Situation 2, many eggs fail to hatch and are killed by sub-freezing temperatures during the winter. Larvae usually enter the winter in first and second instars, which are less cold hardy than the larger third and fourth stage larvae. A high percentage of these larvae succumb to sub-freezing temperatures. Development of surviving larvae begins in the spring and continues until fall. At this time, beetles can be found as large larvae, pupae, callow adults, and a few mature adults. These enter the winter, and usually all pupae, a portion of the callow adults, and most of the mature adults are killed by sub-freezing temperatures the second winter of the 2-year cycle (Amman 1973; Reid 1962; Safranyik 1978). Those that survive will complete development and emerge to infest trees in July and August, thus completing their 2-year cycle. Mortality due to all causes can be high during the 2 years.

Timing of the life cycle is critical where the 2-year cycle occurs, and MPB are literally at the mercy of the weather. Either a slight delay or

a slight speed-up of the life cycle due to local temperatures can place the beetles in jeopardy. When timing is perfect for beetle survival, beetle production from the 2-year cycle can be high.

In areas where the 2-year cycle prevails, foliage of infested trees usually is light green with a few orange needles 1 year after beetle attack.

Situation 3: The third situation occurs in transition zones between low and high elevations. In these transition zones, both 1-year and 2-year life cycles are represented, frequently within the same infested tree. The difference sometimes occurs simply because a portion of a tree trunk receives more direct sunlight, thus more day degrees above the threshold of beetle development, and consequently, more rapid beetle development. -

In these transition zones, eggs laid early will hatch, and development and emergence will generally follow those of 1-year cycle beetles at lower elevations. Eggs laid late will hatch late, if at all, and will generally follow development and emergence of a 2-year cycle beetles. Any unhatched eggs in the fall are killed by cold winter temperatures. Often, beetles in the transition zone will develop to pupal, teneral adult, and adult stages during the first full summer. These stages enter the winter and are highly susceptible to winterkill (Amman 1973; Reid 1962; Safranyik 1978). Thus overall, heavy mortality among this cohort frequently occurs.

It is important to remember that local weather dictates these cycles and makes precise predictions difficult, if not impossible. For example, a series of warm seasons results in the typical 1-year cycle extending to higher elevations. Warmer than average seasons will result in increased beetle survival and, consequently, increased tree mortality. Cooler than average weather during beetle emergence and attack or during brood development can cause a shrinking of the beetle's range to areas of favourable weather (Safranyik 1978).

Host Tree

Although length of cycle sets the stage for dynamics of MPB populations, host tree dimensions play a dominant role, particularly in areas where optimal conditions prevail for the 1-year life cycle.

MPB-Host Tree Interactions - Phloem, the food of developing MPB larvae,

regulates dynamics of mountain pine beetle in areas optimum for the 1-year beetle cycle. Beetle production is directly related to phloem thickness when egg gallery density is high and adequate moisture for beetle development is available throughout the life cycle. Low density of egg galleries will result in low phloem use, and beetle production will be directly related to gallery density (Amman 1972).

At very low densities of attacks and egg galleries, and when the rate of attack is low, beetles will be pitched out or galleries inundated by pitch, resulting in no beetle production and the tree not being killed. Even if the tree is killed, beetle brood may not be produced because of resin in the bark and galleries. The interactions of attacking MPB, blue stain fungi introduced into the tree by MPB, and the host tree have been described (Reid et al. 1967; Safranyik et al. 1975; Shrimpton 1978).

In some cases, phloem may be thick enough for high brood production, but moisture levels in the host tree may fall below that required by the developing beetles, particularly in lodgepole pine harbouring MPB having a 2-year cycle.

Both phloem thickness and moisture level are related to diameter of lodgepole pine (Amman 1978). Consequently, a fairly high correlation exists between diameter and brood production in populations having a 1-year cycle. The close association of beetle production to diameter of lodgepole pine suggests why MPB show such a strong preference for large trees during an outbreak.

The exact mechanism MPB use to select large trees has not been identified. Sight was suggested by Shepherd (1966), whereas Safranyik et al. (1975) suggested random selection involving the greater surface area of large trees. Another possibility is olfaction, whereby MPB detect the greater terpene quantities found in phloem of large rather than small diameter trees and in thick rather than thin phloem (Cole et al. 1981).

Life Cycle-Tree Loss Interactions - Not surprisingly, tree losses are related to the life cycle of MPB. When beetle populations build to epidemic proportions, tree losses are heavy where the 1-year life cycle prevails. Losses generally are progressively less as elevation and latitude increase, simply because beetle survival declines as the beetles infest trees where part of the population completes the life cycle in 1 year and the remainder requires 2 years. Least tree loss usually will occur where the life cycle requires 2 years. As an example, on the north slope of the Uinta Mountains in northern Utah

during a large MPB infestation from 1955 to 1963, losses of lodgepole pine 22.9 cm diameter at breast height (dbh) and larger were 36.5 percent at 2,650 m elevation, but only 1 percent at 3,050 m or greater. The lowest elevation for lodgepole pine is about 2,590 m in this area. Losses in northwestern Wyoming showed tree losses similar to those in northern Utah when adjusted for latitude (Amman et al. 1973). In northwestern Wyoming, losses of trees ranged from 33 percent at 2,440 m elevation to 10 percent at 2,835 m (Amman and Baker 1972).

During periods of several years when temperatures are warmer than average, 1-year life cycles become more prevalent in the transition zone between 1-year and 2-year cycle beetles, permitting greater beetle survival and hence greater tree losses. An example is whitebark pine losses between 2,740 and 3,050 m elevation in northwestern Wyoming (Baker et al. 1971): 20 percent of the trees were killed and then the infestation died even though potential for infestation continued to be great because of the large diameter trees with thick phloem. Trees killed the last year of the infestation revealed many beetle pupal chambers but no emergence, thus suggesting the beetle cycle was extended because of cool weather. Beetles entered winter in stages very susceptible to winterkill, and most of the population was killed.

Another aspect of MPB dynamics is beetle emigration. Dynamics of local populations can be greatly altered by emigration of large numbers of beetles from nearby stands, especially those at lower elevations. Beetle populations are more likely to build up at low elevations, and many more beetles emigrate to higher elevations than vice versa. The emigration of large numbers of beetles increases the amount of mortality above what would normally be expected from resident populations at mid to high elevations. Some areas might never have an infestation if it were not for emigrating beetles that increase the resident population, thus making an outbreak possible.

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