Mountain Pine Beetle: Biology Overview

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ABSTRACT: The general biology and ecology of the mountain pine beetle in lodgepole pine forests was reviewed with emphasis on insect-host interaction and causes of outbreaks. During endemic periods the beetles normally infest trees of low vigor such as injured, diseased or otherwise weakened trees and windfalls, usually in association with secondary bark beetles. Attack success in such trees tends to be high even at low attack densities but brood production is usually low. When the beetle populations switch from endemic to epidemic, the beetles infest proportionately more of the larger diameter trees in the stand. Many of these trees have thick phloem. Normally, such stands are more than 60 years old and the average diameter for trees 10 cm and larger is about 20 cm. Precisely which factors are responsible for triggering outbreaks is uncertain; however, all factors that would significantly reduce host resistance or increase the size of the beetle population above a threshold necessary for colonizing at least some of the large diameter trees with thick phloem could trigger outbreaks.

INTRODUCTION

The mountain pine beetle, Dendroctonus ponderosae Hopk., (Coleoptera: Scolytidae), a native insect in the pine forests of western North America, has been referred to as the most destructive bark beetle (Wood 1963). In areas where the beetle is common, it is the most important pest of mature lodgepole pine, Pinus contorta var. latifolia Engelm. During endemic periods, populations are innocuous, and only a few scattered infested trees are to be found. However, during outbreaks, which occur at irregular intervals and may persist for periods of 5 to 20 years, more than 80% of the host trees with a DBH of 10 cm or more may be killed over large areas.

In recent years, the losses caused by the mountain pine beetle, particularly in lodgepole pine, have been devastating. In British Columbia, for example, losses resulting from the 1983 attacks alone were estimated at 41 million trees killed in infested areas totaling 482,000 ha (Wood and others 1985). In infested stands managed for commercial production, the value of losses during epidemics is usually considerably greater than that indicated by the volume loss because most mortality is among the larger diameter trees. Outbreaks usually affect management plans and may create marketing problems. Outbreaks change stand density, age and species composition of stands, the size distribution of pine, and aesthetic values. Outbreaks also increase fuel loading, and hasten succession to the climax forest type.

The objectives of this overview are to provide a brief account of the population biology of the beetle in lodgepole pine forests, to highlight key features, and to identify gaps in the knowledge as a background to the main theme of the symposium. For more detailed descriptions of the population biology of the mountain pine beetle the reader is referred to Amman and Cole (1983) and other publications cited in this paper.

BIONOMICS

Geographic Distribution and Host Trees

The mountain pine beetle occurs in forests from northern Mexico (latitude 31°N) to northwestern British Columbia (latitude 56°N) and from the Pacific Ocean east to the Black Hills of South Dakota. It occurs up to about 750 m near the northern limits and up to about 3650 m near the southern limits of the beetles' range (Safranyik 1978).

The main hosts are lodgepole pine, ponderosa pine (P. ponderosa Laws.), western white pine (P. monticola D. Don), and sugar pine (P. lambertiana Douglas) (Amman 1978). This list of principal hosts is based on the commercial impact and intensity of epidemics. Other species of pine, including several exotic species within the range of the beetle, are infested and killed. Some non-host trees (e.g., Picea) are occasionally attacked and killed, but populations are usually not maintained in such trees.

Life Cycle

In the optimal portion of its range, the mountain pine beetle normally completes one generation per year. Brood adults typically mature in July. Young beetles are dark brown to black, and range in length from 3.5 to 7.5 mm. In order to complete maturation, they feed on the inner bark and on spores of blue stain fungi and yeasts which line the walls of the pupal chambers. During
maturation feeding the flight muscles increase in size (Reid 1958) and the mycangium (a special structure on the head) becomes charged with fungal spores, which ensures transport of the fungi to new trees (Safranyik and others 1979).

Ambient temperatures are instrumental in determining the onset of emergence, the length of the emergence period, diurnal rates of emergence, and flight activity. Emergence normally begins after several days of warm, dry weather, but there is no apparent relationship between the duration of such warm periods and the onset of emergence (Safranyik 1978). Emergence and flight start at about 16°C, and rates of emergence are reduced at temperatures greater than 30°C. Peak daily emergence normally occurs during a period of 2-3 hrs in mid-afternoon when the temperature exceeds 20°C. The median dates of annual emergence can vary by as much as 1 month, but normally vary by 10 days or less. The period of peak emergence normally lasts a week to 10 days, but can vary from a few days to 3 weeks.

Beetles that do not disperse from the stand in which they develop usually locate suitable host trees within 2 days of emergence, but are capable of searching for several days. In release-recapture experiments using marked beetles in central British Columbia, one beetle was trapped at a baited tree 11 days after release more than 1 km from the release site. In the absence of pheromones, beetles tend to disperse downwind, mainly below the canopy in the clearbole zone, and search upwind only after an attractive pheromone plume is encountered. Very little is known about beetle flight above the canopy (other than that it occurs), or about long-range dispersal. Collection of mountain pine beetles in high-elevation snowfields in eastern British Columbia, Alberta, Washington (Furniss and Furniss 1972), and circumstantial evidence from elsewhere in the United States (Borden and others 1943), indicates that long-range dispersals occur during outbreaks and may be significant factors in the spread of epidemics.

Searching adult beetles usually select and attack living trees during late July or early August. Fresh felled trees or windfall may also be attacked. Searching beetles land at random on host and non-host trees, hence one of the dominant theories of host selection states that initial attack by the pioneer beetles occurs at random, as opposed to being directed by some stress-induced “primary attraction.” There is evidence, however, that dispersing adults land preferentially on lodgepole pines suffering from injury or disease (Gara and others 1984). As the pioneer female beetles bore into the bark, they release semiochemicals which attract both sexes and result in the aggregation of beetles on the focus tree, and eventually to close-range redirection of responding beetles to nearby trees (Borden and others 1986). In lodgepole pine, the beetles are strongly oriented to large-diameter trees. Vision is believed to play a key role in locating the host (Shepherd 1966). In addition to semiochemicals, physical and physiological host factors and beetle population size are thought to be important determinants of the density and distribution of attacks on the bole. On individual trees, mass attacks are normally completed within 1-2 days.

During gallery establishment, the beetles carry spores of the blue stain fungi, yeasts, and bacteria. These spores slough off along the walls of the galleries and grow in the living tissues. Although the roles of these organisms are not completely known, the blue stain fungi quickly invade and kill live cells, thereby preventing them from producing resin, which is the main defense of the tree against invasion by the beetle-microorganism complex. Blue stain fungi also effect a rapid reduction of moisture in the sapwood.

The female beetle bores through the bark and constructs an egg gallery averaging 25-30 cm in length in the phloem parallel to the grain. Mating takes place in the lower end of the egg gallery. The male often leaves after mating. The female plugs the gallery entrance and packs the lower end with boring dust. Usually 60-80 eggs, about 2 per cm, are laid singly in niches cut into the sides of the gallery. The eggs usually hatch in 1-2 weeks and the larvae feed in the phloem, roughly at right angles to the gallery. The larvae normally become dormanit in late October or November and begin feeding again in April. Pupation takes place during mid to late spring and development is completed during late June to mid July.

There are exceptions to the 1-year cycle described above, and they depend primarily upon climate and weather (Safranyik 1985). The most common exceptions occur when many parent beetles establish two broods in a single warm, dry year, or in very cool years or at high elevations and latitudes where a proportion of the brood may require more than 1 year to complete development.

**Brood Survival**

Systematic studies of the nature and effect of factors affecting brood survival within and among trees have only been done on high endemic, epidemic, and postepidemic populations of the mountain pine beetle. Consequently, we have a poor understanding of brood survival and mortality factors in endemic populations.

It is generally believed that the same factors of mortality operate in both endemic and epidemic populations; however, the relative impact of some of these factors on brood survival, alone or in interaction with other factors, is considerably different at the two population states. For example, during endemic periods, often due to the low rates of attack, low attack densities, and perhaps also because of higher tree resistance, much higher proportions of unsuccessful attacks and higher brood mortality can occur than during epidemic periods.

Several life table studies from the United States (Amman and Cole 1981) suggest that during epidemics none of the natural, within-tree mortality factors investigated (competition,
predators and parasites, pathogens, drying of the bark, and resinosis) regulate beetle populations; survival of beetles at these times is more closely related to tree diameter and phloem thickness than any other factor. Reid (1963), based on population studies of a small infestation in southeastern British Columbia, found that tree diameter was the most important factor determining beetle survival.

The life table studies corroborated previous work (Cole 1974, 1975) showing that in areas where mountain pine beetle has mainly a 1-year life cycle, winter temperatures and drying of the phloem are the two most important causes of within-tree mortality and their effects are inversely related to tree diameter. With the exception of the predaceous fly, Medetera, beetle mortality resulting from predators, parasites, disease and resinosis was considerably less than that recorded for temperature and bark drying; Medetera showed a density dependent response over time. Reid (1963) too showed the importance of low temperature and subcortical moisture for affecting brood survival within trees, but he also found competition (in terms of egg gallery density) and resinosis to be important factors.

In general, mortality factors that are most important during the 1-year life cycle cause similar levels of mortality when more than 1 year is required to complete a generation (Schmitz 1985). However, at higher elevations and northern latitudes, cool temperatures that delay development and increase winter mortality replace food (phloem thickness) as the main factor limiting population survival.

In the life table studies referred to above, about one-half of total mortality was caused by unknown factors. This is a rather typical result for bark beetle population studies in general and emphasizes the need for better knowledge of mortality factors and improved experimental procedures.

Mortality within trees is just one component of total mortality in each bark beetle generation. We have inadequate knowledge of mortality among emerged beetles during the dispersal-host finding phase. This mortality may be 60% or higher, depending on population levels in relation to host availability, weather, and other factors, and may be one of the key factors limiting population growth at endemic and postepidemic levels.

Epidemiology

Under endemic conditions the mountain pine beetle often infests trees of poor vigor which were first infested by secondary bark beetles such as Ips and Pityophthorus spp. (Amman 1978), or attack injured, diseased, defoliated or otherwise stressed trees, and windfalls. High endemic or incipient infestations, which characteristically kill small groups of trees, are often found in draws, gullies, along edges of stand openings, or in areas subjected to soil compaction or wide fluctuations in the water table (Safranyik and others 1974). These incipient infestations may develop into outbreaks in a few years or may continue, especially in lodgepole pine stands of poor site quality, until most of the large-diameter pine component are killed. A major exception to this pattern of outbreak development occurs when local populations are augmented by the influx of large numbers of beetles from nearby infested stands, especially those at lower elevations. In this case, low populations and damage levels in a given year in some areas could be followed by epidemic infestations in the following years.

Outbreaks in lodgepole pine last from 3 to 20 years, range in size from a few hectares to hundreds of square kilometers, and invariably deplete the large-diameter component of stands (Safranyik and others 1974). In areas with cooler climates, such as areas at high elevations and northern latitudes, the intensification and spread of outbreaks tend to be less but outbreaks may persist longer than in areas within the beetle's optimum range.

During mountain pine beetle epidemics, large populations of secondary bark beetles usually build up in the tops and other sections of the bole and large branches of trees killed by mountain pine beetle. Following the decline of mountain pine beetle epidemics, these secondary bark beetles, especially Ips and Pityogenes, attack and kill some of the remaining pines, mostly in the smaller diameter classes. Occasionally, tree killing can be extensive, but it rarely lasts longer than 1-2 years.

CAUSES OF OUTBREAKS

Although a great deal is known about the population ecology of the mountain pine beetle in lodgepole pine, our knowledge of how the transition from endemic to epidemic populations occurs is uncertain.

In natural lodgepole pine stands, outbreaks usually occur when the average age of the pine component is about 80 years or more and the average diameter of the pine greater than 10 cm is about 20 cm. Outbreaks usually develop in areas that are climatically most suited for beetle development and survival. Proportionately more of the large diameter trees are killed (Hopping and Beall 1948; Cole and Amman 1969). Brood production from infested trees is directly proportional to the thickness of the inner bark (Amman 1972; Berryman 1976).

Resin production in response to invasion of the beetle-blue stain fungi complex is a measure of host resistance to attack (Reid and others 1967), and is normally greatest in the largest diameter, fastest growing trees at a given age and site quality (Shrimpton 1973). At the stand level, resistance tends to be the greatest near the culmination of current annual increment (between 40 to 60 years, depending on site quality) and declines rapidly with increasing age (Safranyik and others 1975). The culmination of stand resistance corresponds to the attainment of the greatest basal area, biomass, and nitrogen.
accumulation in lodgepole pine ecosystems following a stand-replacing fire (Fahey and Knight 1986).

As average phloem thickness is related to basal area growth during the preceding 6- to 10-year period (Shrimpton and Thomson 1985), both phloem thickness and resinosis are directly related to tree or stand vigor. Consequently, there is an apparent paradox in our information: if epidemic infestations can only be maintained in large diameter trees with thick phloem and if these are also the trees that tend to be the most resistant, how then can the switch from endemic to epidemic occur at all? We do not have definite answers, but a plausible explanation is as follows: It is generally acknowledged that the degree of host response to attack and host suitability for mountain pine beetle reproduction is dependent on beetle numbers, at least at low population levels (Raffa and Berryman 1983). Consequently, as the beetle population increases, trees of higher resistance become available for colonization and outbreaks are triggered when a threshold of beetle numbers is attained that can successfully colonize large diameter trees with thick phloem (Berryman 1978). This beetle population threshold may be exceeded in stands suffering from temporary weakening such as that caused by drought or defoliation, or from decline of tree vigor following attainment of physiological maturity (reduction of phloem thickness follows growth reduction with considerable time lag). The threshold may also be exceeded when endemic subpopulations within scattered weakened trees are close enough to concentrate attacks on one tree or a small group of trees of medium to large diameter and moderate to thick phloem (Amman 1978), or when large numbers of beetles disperse into a stand from other infestations. If weather conditions are unfavorable for the beetle, these incipient infestations will decline and several years may elapse before conditions for the development of an epidemic occur again.

Better understanding of outbreak development is of great practical importance for development of better systems for predicting outbreak hazard, and for development of more effective methods of management to reduce losses. More knowledge is urgently needed on population dynamics in the endemic state, qualitative differences between endemic and epidemic beetle populations, primary attraction and chemical communication, the role of host tree injury and stress factors in triggering outbreaks, and the role of dispersal in the spread of epidemics.

REFERENCES


Hopping, G.R.; Beall, G. 1948. The relation of diameter of lodgepole pine to incidence of attack by the bark beetle (Dendroctonus monticolae Hopkins) Forestry Chronicle. 24: 141-145.


