Mountain Pine Beetle Epidemiology in Lodgepole Pine

Les Safranyik

Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre,
506 West Burnside Road, Victoria BC V8Z 1M5

Abstract

The following brief synthesis of mountain pine beetle epidemiology is based on host-beetle interaction. In the first part I briefly describe the relationship between the dynamics of lodgepole pine and mountain pine beetle. The second part describes the phases in the infestation cycle and their main characteristics. This synthesis is based on published information on infestation behaviour in western Canada, augmented by personal experience relating to the subject area.

Lodgepole pine stand dynamics and the epidemiology of the mountain pine beetle

The mountain pine beetle is native to the pine forests of western North America. As a consequence of the close interaction between the mountain pine beetle with its associated blue stain fungi and lodgepole pine (Safranyik et al. 1975), mountain pine beetle epidemiology is a reflection of the population dynamics of lodgepole pine.

The female beetles require a minimum bark thickness (Fig. 1) and the presence of bark scales and ridges in the bark to establish successful attacks (Safranyik 1971). Hence, the potential attack sites on the bole are largely determined by the density and distribution of these bark characteristics. Young trees with thin bark and small diameter (dbh) older trees (Fig. 2) are rarely attacked or sustain lethal attacks. Because beetle brood production is much lower in small dbh trees compared with large dbh trees (Fig. 3), populations breeding in small trees grow at much slower rates compared to large trees.

Attacks by the mountain pine beetle are mediated by blue stain fungi. The spores of blue stain fungi are carried into the tree by the beetles. The spores germinate quickly, penetrate and kill living cells in both the phloem and xylem (Safranyik et al. 1975). This process aids the establishment of successful attacks in the tree. Trees respond to the invasion by the beetle-blue stain complex with a flow of liquid resin from resin ducts (primary resin) damaged by the attacking organisms and production of additional resin in living cells next to the damaged area (secondary resin). When resin production is rapid and massive and the phloem and sapwood next to the wound becomes impregnated by resinous substances, beetles are killed or repelled and the fungi are confined and die.
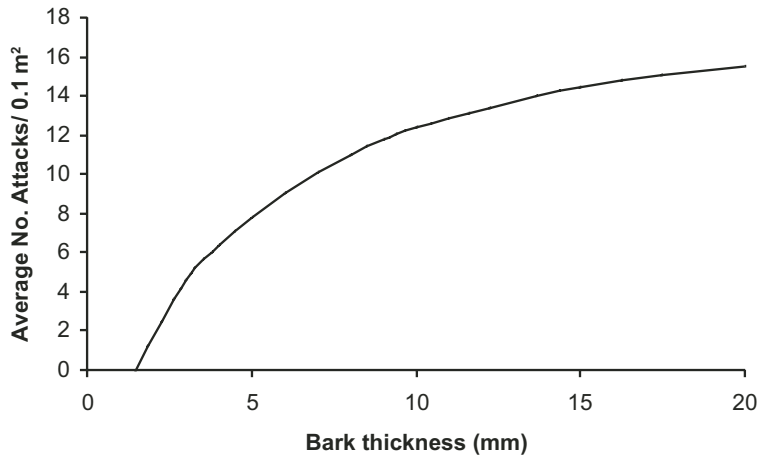
Figure 1. Example of the relationship between the combined thickness of the bark and phloem and the average number of mountain pine beetle attacks in lodgepole pine. Horsethief Creek data, 1966. (Redrawn from Safranyik 1971.) Minimum bark thickness for attack averaged 2.4 mm.
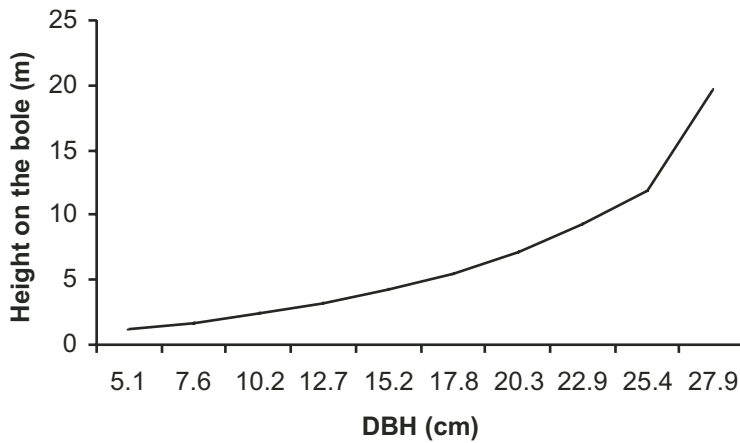

Figure 2. Relationship between the average height of the 2.4 mm total bark thickness and dbh on bole of lodgepole pine. (From Safranyik 1968.) The height on the bole corresponding to ca 2.4-mm-thick bark represents the theoretical maximum attack height.
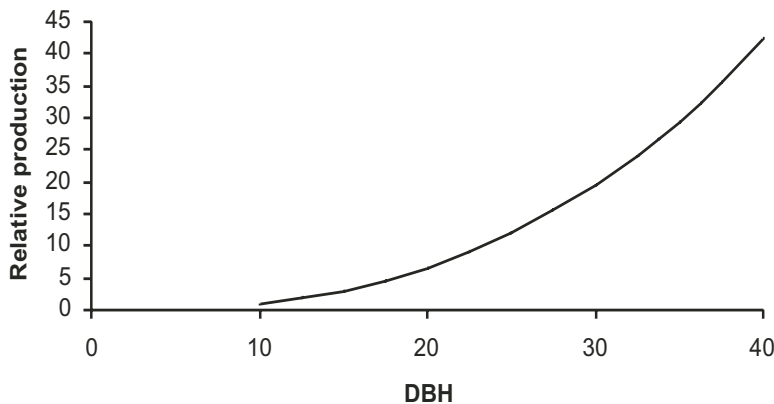

Figure 3. Brood productivity of lodgepole pine trees of different dbh relative to a 10-cm-dbh tree. (Based on Safranyik et al. 1975 and Safranyik 1988.)

Host resistance increases with age, approximately in parallel with the increase in the Current Annual Increment (CAI) (Safranyik et al. 1975) and culminates at an age when natural stands attain maximum stocking on all physiographic sites. Near the culmination of CAI, on at least the better sites, many trees are of sufficient size and density to sustain an increasing beetle population. However, mainly due to high tree resistance, attacks at this stage of stand development are intermittent and confined to a few scattered, weakened or damaged trees.

The increased competition among trees for resources (that follows the attainment of maximum density and the culmination of CAI), coupled with a decline in tree resistance, increases the abundance in space and time of low vigour trees in most unmanaged stands. These trees are frequently attacked by a number of secondary bark beetle species. However, some of the trees will be co-attacked by mountain pine beetle. This time period marks the beginning of the establishment of sustainable endemic mountain pine beetle populations in at least some of the stands. Since these mountain pine beetle populations exist mainly in suppressed and otherwise weakened trees, stand hygiene is an important factor in the maintenance of endemic beetle activity.

A large number of factors interact to restrain the potential of mountain pine beetle populations from increasing. These include insect predators and parasites, avian predators, mites, nematodes, disease, competition for food and space, tree and stand factors, and climate and weather. During endemic periods, populations suffer very high levels of mortality from a combination of these factors, so that reproduction and mortality tend to balance. Some of the most important mortality factors are related to the scarcity and patchy distribution of suitable trees, host quality and inter-specific competition. The brood trees are frequently confined to the smaller diameter classes; trees with thin phloem that have been attacked by secondary bark beetle species, both prior to and following mountain pine beetle attacks. Attacks by some of the secondary species occur during the late spring period. This, combined with small tree size, leads to faster drying and deterioration of the phloem compared with either trees of larger size or trees that had been attacked only by mountain pine beetles later in the season. Also, as the sub-cortical cooling rate during the winter is inversely related to tree size, winter mortality is greater in small diameter trees.

Incipient infestations, which are the beginning stages of an outbreak, develop when local beetle populations have grown to a minimum size sufficient to successfully mass attack the average large diameter component of stands. Because tree resistance tends to increase with tree diameter (Shrimpton 1973), the main factor(s) for the development of incipient populations are those that affect either a decline in tree resistance or an increase in beetle population size. The decline in tree resistance can be either temporary such as following periods of drought, or permanent due to senescence or disease. A number of consecutive years with warm and dry weather during the flight and dispersal period combined with mild winters favour sustained increases in beetle populations. Hence, a decline in host resistance combined with favourable conditions for beetle establishment and survival are thought to be the main factors for the development of incipient infestations.

Outbreaks exist at the landscape level. Outbreak populations develop because of the growth and expansion in space and time of incipient populations and local endemic populations, and long-range dispersal. Large areas of susceptible host, such as mature lodgepole pine, combined with continued, favourable weather conditions for beetle establishment, development, and survival are the main causes of outbreaks. During outbreaks the following factors are the main determinants of yearly changes in population and damage levels: 1) size of the parent beetle population; 2) stand characteristics such as species composition, density, age and diameter distribution; 3) the spatial distribution of stands of different susceptibility; and 4) weather factors. Outbreaks are loosely synchronized over much of the distributional range of the mountain pine beetle. This may be due to the so-called Moran effect (Moran 1953). This theory states that if regional populations are under the influence of the same density-dependent factors, they will be correlated under the influence of density-independent factors such as the effects of climate and weather.

Outbreak populations collapse primarily from one or a combination of the following two factors: 1) unseasonably cold weather conditions during the late fall to early spring period; 2) the large diameter susceptible host component of stands has been killed. In the final stages of population decline, increased mortality from natural enemies and competitors can have an impact. At the landscape level, within the outbreak areas, the relative severity of mortality in the various stands will generally reflect tree and stand susceptibility as defined in Shore and Safranyik (1992). Mortality will generally be confined to the larger diameter classes. Locally, however, most of the host trees can be killed down to 8-10 cm dbh.

The course of epidemics

We recognize four phases in the population cycle of the mountain pine beetle: endemic, incipient epidemic, epidemic and post-epidemic (declining) populations. These four phases represent distinct differences in beetle population size and damage potential. There is also some suggestion of changes in beetle population quality during the population cycle. However, this aspect of beetle biology is insufficiently understood and needs further study.

Endemic populations are those that exist between outbreak collapse and the development of incipient populations. Endemic populations are in a dynamic balance with their environment in which the host population appears to be the most important. For populations to maintain this balance (to remain more or less static) in time and space for several generations, they must suffer very high levels of generation mortality from a combination of factors, such as host resistance and nutritional quality, natural enemies, competitors, and weather factors. The following example will illustrate this point. Female beetles lay about 60-80 eggs, about two-thirds of which are female (Reid 1962). Based on this sex ratio, an average of 60 eggs per female parent represents 40 potential female offspring. Only one of these eggs needs to become an adult to establish a successful attack and replace the parent female. Hence, in order for the population to remain static between successive generations, brood mortality must be in the order of $(39/40) \times 100 = 97.5\%$.

Endemic beetle populations have the following characteristics:
- Infest weakened and decadent trees;
- Frequently found in trees attacked by secondary bark beetle species. Hence, trees containing mountain pine beetles can be very difficult to locate on the ground and even from the air since many of these trees will be in the intermediate to suppressed crown classes, the faded crowns of which are partially hidden below the crowns of taller, uninfested trees;
- Currently attacked trees are often not located near brood trees;
- There is no obvious relationship between the probability of attack and tree dbh; and
- Yearly tree mortality is normally less than volume growth.

Historically, in British Columbia, the duration of the endemic phase varied between 10 to 15 years.

Incipient epidemic populations are those that can successfully mass attack the average large diameter tree in a stand. The main factors responsible for the development of incipient epidemic populations have been described. The minimum beetle population size necessary for colonizing the larger diameter component in a stand is called the epidemic threshold (Berryman 1982) population level. In most situations, incipient epidemic populations are the beginning stages of epidemics. Exceptions are situations where stands suffer from temporary weakening such as drought conditions in younger stands. In these situations incipient populations usually decline to endemic levels once the stands have recovered.

Incipient epidemic populations have the following characteristics:
- Most infested trees are in the larger diameter classes;
- Clumps of infested trees are scattered and confined to some stands;
- The infested clumps vary considerably in size and number from year to year but tend to grow over time; and
- Frequently, the groups of infested trees first appear in the following situations: draws and gullies, edges of swamps or other places with wide fluctuations in the water table; places where lodgepole pine is growing among patches of aspen, perhaps indicating the presence of root disease; dry, south and west-facing slopes.

Initially, incipient populations grow relatively slowly, so that averaged over a number of generations the rate of increase may not exceed twofold. As a consequence, there may not be much noticeable change in infestation levels for five or more years. In some cases, infested spots may even die out for a year or two. Eventually, however, in most situations there will be sustained yearly growth in beetle population size with corresponding increases in the size and number of infested spots. Spot infestations will coalesce into larger patches and new infested spots may develop in adjacent stands. This situation marks the beginning of the onset of epidemic level infestations. This pattern of beetle population growth is typical in areas that contain large contiguous areas of mature lodgepole pine.

Epidemic populations result from the growth of incipient populations in time and space over the landscape as a result of sustained favourable weather for beetle establishment and survival combined with an abundance of susceptible hosts. Epidemic populations have the following characteristics:
- Resilient to large proportional losses through natural mortality;
- Generation mortality is usually in the range of 80% - 95%, corresponding to potential rates of population increase of twofold to eightfold. The usual annual rate of increase, however, is twofold to fourfold when measured over the entire epidemic area.
- Infestations are widespread and exist at the landscape level.
- There are usually large annual increases in both infested areas and numbers of infested trees.

During epidemics in unmanaged stands, tree mortality is usually proportional to tree dbh above a certain minimum value. The minimum dbh where little or no mortality occurs varies with stand characteristics and infestation intensity, but is usually near 10 cm. The expected rate of mortality above this minimum dbh is 1.5% - 4.0% with every 1 cm increase in dbh. As a consequence, trees in the larger dbh classes are often severely depleted. Expressed in terms of the number of trees killed in a dbh class in a given area (N_k), the relationship between mortality and dbh class (D_c) is as follows:

$$N_k = 0, D_c \leq a/r$$
$$N_k = N_c\,(\,rD_c - a), \ a/r < D_c < (1+a)/r$$
$$N_k = N_c, D_c \geq (1 + a)/r$$

where N_c, a, and r, respectively, are the number of trees in dbh class D_c, a = constant; therefore the minimum dbh for killed trees is a/r, and r = mortality rate per unit dbh above a/r. The other symbols were previously defined. This relationship indicates that tree mortality is a function of both dbh class and the number of live trees within that dbh class. Interestingly, the same relationship can be derived based on an assumption of random search by the attacking beetles and landing proportional to the silhouette (dbh) of trees above a minimum size (Safranyik et al. 2004).

Outbreaks can re-occur in the same stands until the large dbh component has been severely depleted. Suppression of infestations at this population phase is very difficult due to the very large proportion of the beetle population that must be destroyed annually to affect a decline in infestation trend. Using the

number of infested trees as an index of beetle population level and the ratio of the number of currently infested trees ("green attack") to the number of trees infested by the parent generation of beetles ("red attack"), as an index of beetle population trend, the rule of thumb for suppression is as follows:

$P > 100\{1 - (R):(G)\}$ where P is the percent of infested trees treated, R is red attack and G is green attack.

For example, if the ratio of green attack to red attack were three-fold, more than 67% of the infested trees would need treatment to affect a decline in population and damage levels. It is very likely that a similar level of control effort would have to be maintained for several years until the infestation collapsed.

Depending primarily on the cause of epidemic collapse, the size distribution of trees attacked by post-epidemic populations may be different from that attacked during epidemics. For example, following sudden major declines in beetle numbers due to lethal low temperature events, the residual beetle population generally breed in the same type of trees that were attacked prior to the decline. However, due to the much lower beetle numbers, many trees may only be partially attacked and in some fully attacked trees, the rate of accumulation of attacks will be reduced. Consequently, brood survival will be reduced due to increased host resistance. Inter-specific competition for food and space is another major factor impacting beetle survival (Safranyik et al. 1999). When the collapse of epidemics is primarily due to local depletion of suitable hosts, subsequent generations of beetles breed in trees of reduced nutritional quality or increased resistance, and will probably suffer mortalities of similar magnitude as those occurring in endemic populations.

In British Columbia, the historical average duration of epidemics is approximately 10 years, normally lasting more than 5 years; the longest recorded epidemic continued for 18 years. Based on the assumption of mean outbreak duration of 10 years, minimum duration of 5 years, and a geometric temporal distribution of outbreak terminating events, two models were developed for predicting the probability of collapse as a function of years from the start of the outbreak (Fig. 4). Model 1 is based on a fixed expected probability of outbreak collapse in year i (P) for years 6 to 18 given that it has not collapsed prior to year i In Model 2, the expected probability of collapse increased with years after year 6.

$$\text{Model 1: } Y1_i = 0, i \leq 5$$

$$Y1_i = \sum_{j=1}^{n} P(1-P)^{(j-1)}$$

i = years from the beginning of the outbreak; $Y1_i$ = the cumulative distribution of the probability of outbreak collapse as a function of years from the start of the outbreak. $n = (i - 5)$; P = expected (average) probability of outbreak collapse $(1/(10-5) = 0.2)$ for years 6-18; $\sum$ = summation sign.

In Model 2, P_j is calculated as the product of the average probability of outbreak collapse (P in Model 1) and the ratio $(m + 1 - i)/(m - i)$, where m = maximum observed outbreak duration (18 yrs.).

$$\text{Model 2: } Y2_i = 0, i \leq 5$$

$$Y2_i = \sum_{j=1}^{n} \left[\left\{ \prod_{k=1}^{j} (1-P_{k-1}) \right\} P_j \right]$$

P_j = probability of outbreak collapse in year j given that it has not occurred in preceding years; $\prod$ = product sign, $Y2_i$ = the cumulative distribution of the probability of outbreak collapse as a function of years from the start of the outbreak and the other symbols are as stated earlier.

Figure 4 indicates that based on Model 2, the probability of the collapse ($Y2_i$) of the current outbreak next year and 3 years from now is approximately 83% and 94%, respectively, assuming that it started in 1993. These probabilities are approximately 12% higher than the corresponding estimates based on Model 1 ($Y1_i$). Models 1 and 2 were based on outbreak characteristics preceding the current of outbreak. Sustained changes in climatic conditions may alter the course of current and future outbreaks.
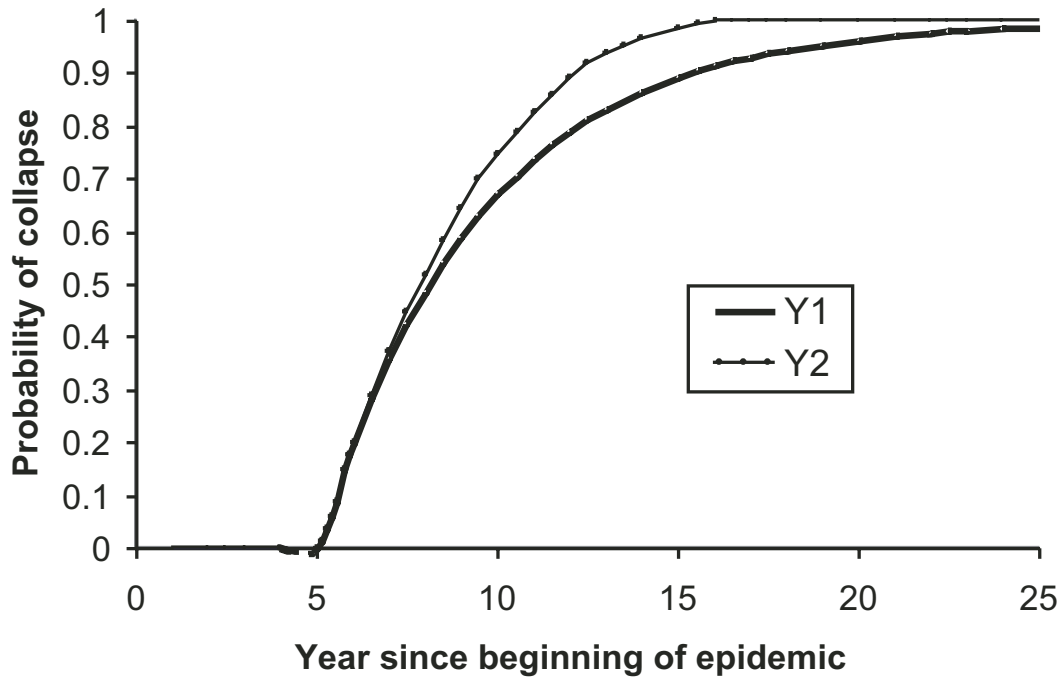

Figure 4. Predicted probability of outbreak collapse as a function of years since the start of the outbreak. Curves Y1 and Y2 are based on Model 1 and 2, respectively (see text for details).

Management implications

The interactions between lodgepole pine and the mountain pine beetle with its associated blue stain fungi have the following management implications:

- Long-term management should focus on lodgepole pine, not the mountain pine beetle.
- In spite of the best efforts of prevention, outbreaks will occur which require efficient control strategies and tactics.
- Effective direct control programs are based on early detection and implementation, and continuous commitment.

Les Safranyik is Emeritus Research Scientist with the Canadian Forest Service, Pacific Forestry Centre.

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