

Part 1

Biology



Chapter 1

The biology and epidemiology of the mountain pine beetle in lodgepole pine forests

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Abstract

The biology, habits and epidemiology of the mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae), are reviewed with particular reference to lodgepole pine, *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm., the main host in Canada. Critical aspects of mountain pine beetle life history (i.e., those that have large impacts on establishment and survival) include (i) efficient host selection and dispersal, (ii) a highly evolved mutualistic relationship with blue stain fungi that aids the beetle in overcoming host resistance, (iii) a semiochemical communication system that mediates mass attack and regulates attack density, (iv) stage-specific development thresholds that ensure synchrony of development within and among growing seasons, and (v) development rates specific to sub-populations that ensure univoltinism over a large part of the geographical range.

Mountain pine beetle populations exist in one of four phases: endemic, incipient epidemic, epidemic (i.e., outbreak) and post-epidemic (i.e., declining). Each of these phases is defined in terms of population size relative to the abundance of available host. Endemic populations principally exist in weakened, often small-diameter trees, and interactions with other bole-infesting bark beetle species are an important determinant of mountain pine beetle establishment and survival. Incipient-epidemic populations develop when the larger-diameter host trees can be successfully colonized either because of a local decline in host resistance or increases in population size due to immigration or favourable breeding conditions, or a combination of these factors. Epidemics exist at the landscape level, and develop mainly as a consequence of large, highly contiguous areas of susceptible host and favourable weather conditions. Epidemics decline either due to adverse weather conditions, or depletion at the landscape level of the host component in which increasing populations can be maintained (i.e., large-diameter trees).

Due to the nature of the interaction between the mountain pine beetle and its host trees, effective management requires detailed yearly surveys and prompt, thorough action against emerging incipient-epidemic infestations. However, given that the mountain pine beetle has evolved as a natural disturbance agent of pine forests, long-term mitigation of large-scale epidemics can only be achieved through management strategies that reduce the susceptibility of lodgepole pine over the landscape.

Résumé

La biologie, les mœurs et l'épidémiologie du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopk. [Coleoptera: Scolytidae]) sont examinées en rapport avec le pin tordu latifolié (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), hôte de prédilection du ravageur au Canada. Les principaux aspects du cycle vital du dendroctone du pin ponderosa (c.-à-d. ceux qui ont une incidence importante sur l'établissement et la survie de l'insecte) comprennent : i) une sélection d'hôte et une dispersion efficaces; ii) un mutualisme très évolué avec des champignons agents du bleuissement qui aident le ravageur à vaincre la résistance de l'hôte; iii) un système de communication sémiachimique qui sert d'intermédiaire aux attaques massives et règle la densité des attaques; iv) des seuils de développement propres au stade, qui assurent une bonne synchronisation du développement au cours d'une même saison de croissance et d'une saison à l'autre; v) une vitesse de développement propre à chaque sous-population, qui assure le maintien de l'univoltinisme à l'échelle d'une grande partie de l'aire de répartition du ravageur.

Les populations de dendroctones du pin ponderosa passent par quatre stades : le stade endémique, le stade de préinfestation, le stade de l'épidémie (c.-à-d. l'infestation) et le stade postépidémie (c.-à-d. le déclin de l'infestation). Chacun de ces stades se définit en fonction des effectifs du ravageur par rapport à l'abondance de l'hôte. Les populations endémiques sont associées principalement aux arbres affaiblis, souvent de petit diamètre, et les interactions avec les autres espèces de scolytes qui infestent le tronc jouent un rôle déterminant dans leur établissement et leur survie. Les populations atteignent le stade de préinfestation lorsqu'elles parviennent à coloniser des hôtes de fort diamètre en raison soit de la baisse localisée de la résistance des hôtes, soit de l'augmentation de leurs effectifs due à l'immigration ou à des conditions propices à la reproduction, ou d'une combinaison de ces deux facteurs. Les populations d'épidémie se retrouvent à l'échelle du paysage, et elles se propagent principalement en raison des vastes régions contiguës d'hôtes vulnérables et de conditions météorologiques favorables. Le déclin de l'épidémie se produit soit en raison de conditions météorologiques défavorables, soit de la diminution à l'échelle du paysage du nombre d'hôtes permettant la croissance des populations du ravageur (c.-à-d. des arbres de grand diamètre).

En raison de la nature de l'interaction entre le dendroctone du pin ponderosa et son hôte, une gestion efficace de la situation exige des relevés annuels détaillés et l'application rapide et rigoureuse de mesures contre le ravageur au stade de préinfestation. Toutefois, comme le dendroctone du pin ponderosa a évolué en agent de perturbation naturelle des forêts de pins, l'atténuation à long terme des épidémies à grande échelle ne peut se réaliser que par des stratégies d'aménagement qui réduisent la vulnérabilité du pin tordu latifolié à l'échelle du paysage.

Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae), is the most destructive biotic agent of mature pine forests in western North America. Normally, mountain pine beetle populations are innocuous, infesting only a few damaged, decadent or suppressed trees scattered throughout a forest. However, populations periodically erupt into

large-scale outbreaks capable of causing the mortality of mature trees over many thousands of hectares (Fig. 1). In Canada, the most extensive outbreaks have been situated within the southern interior regions of British Columbia (Unger 1993), while in the United States the largest epidemics have occurred in the Rocky Mountain states (Amman and Cole 1983). In addition to extensive timber losses, mountain pine beetle epidemics may increase fuel loading, alter successional trajectories, affect watershed quality, wildlife composition, and recreational values (Safranyik et al. 1974; McGregor 1985).

Due mainly to the severity of these impacts on forest resource values, the biology and management of the mountain pine beetle has been researched extensively over the past 50 years both in Canada and the United States, and a large body of published information exists. The earlier publications are referenced in Safranyik et al. (1975) and Berryman (1976), while examples of more recent work are found in Amman and Cole (1983), Borden et al. (1983b), Cole et al. (1985), Raffa and Berryman (1986), Bentz et al. (1991), and Carroll and Safranyik (2004).

The following review of the biology, habits and population dynamics of the mountain pine beetle is based on the published literature augmented by unpublished data from our files. We will concentrate on the biology of mountain pine beetle in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) due to the extent, severity and commercial impacts of epidemics in lodgepole pine forests. We have emphasized the interactions between the beetle with its associated blue stain fungi and lodgepole pine, with particular reference to western Canada.



Figure 1. Mountain pine beetle-caused mortality in a lodgepole pine forest in central British Columbia, Canada.

Distribution, life history, and habits

Taxonomy

Detailed descriptions of the taxonomy of the mountain pine beetle are given in Wood (1982) and Amman and Cole (1983). The following is a brief overview. Hopkins (1902) described *D. ponderosae* from specimens collected from ponderosa pine (*Pinus ponderosa* P. Laws. ex C. Laws) in the Black Hills, South Dakota. The early common name, Black Hills beetle, and more details on biology and habits were provided by Hopkins (1905). The mountain pine beetle (*D. monticolae* Hopk.) was described four years later (Hopkins 1909); the known hosts at the time comprising sugar pine (*P. lambertiana* Dougl.), western white pine (*P. monticola* Dougl. Ex D. Don), lodgepole pine and ponderosa pine. The Jeffrey pine beetle (*D. jeffreyi* Hopk.) was described the same year with hosts listed as Jeffrey pine (*P. jeffreyi* Grev. and Balf.) and ponderosa pine.

Experimental mating of *D. ponderosae* and *D. monticolae* (Hay 1956) indicated that these were actually one species that varied by region and host in some characteristics such as body size. In a comprehensive treatment of the genus *Dendroctonus*, Wood (1963) combined *jeffreyi*, *monticolae*, and *ponderosae* into a single species: the mountain pine beetle, *D. ponderosae*. Later (e.g., Lanier and Wood 1968; Pitman et al. 1968; Renwick and Pitman 1979; Zúniga et al. 2002), additional evidence supported the synonymy of *ponderosae* and *monticolae*, but indicated a distinctiveness of *jeffreyi*. Additional genetic studies showed differences in mountain pine beetle populations breeding in two varieties of lodgepole pine (*P. contorta* var. *murrayana* and *P. contorta* var. *latifolia*) (Stock et al. 1978) suggesting genetic variation among widely separated beetle populations (Stock and Guenther 1979) that might be partially related to host tree species (Stock and Amman 1980).

Life stages

The mountain pine beetle has four life stages: egg, larva, pupa and adult (Fig. 2). Apart from the dispersal phase by mature adults, all of the life stages occur within the subcortical tissues of their host trees. Adult beetles construct egg galleries in newly attacked trees parallel to the direction of the stem (Fig. 2a). Once mated, the females deposit their eggs (approximately 60 per female on average) singly into niches cut in the sides of the gallery and cover them with boring dust (Fig. 2b). Eggs are pearly white to cream coloured, ovoid, and average about 1 mm in diameter. Egg size is positively related to beetle size (McGhehey 1971), and increases with distance along galleries, perhaps due to the ingestion of nutritious phloem by females during gallery construction (Elkin and Reid 2005). Unfertilized eggs remain a uniform colour whereas the colour of fertilized eggs changes with time during embryogenesis. Reid and Gates (1970) classified eggs into four development stages based on appearance. Stage 1 eggs are 1 – 2 days old and homogeneously opaque; stage 2 eggs are 2 – 3 days old and clear at one end; stage 3 eggs are 3 – 4 days old and clear at both ends; stage 4 eggs are 4 – 5 days old and have a clearly developed head capsule visible.

Larvae pass through four growth stages called instars, each of which is terminated by moulting. They have brown sclerotized heads and white to greyish bodies (Fig. 2c). The width of the head capsule increases with larval instar. On average the head capsule ranges in width from 0.50 mm (first instar) to 1.25 mm (fourth instar). The mature (i.e., fourth instar) larva is about 6 mm long (Fig. 2c). The larvae feed individually on the phloem tissue in the inner bark by excavating mines or tunnels that usually extend at right angles to the parent egg gallery. The larval mine generally becomes wider with each successive instar. When encountering another larval mine, some larvae will cross it or mine under it (Amman and Cole 1983); however, parental galleries are rarely crossed. Larvae will also occasionally back down their mines and commence feeding either in a new direction or along the sides of the original mine.

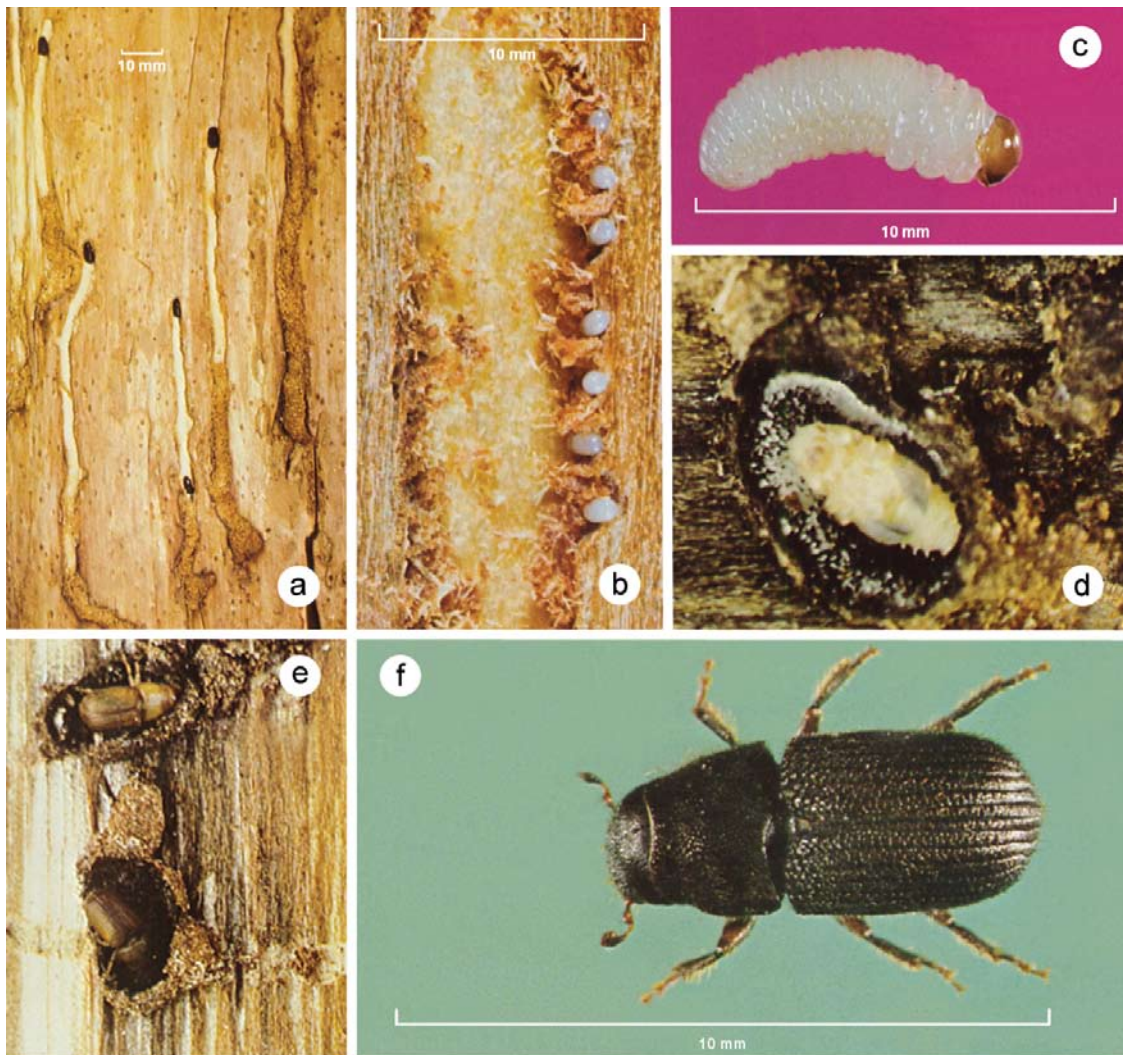


Figure 2. (a) Mountain pine beetle parental galleries in the phloem before eggs hatch, (b) eggs in niches in the parental gallery, (c) a mature (i.e., fourth instar) larva, (d) pupal chamber with pupa, (e) newly formed, teneral adults, (f) and a mature adult. Adapted from Safranyik et al. (1974).

During the latter part of the fourth larval instar, the feeding area is enlarged and cleared of debris. The prepupal and pupal periods are passed in this chamber (Fig. 2d). The pupae are white at first, changing to light brown, and are about 5 mm long. The legs and wings are folded beneath the body and the abdominal segments are exposed (Fig. 2d). This is the earliest stage in which the sexes can be determined (Fig. 3a [Schofer and Lanier 1970]).

At first, adults are pale coloured and soft. These new beetles are commonly called teneral or callow adults (Fig. 2e). They harden and become dark brown to black before emergence. Mature adults range in length from 3.7 to 7.5 mm and have stout, cylindrical bodies (Fig. 2f). Normally the females are larger than the males. For example, the mean pronotal width of female and male beetles from a population in southeastern British Columbia measured 2.08 and 1.94 mm, respectively (McGhehey 1971). The sexes can be reliably identified based on the dimorphism of the posterior margin of the seventh abdominal tergite (Fig. 3b,c [Hopkins 1909; Lyon 1958]). The pointed margin of this tergite on the male is used as part of a stridulation mechanism to produce a high-pitched rasping sound (Michael and Rudinsky 1972). Male stridulation can also be used for separation of the sexes. However, as some males do not stridulate, this method is less reliable than that based on the shape of the seventh abdominal tergite.

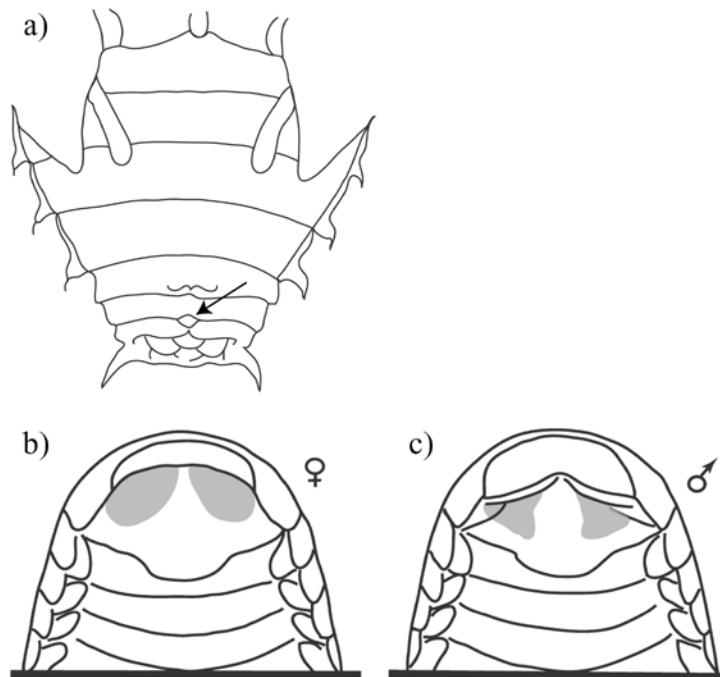


Figure 3. Ventral aspect of mountain pine beetle pupa (a) with arrow indicating characteristic lobe of females (absent in males [Schofer and Lanier 1970]), and dorsal view (elytra and wings removed) of the abdomen of female (b) and male (c) mountain pine beetle adults. Note that the posterior margin of the seventh tergite of females is gently curved, whereas in males it is angular (Lyon 1958). Adapted from Amman and Cole (1983).

Geographic distribution, host trees

The range of the mountain pine beetle extends from northern Mexico (latitude 31° N) to northwestern British Columbia (latitude 56° N), and from the Pacific Coast east to the Black Hills of South Dakota (Fig. 4). In Canada, the beetle is found as far east as the Cypress Hills on the Alberta – Saskatchewan border. The elevational range is from sea level to about 750 m near the northern limit, and up to 3650 m in the most southerly regions (Safranyik 1978).

In western Canada, the principal hosts of the mountain pine beetle are lodgepole pine, ponderosa pine, and western white pine. However, all native pines within the beetle's range, other North American pines (e.g., eastern white pine, *P. strobus* L. and jack pine, *P. banksiana* Lamb.) and some exotic species (e.g., Scots pine, *P. sylvestris* L.) can be infested and killed. Interestingly, host species can cause variation in several life-history parameters such as survival, phenology, fecundity, development rate, and body size (Knight 1959; Reid 1962 a, b, 1963; Billings and Gara 1975; Amman 1982; Safranyik and Linton 1982, 1983; Amman and Cole 1983; Langor 1989).

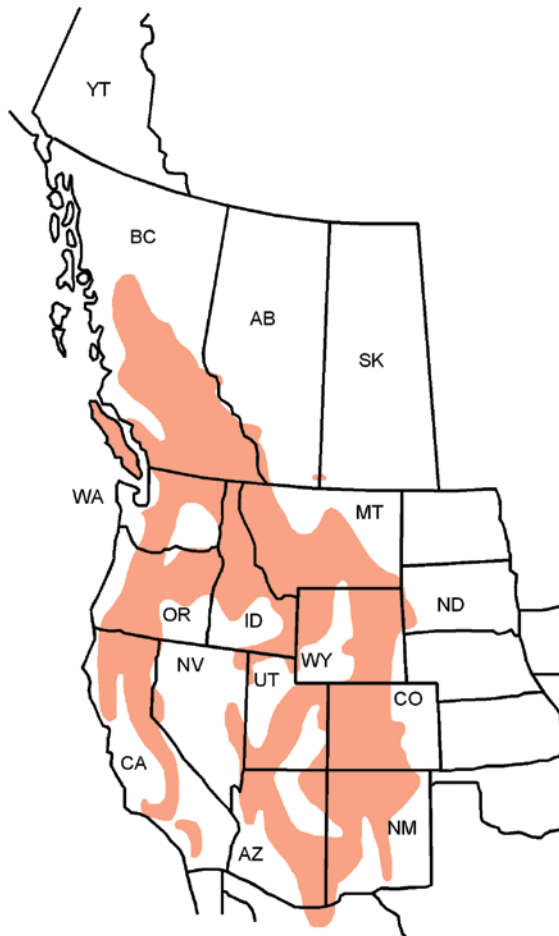


Figure 4. Present range of the mountain pine beetle in North America.

Life cycle

The length of the life cycle varies depending on ambient temperature. Normally throughout most of their range beetle populations have one generation per year (i.e., they are univoltine). During warmer than average summers, parent adults may re-emerge to establish a second brood (Reid 1962a). In cooler summers, such as those that often occur at high elevations, some or all of the brood may require two years to mature.

For univoltine populations, emergence and dispersal, host selection and colonization, and mating and oviposition normally occur during late July to mid August. Within the parental galleries of newly colonized trees, eggs normally hatch within a week or so following deposition and young larvae commence feeding immediately. Larvae often reach third or early fourth instars before temperatures become too cool for continued development. Larvae resume feeding in the spring once temperatures warm sufficiently and complete their development, transforming to pupae by June. New adults occur during late June to mid July. Depending on ambient temperatures, teneral adults require one to two weeks to mature and be capable of emergence and dispersal.

Following mild winters a high proportion of parent beetles often survive within the egg galleries they excavated during the previous season. Some of these beetles may emerge and infest new trees before their progeny complete development. More frequently, early emerging parent beetles construct galleries in the fresh phloem of trees that resisted attack or were only partially attacked (i.e., strip attacked) in the previous season (Rasmussen 1974). Alternatively, surviving parent beetles may continue to extend their galleries and oviposit in the spring if there is sufficient fresh phloem in the trees they originally attacked (Amman and Cole 1983). Progeny produced by early emerging parent beetles have little chance of contributing to population fluctuations because of their lack of coincidence with the general mountain pine beetle population (see Synchrony and Phenology).

Signs and symptoms of attack

Trees attacked by the mountain pine beetle display several distinct signs and symptoms (Fig. 5) and are grouped by the following categories: external-bole signs, crown symptoms, and under-bark symptoms (see Safranyik et al. 1974). External signs on the lower bole of mountain pine beetle-infested trees are usually a combination of (i) pitch tubes surrounding beetle entry holes (pitch tubes are cream to pinkish coloured mixtures of resin and boring dust that are extruded from egg galleries), (ii) boring dust in bark crevices, particularly around the root collar of the tree, (iii) patches of bark flaked off by woodpeckers in search of bark beetle brood, and (iv) small round emergence holes (about 2.5 mm in diameter) through which the new adults have exited trees once they've completed their development (see Fig. 5a,b,c). Flaked bark accumulates on the ground and is readily seen over snow in winter (Fig. 5b), but trees of low vigour may not produce pitch tubes, and boring dust, emergence holes and woodpecker activity are not unique to mountain pine beetle attacks. So, by themselves, these signs of injury are not reliable indicators of mountain pine beetle attack.

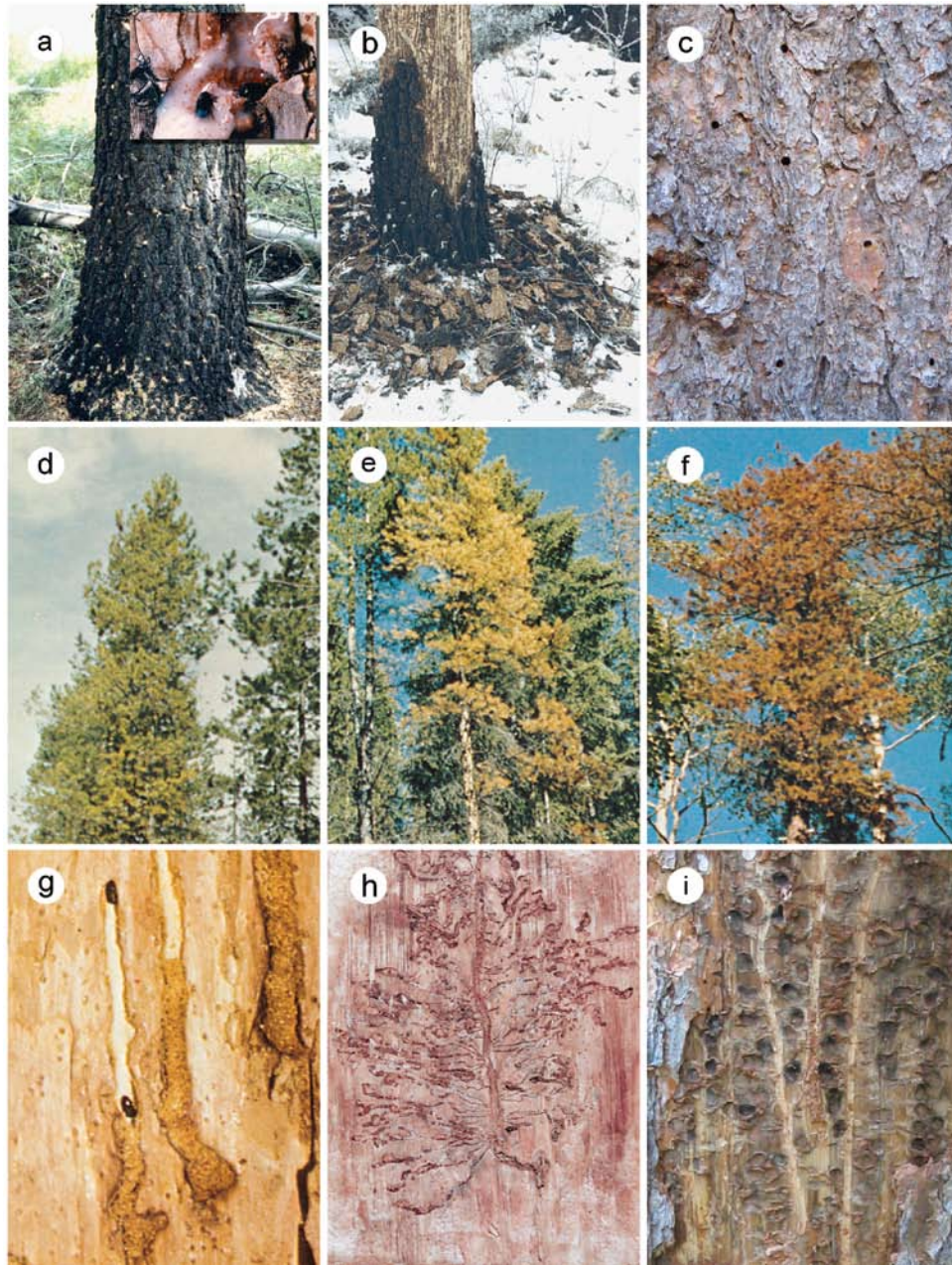


Figure 5. Symptoms of mountain pine beetle attack on the bole (a,b,c), in the foliage (d,e,f) and beneath the bark (g,h,i) of lodgepole pine. Beetles attacking a tree (a) expel light-coloured boring dust that collects around the root collar and bark crevices, while trees often exude pitch around the point of penetration, i.e., pitch tubes (a, inset). During winter, woodpeckers frequently chip away the bark in search of mature larvae (b). As new beetles emerge in the subsequent year, round holes are left in the bark of dead trees (c). The foliage of attacked trees remains green (d), usually until May and June of the year following attack, after which it begins to fade to yellow (e) and finally to red-brown (f) by July and August at approximately the time that new adults emerge. Attacking beetles excavate galleries within the phloem tissue that have a characteristic hook at the bottom and the lower ends are packed with boring dust (g). Larvae construct mines at right angles to the parental gallery (h), terminating in pupal chambers (i) once they've completed development.

Successfully attacked trees are usually killed and their crowns begin to fade from loss of moisture. The first sign of fading is a change in foliage colour from green to greenish-yellow that usually begins in the top of the crown. Later, in sequence, the crown fades to a uniform yellow, bright red and to brown by late summer the year following attack (see Fig. 5d,e,f). In situations where the mountain pine beetle develops on a one-year cycle, all or most of the beetles have emerged by the time the crowns of brood trees have turned brown.

The beginning of the visible symptoms of crown fading depends on a number of factors such as the timing of attack during the year, attack density, tree vigour and weather conditions. In western Canada, the first signs of fading normally occur in late May to early June of the year after attack. However, following hot, dry weather during late summer and early fall, faded crowns may be visible during autumn of the year of attack. Normally, lodgepole pines killed by mountain pine beetle retain some needles 3 to 5 years following attack. So, it is not possible to reliably use crown symptoms to estimate when a tree died, and it follows that aerial assessments of yearly tree mortality are unreliable.

Only the under-bark symptoms are definitive indicators of mountain pine beetle attack. However, the appearance of under-bark symptoms will vary, depending on the time of examination. During late summer, shortly after attack, beetles construct vertical galleries in the phloem with a diagnostic slight hook at the bottom (Fig. 5g). The bottom of each gallery is normally packed with boring dust. Completed galleries are usually approximately 30 cm long, but in some cases they may approach 2 m. Larvae construct their mines perpendicular to the parent gallery (Fig. 5h). During late spring of the year after attack, oval pupal chambers will be visible at the ends of some of the larval mines (Fig. 5i). From then until emergence, larvae, pupae and teneral adults will usually be present within each gallery system. In the case of new, isolated infestations it is advisable to obtain positive identification of adult beetles as confirmation.

Symptoms of mountain pine beetle attack are also visible at the stand level. During the beginning stages of epidemics, infested trees appear in groups (Fig. 6a). Locally, the groups of infested trees will grow in size and number and may coalesce to form larger patches (Fig. 6b). Within the infested patches, proportionately more of the larger-diameter trees are infested. These characteristics of infestations are frequently used for aerial assessment of damage and infestation levels over large areas.

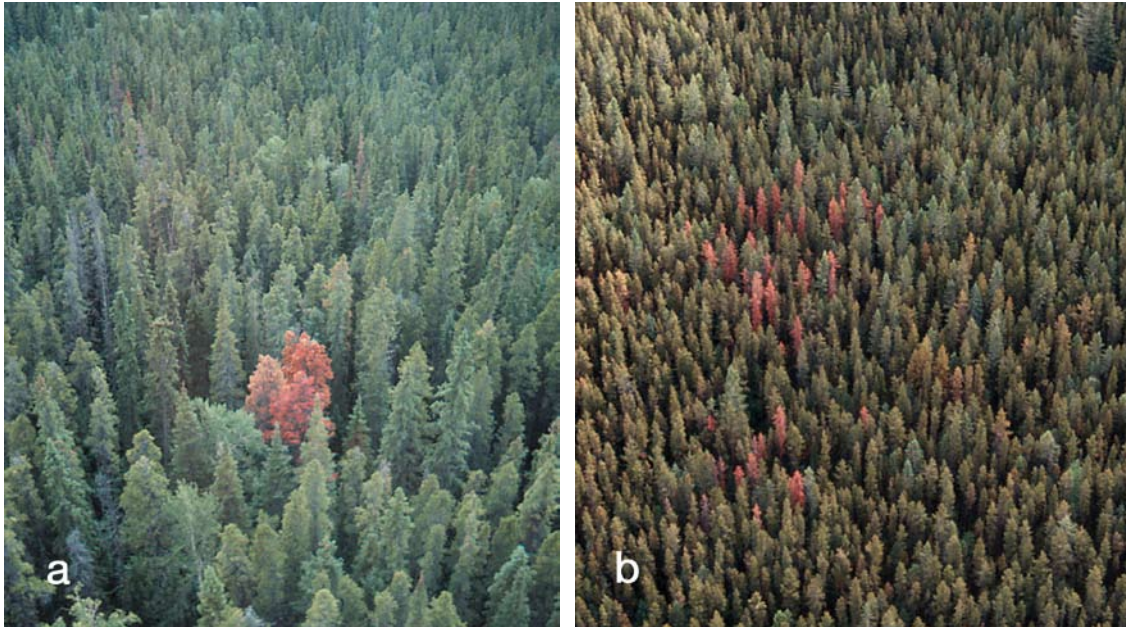


Figure 6. Symptoms of mountain pine beetle attack at the stand level. Infested trees appear in groups (a) during the early stages of epidemics. Often, these groups will grow in size and number and may coalesce to form larger patches (b).

Population processes

Emergence

Although the phase of the mountain pine beetle life cycle beginning with emergence and ending with orientation toward, and colonization of, new host trees is arguably one of the most important aspects of mountain pine beetle ecology, it is perhaps the least understood. During this phase local infestations may grow in size (i.e., spot growth), or new infestations may develop (i.e., spot proliferation).

Prior to emergence, young beetles complete maturation by feeding on the inner bark and on spores of blue stain fungi and other microorganisms that line the walls of their pupal chambers. This enables the flight muscles to increase in size (Reid 1958b), and the mycangia (specialized invaginations of the maxilla) to become charged with fungal (Whitney and Farris 1970) and yeast (Shifrine and Phaff 1956) spores, thereby ensuring transport of necessary microorganisms to new trees (Safranyik et al. 1975). Microorganisms may also be transported from tree to tree by way of sticky spores that adhere to the bodies of emerging beetles (Whitney and Blauel 1972; Six 2003). When the density of new adults is high, their maturation feeding often causes them to coalesce together within a common feeding chamber. The result is that multiple beetles may emerge through a single emergence hole chewed through the bark (Reid 1963; Amman 1969; Safranyik and Linton 1985).

After completion of maturation feeding, it is mostly temperature that determines when emergence begins and the initiation and duration of the dispersal period. Emergence occurs only when ambient temperatures exceed 16°C (Reid 1962a; Schmid 1972; Billings and Gara 1975) and it declines above 30°C (Gray et al. 1972; Rasmussen 1974). Most beetles emerge when temperatures are above 20°C (Fig. 7). This usually occurs during the early to mid-afternoon over the main distributional range in British Columbia. The emergence and flight periods are generally preceded by warm, dry weather, but there is no apparent relationship between the duration of such dry periods and the onset of emergence (Chapman 1967).

The pattern of emergence is determined by several factors. Timing of attack by parent beetles combined with accumulation of heat above the thresholds for development of the various brood stages (Safranyik 1978; Safranyik and Whitney 1985; Bentz et al. 1991) are the primary determinants of life-stage distribution and the subsequent temporal pattern of new adult emergence. Host size (diameter), aspect, height on the bole and brood density also affect emergence. On average, beetles emerge at greater relative rates from large-diameter trees than from trees with small diameters (Safranyik and Jahren 1970). Furthermore, beetles emerge at greater relative rates from the south aspect of the bole compared with the north aspect, and the rates of emergence generally decrease with height on the stem. In addition, large female beetles tend to emerge earlier than small females.

Safranyik and Jahren (1970) found that rates of daily emergence were proportional to cumulative degree-days above 14.4°C, and captures of released mountain pine beetles were directly related to heat accumulation above 16°C (Safranyik et al. 1989). The pattern of daily emergence is controlled by an endogenous rhythm as emergence in the field and in the laboratory exhibit distinct diel periodicity even in total darkness and at constant temperatures (Reid 1962b; Watson 1970; Billings and Gara 1975).

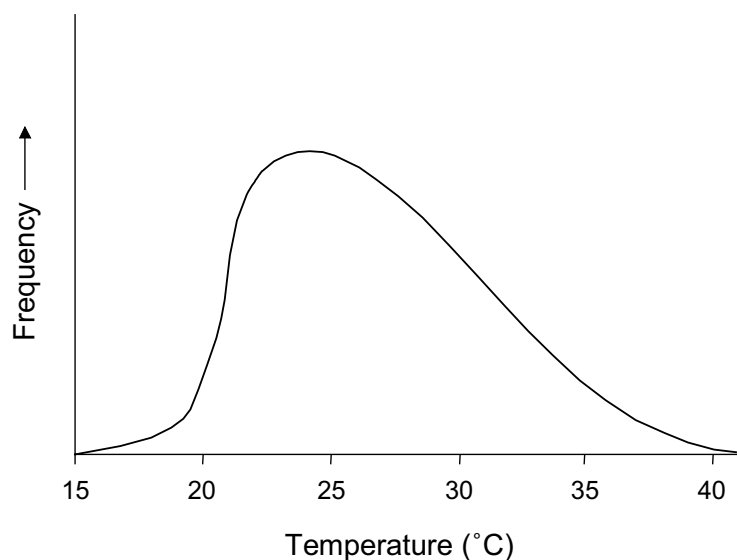


Figure 7. Frequency of emergence of mature mountain pine beetle in relation to temperature. Adapted from McCambridge (1971).

From year to year, the peak of emergence may vary by as much as 1 month, but normally it varies by less than 10 days (Reid 1962a; Safranyik 1978). Throughout most of the beetle's range in western Canada, emergence usually peaks between mid-July and mid-August. The window of peak emergence normally lasts 7 to 10 days, but can be as long as several weeks during cool or rainy periods (Safranyik et al. 1975).

Although the estimated lower and upper temperature limits for beetle flight are 19° and 41°C, respectively (McCambridge 1971), most beetles fly when temperatures are between 22° and 32°C (Safranyik 1978). Within the optimum temperature range, flight propensity increases with increasing light intensity and relative humidity almost up to the saturation point. Once temperatures exceed 35°C, flight propensity begins to decline with light intensity (Shepherd 1966), and above 38°C flight is severely restricted (McCambridge 1971). Since beetles are able to fly at low light intensities, the pattern of daily emergence is more the result of temperature than light intensity (Reid 1962a).

In general, bark beetles do not fly in winds that exceed their maximum flight speed (Seybert and Gara 1970; Meyer and Norris 1973). For large-bodied bark beetles like the mountain pine beetle, the maximum wind speed for flight, and therefore the probable maximum flight speed, is approximately 2 ms⁻¹ (Rudinsky 1963).

Dispersal

The initial flight by newly emerged mountain pine beetles tends to disperse them widely throughout the forest (Raffa and Berryman 1980; Safranyik et al. 1992). Indeed, even in the presence of aggregation pheromones, the majority of beetles may disperse out of a stand (Safranyik et al. 1992). That beetles tend not to respond to aggregation pheromones immediately following emergence suggests that a flight period may enhance their host-seeking behaviour. This interpretation is supported by Shepherd (1966) who found that flight exercise increased the responsiveness of mountain pine beetle to host stimuli.

During short-range, within-stand dispersal, most beetles fly several metres above the ground – below tree crowns, but above the undergrowth (Schmitz et al. 1980; Safranyik et al. 1989). The direction of this flight is normally downwind until beetles encounter an attractive odour plume at which point they turn and fly back upwind toward the source (Gray et al. 1972; Byers 1999). Beetles that do not disperse from the stand in which they develop usually locate suitable host trees within two days of emergence, but are capable of searching for several days. In a two-year mark-release-recapture study in a lodgepole pine stand (Safranyik et al. 1992), the number of beetles recaptured following release decreased exponentially with distance from the release point, and about 90% of the recaptured beetles were trapped within 30 m. Although shorter dispersal flights may allow greater investment of energy in reproduction (Elkin and Reid 2005), longer flights may enable beetles to locate habitats with higher quality host trees.

There is a paucity of information about long-range, above-canopy dispersal by the mountain pine beetle. However, Safranyik et al. (1992) found that, based on the vertical distribution of flying beetles, up to 2.5% of a population may attempt long-range dispersal above the canopy. This estimate was determined from a relatively small population and would likely be much higher during an outbreak when locally available host trees have been depleted. Given that beetles fly during periods of warm, fair weather that are often accompanied by air inversions near the ground and by upward convection currents (Chapman 1967), it has been suggested that some beetles are caught in, and directed by, warm convective winds and could easily be carried 20 km or more (Furniss and Furniss 1972). This thesis is supported by collections of mountain pine beetles from snowfields above the timberline, many kilometres from potential host trees. In addition, there is compelling evidence for long-distance dispersal at the scale of hundreds of kilometres. During an outbreak that occurred in the extreme southwestern region of Alberta and adjacent British Columbia in the early 1980s, mountain pine beetles were discovered attacking planted pine trees in community parks and on residential properties 200 to 300 km downwind across the prairies (Cerezke 1989). More recently, mountain pine beetle infestations were discovered in the Peace River region of northeastern British Columbia, an area that was historically considered climatically unsuitable for mountain pine beetle (Safranyik et al. 1974; Carroll et al. 2004). Assessments of these infestations revealed that they originated in a single year (i.e., they did not increase from local populations), most probably as a consequence of long-distance dispersal from outbreak populations located several hundred kilometres to the southwest, across the Rocky Mountains (ALC, personal observation). These observations suggest that long-range dispersal could contribute to the spread of epidemic populations.

Host selection and colonization

Some debate exists as to the mechanism of initial host selection by pioneer beetles. Evidence suggests that vision plays a key role in locating host trees. Several authors have reported tree diameter as a landing stimulus (Hopping and Beall 1948; Cole and Amman 1969), and that large, dark silhouettes (Shepherd 1966) and vertically oriented cylinders (Billings et al. 1976) are attractive to beetles. By contrast, other studies suggest that beetles land at random during the pre-aggregation phase and that the greater number of beetles landing on larger trees is simply due to their larger surface area (Burnell 1977; Hynum and Berryman 1980).

Although the dominant theory of host selection by mountain pine beetle proposes that pioneer females utilize a combination of random landings and visual orientation followed by direct assessment of host suitability after landing (e.g., Wood 1982; Pureswaran and Borden 2003a), there is evidence that dispersing adults orient to lodgepole pine trees suffering from injury or disease (Gara et al. 1984a). Furthermore, Moeck and Simmons (1991) showed that mountain pine beetles are attracted to odours of host material in the absence of visual cues.

After pioneer beetles land on a potential host tree, the decision to initiate a gallery is made based upon gustatory assessment of compounds present in the bark (Raffa and Berryman 1982a). If a tree is considered acceptable, females begin to construct a gallery and in the

process instigate a mass attack. A mass attack involves a complex synergism of host-produced (kairomones) and beetle-produced (pheromones) volatile chemicals (Borden 1982). As pioneer females penetrate the bark they oxidize the host monoterpene α -pinene to produce the aggregation pheromone *trans*-verbenol, which is preferentially attractive to males (Pitman et al. 1968; Pitman and Vité 1969; Billings et al. 1976; Libbey et al. 1985). Once males arrive they release *exo*-brevicomin, which at low concentrations attracts mainly females (Borden et al. 1983a, 1987; Conn et al. 1983; Libbey et al. 1985). The kairomones α -pinene and myrcene synergize the aggregation pheromones resulting in a mass attack (Renwick and Vité 1970), a process that is normally completed in one to two days on an individual tree. In trees where attack densities are low, females may abandon their egg galleries, even after laying a complement of their eggs (Amman 1975, 1980).

To minimize the effects of intraspecific competition, the mountain pine beetle has evolved a mechanism to terminate host colonization on individual trees at or near optimum attack densities [approximately 60 attacks per m² of bark (Raffa and Berryman 1983b)] using chemical cues. Attack density is regulated in part by the production of high concentrations of *exo*-brevicomin and frontalin (Ryker and Libbey 1982; Ryker and Rudinsky 1982; Raffa and Berryman 1983b; Borden et al. 1987) and 2-phenylethanol (Pureswaran et al. 2000) by males, the release of 1-octen-3-ol by females (Pureswaran and Borden 2004), and by the production of the anti-aggregation pheromone verbenone (Pitman and Vité 1969) by intestinal and gallery-inhabiting microbes within both sexes of beetles (Hunt and Borden 1990). This process is not fully understood, and at least three hypotheses have been advanced to explain the process of switching attacks from a “focus tree” to a neighbouring “recipient” tree (Geiszler et al. 1980; Bentz et al. 1996). The first of these theories is that production of the anti-aggregation pheromone, verbenone, through autoxidation of the kairomone α -pinene and microbial conversion of *trans*-verbenol (Hunt and Borden 1989), in combination with the inhibitory effects of high concentrations of frontalin and *exo*-brevicomin, leads to close-range redirection of beetles to nearby trees (e.g., Ryker and Yandell 1983; Borden et al. 1987). A second theory is that cessation of resin exudation from the host tree as it becomes fully utilized (Renwick and Vité 1970), and secondarily the production of inhibitory compounds, leads to the termination of attacks. Thirdly, some authors have proposed that an increasing concentration of *trans*-verbenol emitted from the focus tree envelopes neighbouring trees leading to their subsequent acceptance and attack (Coster and Gara 1968; Geiszler and Gara 1978; Geiszler and Gallucci 1980). Several studies have shown that switching of attacks to a recipient tree often occurs before the original focus tree is fully utilized (Geiszler and Gara 1978; Bentz et al. 1996), thereby precluding the second theory. Raffa and Berryman (1983b) and Bentz et al. (1996) have suggested a combination of the first and third hypotheses where the inhibitory effects of the anti-aggregation pheromones are short range, perhaps affecting the distribution and density of attacks within a tree rather than among trees (Raffa and Berryman 1983b; Renwick and Vite 1970), while plumes of the aggregation pheromones that encompass neighbouring trees are responsible for redirection of attacks. In support of this interpretation, observations (e.g., Raffa and Berryman 1983b) and model analyses (Logan et al. 1998; Powell et al. 1998) indicate that when mountain pine beetle populations are very small (i.e., when attack densities are low) the pattern of

successfully attacked trees is mainly determined by the distribution of susceptible trees. In epidemic infestations, however, the availability of susceptible trees is less important and the success of switching attacks is more dependent on factors such as distance between the focus and recipient tree (Mitchell and Preisler 1991; Preisler and Mitchell 1993).

Beetle-host interactions

The mountain pine beetle preferentially attacks large trees. This is because characteristics of the stem that are related to tree size are the primary determinants of a tree's potential to produce beetles once it has been successfully colonized (Safranyik et al. 1975; Amman and Cole 1983).

Total attacks and brood production per tree are positively related to tree age and diameter at breast height ([dbh] i.e., 1.3 m) of lodgepole pine trees (Fig. 8). This is due in part to the fact that larger trees have thicker bark (Fig. 9a). Mountain pine beetles require a minimum thickness of bark (≈ 1.5 mm) beneath which to construct their galleries (Fig. 9b). When beetles attempt to excavate egg galleries in thin bark, they often break through to the outside. If this occurs, beetles will abandon the tree. Thick bark also affords protection from natural enemies, temperature extremes, and sapwood drying (e.g., Reid 1963; Safranyik et al. 1974). Furthermore, attacking beetles require bark scales, crevices and fissures as points to brace against to initiate boring through the bark (Shepherd 1965). The rough boles of older, larger trees tend to have a much greater density of these potential boring points than smaller, younger trees (Safranyik 1971).

Bark characteristics also affect the spatial pattern of attacks. Beetles initiate galleries with a regular spacing on the bole, apparently because of the regular arrangement of bark niches (Shepherd 1960, 1965). This conclusion is strengthened by the finding that the proximity to previously established attacks has no effect on attack initiation (Safranyik 1971). There is also a horizontal attack gradient around the circumference of the stem (Shepherd, 1960, 1965; Reid 1963; Carson and Cole 1965; Safranyik 1971). In the clear bole zone, the heaviest attacks are usually found on the northern aspect and the lightest attacks on the southern aspect (Fig. 9c). Shepherd (1965) suggested that this is the result of the attacking beetles' reaction to light intensity and temperature. Since most flights occur on bright sunny days, and peak flight is in the early to mid afternoon (Reid 1960), the southern aspect of the bole usually has high light intensities and surface temperatures during this time period, conditions that stimulate beetles to continue flying (Shepherd 1966).

Beetles ultimately prefer large trees due to the positive relationship between tree diameter and phloem thickness (Amman 1969; Shrimpton and Thomson 1985). Brood production by the mountain pine beetle is directly related to phloem thickness (Amman 1969, 1972b; Berryman 1976; Amman and Cole 1983) given the greater quantity of the resource and perhaps its greater nutritional value. In trees with thick phloem, beetles lay more eggs per centimetre of gallery (Amman and Cole 1983), experience less intraspecific competition as larvae (Cole 1973), develop faster (Amman and Cole 1983), and ultimately produce larger brood beetles (Amman and Pace 1976) compared to beetles in trees with thin phloem.

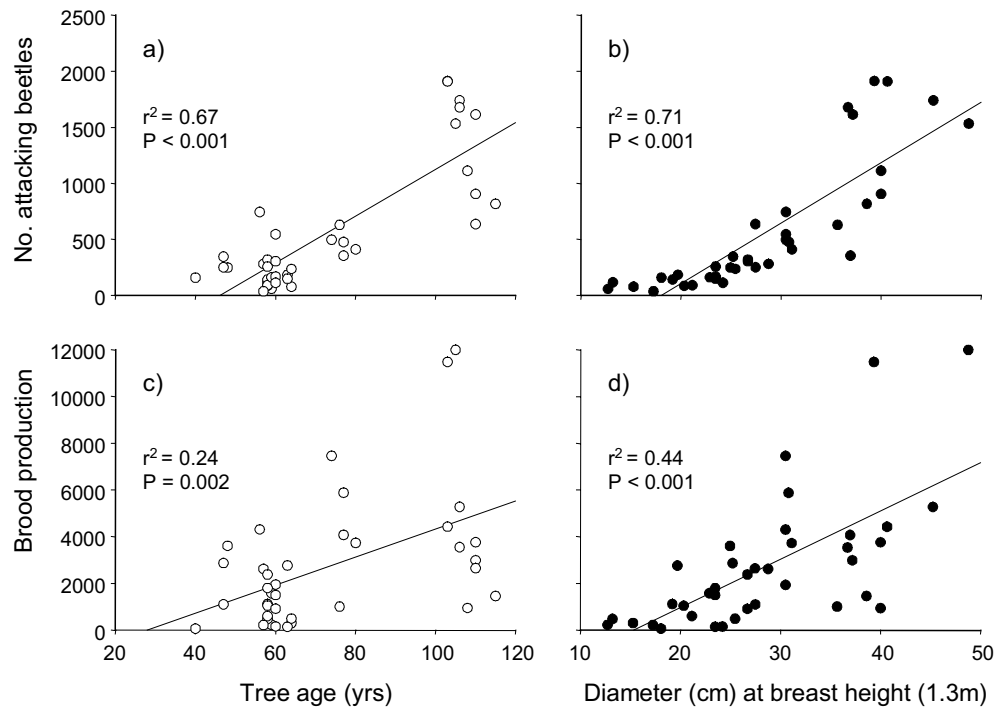


Figure 8. The number of attacking beetles and the number of brood produced per tree in relation to (a, c) tree age, and (b, d) the diameter of trees at breast height for an incipient mountain pine beetle population from southeastern British Columbia. Adapted from Safranyik (1968).

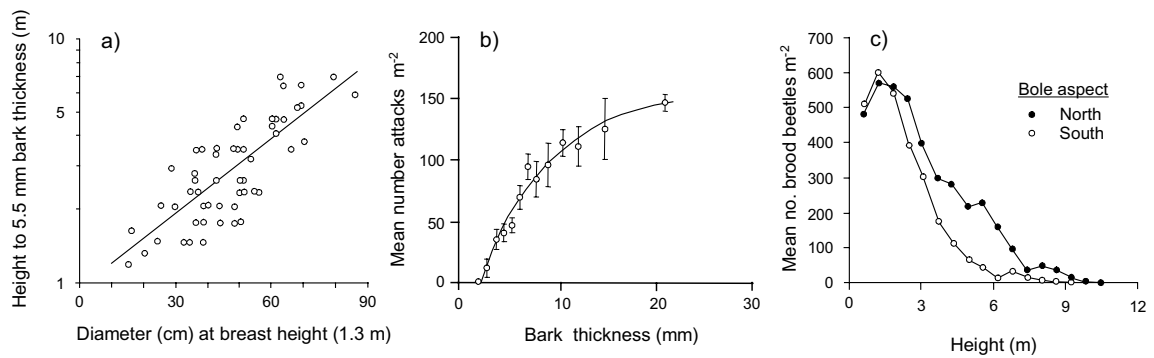


Figure 9. (a) The diameter at breast height in relation to the height on the bole at which the bark is at least 5.5 mm thick, (b) the mean (± 1 S.E.) density of mountain pine beetle attacks in relation to the combined thickness of the inner and outer bark, and (c) the mean number of brood beetles per m² of bark versus height on the bole of the North and South sides of lodgepole pine trees. Data were collected from an incipient mountain pine beetle infestation from southeastern British Columbia. Adapted from Safranyik (1968).

Although phloem thickness is generally positively correlated with tree diameter, stand conditions often affect this relationship. For example, senescing or unthrifty trees tend to have thin phloem (Berryman 1982a). In addition, competition among trees within a stand may affect phloem thickness. The number of attacking beetles and the number of brood produced are both positively related to the volume of a tree's live crown and the sum of the distances to its nearest neighbours (Fig. 10). Trees with larger crowns growing at greater distances from neighbouring trees suffer less competition for resources and in turn have thicker, potentially more nutritious phloem (Safranyik 1968). Variation in phloem thickness as a consequence of stand conditions likely explains why tree age and diameter explain much more of the variability in the number of attacking beetles (Fig. 8a,b) than the subsequent number of brood produced (Fig. 8c,d).

Because the combined thickness of the bark and phloem tends to decline with height on the bole, the density of attacks is a decreasing function of infested height (Fig. 9c). As a consequence of these relationships and the effect of tree size on beetle landing rates, young trees with thin bark, and small-diameter, older trees are rarely attacked or killed. Moreover, because brood production is much lower in small-diameter trees compared with large ones, populations breeding in small trees have a much lower potential rate of increase compared to those infesting large trees. In practical terms, this means that on average lodgepole pine trees up to 25 cm in diameter are beetle sinks (i.e., more beetles attack than emerge), whereas trees over 25 cm in diameter are beetle sources (i.e., more beetles emerge than attack [Safranyik et al. 1974]).

Although the mountain pine beetle prefers to colonize larger trees within a stand, such trees are normally the fastest growing, most vigorous trees at a given age and site quality (Shrimpton 1973a). As a consequence, they are also the best able to defend themselves from attack. Successful colonization by the mountain pine beetle depends on the death of its host tree. This intense selection pressure has resulted in the evolution of a complex array of defenses that enable lodgepole pine to resist attack. These defenses include resins released from constitutive resin ducts severed as beetles bore through the bark (Smith 1963; Shrimpton and Whitney 1968; Reid and Gates 1970; Berryman 1972), and secondary induced resinosis by tissues surrounding the wound (Reid et al. 1967; Shrimpton and Whitney 1968; Berryman 1972; Shrimpton 1973b; Raffa and Berryman 1982b; 1983a,b). The flow of constitutive resin slows attacking beetles and their accompanying microorganisms and may even expel them from a tree [i.e., pitch out (see Fig. 11)]. The induced response involves localized breakdown of parenchyma cells, the formation of traumatic resin ducts, and ultimately the production of secondary resin comprising increased concentrations of terpene and phenolic compounds (Raffa and Berryman 1982b; 1983a). The phloem becomes saturated and liquid resin exudes through the sites of attack. If the induced response is rapid and extensive, the beetles and associated microorganisms will be confined and killed in a lesion of dead tissue.

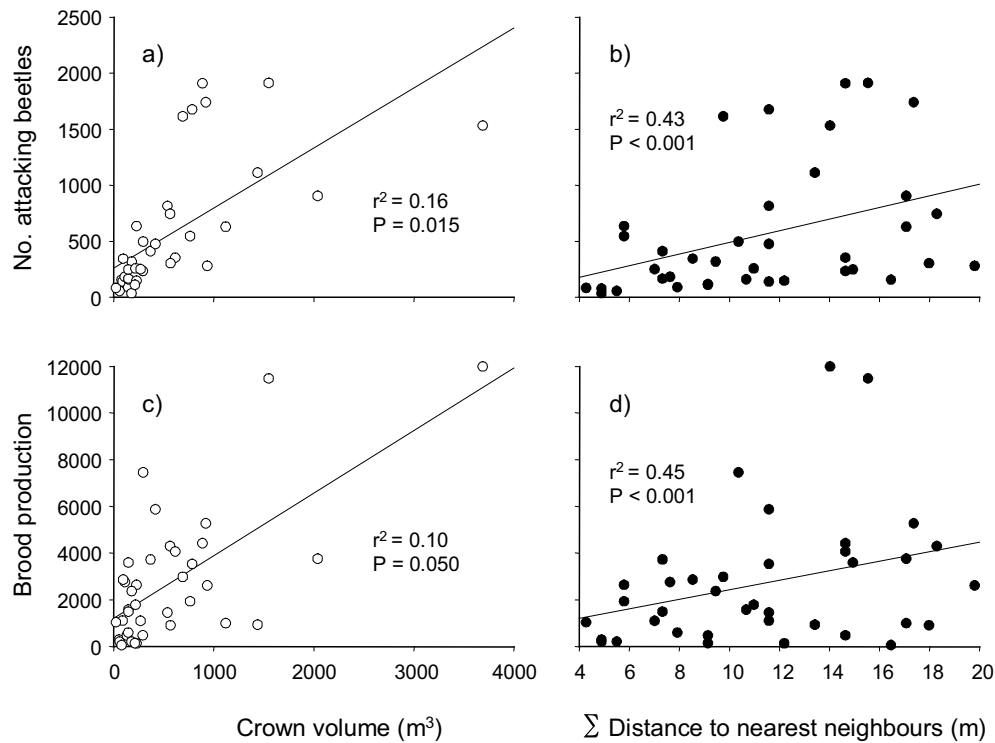


Figure 10. The number of attacking beetles and the number of brood produced per tree in relation to (a, c) volume of the live crown, and (b, d) the sum of the distances to each of the three nearest neighbours larger than 10 cm diameter at breast height (1.3 m) for an incipient mountain pine beetle population from southeastern British Columbia. Adapted from Safranyik (1968).

The mountain pine beetle employs two strategies to overcome the defenses of lodgepole pine. The first relies upon cooperative behaviour in the form of mass attack as described above. By rapidly concentrating attacks on selected trees in response to aggregation pheromones, the beetles exhaust the host's defensive response (Safranyik et al. 1975; Berryman 1976; Raffa and Berryman 1983b; Berryman et al. 1989). If sufficient beetles arrive at a rate that exceeds the resistance capacity of a particular tree, then colonization will be successful.

The second strategy derives from a mutualistic relationship between the mountain pine beetle and several species of blue stain fungi. Spores of these fungi are acquired and disseminated via the mycangia, which are paired invaginations of the exoskeleton of the maxillae present in both sexes (Whitney and Farris 1970) (Fig. 12a). The fungal spores are inoculated into trees as beetles bore through the bark. They germinate quickly and penetrate living cells in both phloem and xylem (Safranyik et al. 1975; Ballard et al. 1982, 1984; Solheim 1995) (Fig. 12b) causing desiccation and disruption of transpiration (Mathre 1964), effectively terminating resin production by the tree. As the fungus colonizes a tree, the mountain pine beetle brood develops. At the end of larval development, coincident with pupation, the fungi line the pupal chambers with a dense layer of asexual propagative spores (conidiophores and conidia; Fig. 12c). Newly eclosed beetles feed on the fungi for a period of days to weeks before emergence, during which time the mycangia are charged with spores (Whitney 1971).

The mountain pine beetle may benefit from its association with blue stain fungi in several additional ways (reviewed by Six and Klepzig 2004). Colonization of the phloem and sapwood by the mycangial fungi may: (i) protect beetle broods from antagonistic species of fungi (Whitney 1971), (ii) improve the moisture composition of phloem for larvae (Reid 1961), and (iii) provide nutrients required to complete development (Six and Paine 1998).

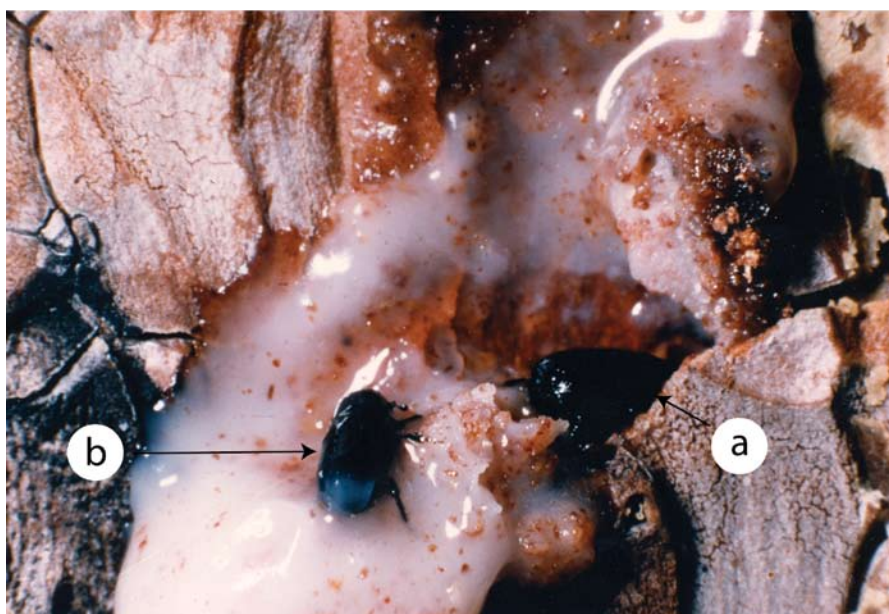


Figure 11. Defensive resin exuded by lodgepole pine in response to attack by the mountain pine beetle. Note the female beetle (a) penetrating the bark, and male (b) partially engulfed by resin.



Figure 12. Maxilla of mountain pine beetle (a) showing mycangium (indicated by arrow) with fungal material protruding. Cross section of a lodgepole pine tree killed by mountain pine beetle with characteristic blue staining of the sapwood (b) as a consequence of fungal colonization. Mountain pine beetle pupal chamber (with pupa) lined with a dense layer of blue stain fungi spores (c).

Two species of blue stain fungus, *Ophiostoma clavigerum* (Robinson-Jeffrey & Davidson) Harrington and *O. montium* (Rumbold) von Arx, are consistently associated with mountain pine beetle (Whitney and Farris 1970; Six and Paine 1998; Six 2003; Kim et al. 2005). Interestingly, recent studies have shown that *O. clavigerum* is mainly acquired and disseminated from the mycangia, whereas the sticky spores of *O. montium* are mainly carried phoretically on the exoskeletons of beetles (Six 2003). Moreover, *O. clavigerum* appears to be a mutualist with a long evolutionary history with mountain pine beetle. By contrast, *O. montium* is a more recent associate that acts antagonistically to mountain pine beetle brood, possibly parasitizing the mutualism between the beetle and *O. clavigerum* (Six and Paine 1998, 1999).

At the stand level, resistance of lodgepole pine to colonization by the mountain pine beetle and blue stain fungi is affected by the normal process of stand aging. Depending on site quality, stands tend to be most resistant between 40 and 60 years of age, and resistance then declines rapidly with age (Safranyik et al. 1974) (Fig. 13a). Resistance begins to decline at about the point when, in fully stocked stands, current annual increment peaks and basal area growth culminates (Safranyik et al. 1974, 1975; Raffa and Berryman 1982b) (Fig. 13b). Thereafter, the vigour of trees declines as they reach maturity and begin to compete for resources. Under these conditions, if trees have reached sufficient size, mountain pine beetle populations can increase rapidly. As a general rule, by the time stands reach 80 to 100 years of age, they are highly susceptible to mountain pine beetle.

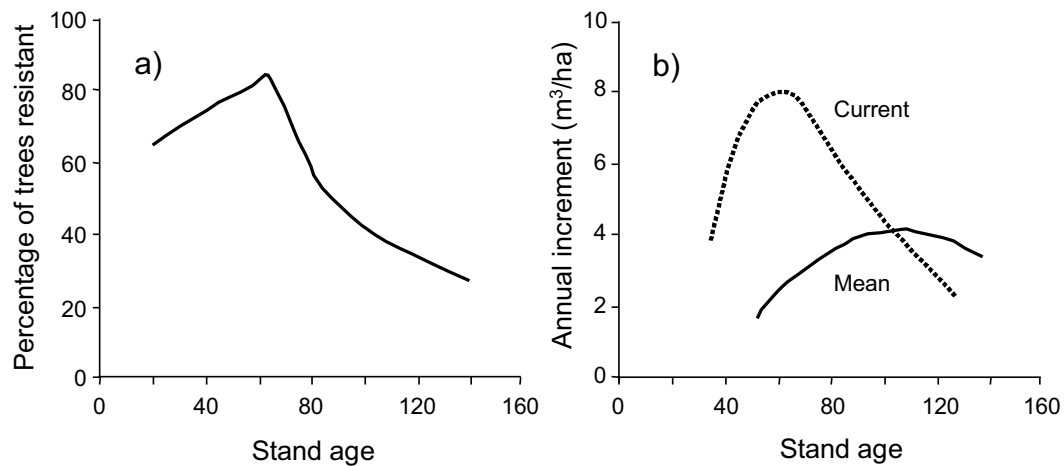


Figure 13. The frequency of trees resistant to inoculation with blue stain fungi in relation to age (a), and the current and mean annual growth increments (b) for a fully stocked lodgepole pine stand growing on a moderately productive site. Adapted from Safranyik et al. (1974).

Cold tolerance

Within the host tree, cold temperature is often the largest single source of mortality in mountain pine beetle populations (Safranyik 1978; Cole 1981). Not surprisingly, the beetle has evolved an effective mechanism by which it can tolerate temperatures commonly encountered during winter within its range. Cold tolerance is acquired through the production and accumulation of glycerol, a polyhydric alcohol, in the hemolymph (i.e., the blood) as temperatures decline during autumn (Somme 1964; Bentz and Mullins 1999). Tolerance to cold varies with life stage. Larvae are the most cold tolerant followed by adults, pupae, then eggs (Safranyik et al. 1974). Reid and Gates (1970) determined the lethal temperature for eggs to be -18°C . Logan et al. (1995) estimated that the lethal temperature range for pupae is between -18° and -34°C , and that for adults between -23° and -34°C . Larval tolerance to cold increases as they mature (Amman 1973; Safranyik et al. 1974; Langor 1989; Safranyik and Linton 1998; but see Bentz and Mullin 1999) even though the first three larval stages contain proportionately the same amount of glycerol (Somme 1964). Lethal low temperatures for larvae have been estimated as manifesting between -23° and -29°C for first instars, -23° and -34°C for second instars, and -29° and -40°C for both third-instar and fourth-instar larvae (Logan et al. 1995).

Given the gradual accumulation of glycerol, cold-hardiness is greatest during the period from December to February when winter temperatures are usually lowest. Late larval instars are the normal overwintering stage and can withstand temperatures near -40°C for extended periods during this time (Wygant 1940; Yuill 1941). However, if low temperatures occur early in the year before the mountain pine beetle is able to produce sufficient glycerol, or late in the winter after the beetle has begun to metabolize it, significant mortality can occur (Wygant 1940; Safranyik et al. 1974). For example, if -30°C were to occur in mid winter, little mortality would be expected. However, if this temperature were to occur at the end of October, or in the middle of March, then nearly 100% mortality can be expected (see Fig. 14). Interestingly, in 1984 and 1985 a major outbreak in the Chilcotin region of central British Columbia collapsed due to a series of days during which temperatures dropped below -30°C in late October and early November, respectively (Safranyik and Linton 1991). The mortality due to unseasonable cold temperatures during the winter of 1984-85 was so severe that surviving brood were restricted to the lower 0.5 m of the bole (below the snowline), and comprised only 10% of the numbers required for replacement of the parent generation.

The effects of cold exposure are normally exerted within the first two to four hours of exposure (Wygant 1940; Yuill 1941; Somme 1964). However, many factors can moderate the effects of low temperatures on mountain pine beetle mortality. Thick bark and deep snow will insulate beetle broods from declining ambient temperatures (Wygant 1940; Safranyik et al. 1974). Also, the rate of decline of subcortical temperatures is slower for large-diameter versus small-diameter trees due to the greater capacity of large objects to store heat (Safranyik and Linton 1998). Beetle attack characteristics will also affect the potential for mortality due to cold. As temperatures approach lethal lows, mortality is negatively related to attack,

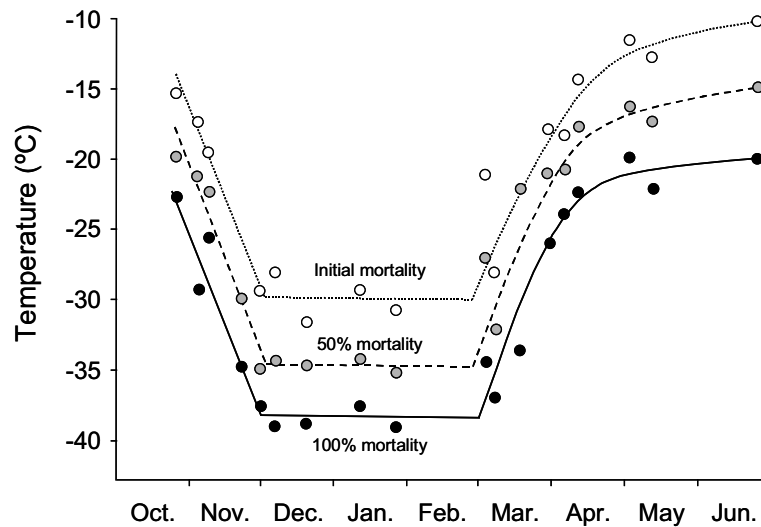


Figure 14. Temperature thresholds at which initial, 50% and 100% mortality of third and fourth instar mountain pine beetle larvae occurs in relation to time of year. Larvae were exposed to low temperatures for 2.5 hours. Adapted from Wygant (1940).

brood and egg gallery densities, due to the insulating effects of air pockets created by gallery construction (Safranyik and Linton 1998). Consequently, for cold weather events to impose significant mortality upon a mountain pine beetle population, temperatures must decline and remain low for several days to ensure that subcortical temperatures reach lethal levels.

Synchrony and phenology

The potential for mountain pine beetle populations to establish and persist within habitats with suitable host trees is largely dependent upon the phenology and synchrony of populations within and among seasons. However, unlike many insects in seasonal environments, the mountain pine beetle does not have a diapause (i.e., an obligatory winter torpor) to functionally synchronize populations with critical phenological events (Logan and Bentz 1999). Development is under direct temperature control, suggesting that in environments with temperature regimes outside a narrow optimal range, population synchrony would degrade over time. Interestingly, the high mortality associated with asynchrony has selected for adaptations that ensure adult emergence is temporally coincident, thereby maximizing chances for successful mass attacks (Raffa and Berryman 1987), and phenologically timed to enable broods to mature to cold-tolerant life stages before winter (Logan and Bentz 1999; Logan and Powell 2001).

Adult emergence is synchronized by stage-specific responses to temperature (Bentz et al. 1991). Late instar larvae have higher temperature thresholds for development than early instars, preventing progression to cold-susceptible advanced life stages before the onset of winter. Due to their lower developmental thresholds, early instars originating from late-hatching eggs are able to “catch up” and become synchronous with the rest of

the population after temperatures have become too cool for late instar larval development (Bentz et al. 1991). To ensure that populations maintain their phenological timing, the mountain pine beetle has also evolved regional differences in its developmental rate. Given the large differences in heat accumulation in the northern versus southern portions of its range, populations of the mountain pine beetle in the north have evolved to develop faster for a given input of temperature than beetles from the south (Bentz et al. 2001). These two adaptations ensure that populations can maintain a synchronous univoltine life cycle that is phenologically coincident with critical seasonal events over an extremely broad range of climatic conditions.

In cooler environments, such as those that occur at high elevations and near the northern edges of its range, heat accumulation is often insufficient for completion of the typical univoltine life cycle and mountain pine beetle populations become semivoltine (Fig. 15). Stretching the life cycle over two years results in severe mortality since the beetles will be forced to overwinter twice, often in cold-susceptible stages, and exposed to natural enemies for a longer period (Amman 1973; Safranyik 1978). Moreover, a two-year life cycle slows the beetle's physiological clock in relation to the chronological clock, prolonging critical life history events such as adult emergence and dispersal (Logan et al. 1995; Logan and Powell 2001). This will significantly reduce colonization success since the mountain pine beetle relies on mass attack to overcome host resistance.

Generally, in areas where mountain pine beetle populations can maintain a univoltine life cycle, the frequency of adverse weather conditions is not great enough to prevent development of outbreaks or to reduce populations to low, endemic levels. By contrast, in semivoltine populations climate becomes a dominant factor affecting both the distribution and abundance of mountain pine beetle (Safranyik 1978).

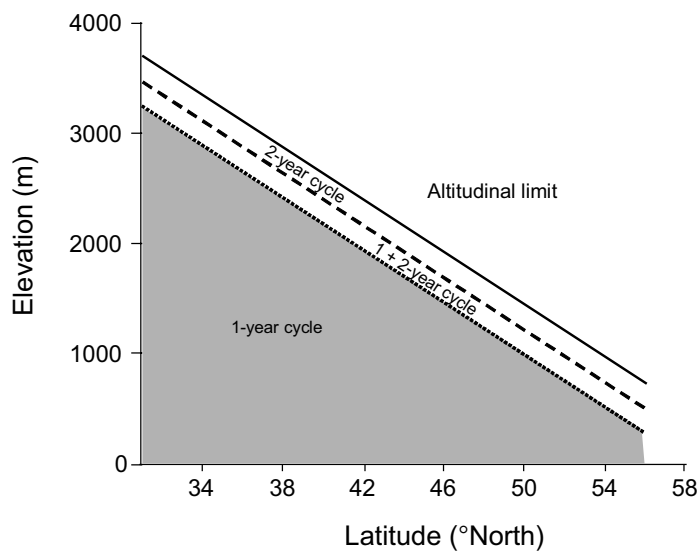


Figure 15. Historic distribution of mountain pine beetle life cycle duration in relation to elevation and latitude. Adapted from Amman (1973).

Population dynamics

Several authors have modelled the dynamics of mountain pine beetle populations (Berryman 1976; Cole et al. 1985; Raffa and Berryman 1986; Polymenopoulos and Long 1990; Safranyik et al. 1999a). It is not our intention to review modelling techniques. Instead we will address the independent and interacting effects of the various aspects of mountain pine beetle life history that determine its population dynamics (i.e., the fluctuation of populations in time and space), some of which may have been included in various modelling efforts.

Mating and oviposition

Prior to mating, females construct the initial 1 to 5 cm of the egg gallery in the phloem tissue across the grain of the wood of their host tree, keeping it clear of boring dust (Reid 1962b). The male joins the female and mating takes place in the lower end of the egg gallery. Nearly all mating occurs after initiation of the egg gallery. Indeed, only 1% or 2% of females are mated prior to emergence and dispersal (Reid 1958a; McCambridge 1970). After mating, males assist females with gallery construction by removing debris, plugging the entrance hole and packing boring dust at the lower end of the gallery. They also guard against the intrusion of other males (McGhehey 1968; Ryker and Rudinsky 1976) and may continue to produce anti-aggregation pheromones (Pureswaran and Borden 2003b). Males often die in the egg gallery and are sealed in by the female as she continues packing the lower end of the gallery with debris. However, males may leave galleries to seek additional females. The quantity of spermatozoa produced by males increases for several days after emergence (Cerezke 1964).

Male mountain pine beetles are polygynous and multiple mating is the norm; however, mating frequency is much reduced after females commence egg laying (Reid 1962b). In nature the male:female sex ratio is near 1:2, but under laboratory conditions, a ratio as low as 1:4 did not affect mating success (Reid 1958a). Sperm remains viable in the spermatheca for at least one year so that re-emerged females do not have to mate again to produce viable eggs.

Within the host tree, the behaviour of female adults in relation to egg gallery construction, egg laying and flight preparation are determined to a large extent by moisture and temperature conditions (Reid 1962b). Oviposition ceases when the moisture content of the phloem and outer sapwood falls below 105% and 60% of oven dry weight, respectively. Under drier conditions than these, the female beetle ceases egg laying, builds up its flight muscles, and re-emerges to make a second flight and attack. The lower temperature threshold for boring and oviposition activity is between 2° and 7°C, depending on the vigour of the individual beetle. The rate of egg gallery construction, egg density, and the numbers of eggs laid per day all increase with temperature above the lower threshold in a curvilinear fashion (Amman 1972a). The upper temperature limits for boring and oviposition have not been investigated. However, for the closely related Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, Rudinsky and Vité (1956) reported that egg gallery construction continued at 32°C, but restlessness and excessive activity hindered organized boring.

Under favourable conditions of moisture, temperature, and attack density, individual beetles can construct egg galleries up to 1.5 m in length and lay over 200 eggs (Reid 1962b). Generally, however, egg galleries are less than 30 cm long and contain fewer than 75 eggs. Large beetles lay more eggs and construct longer egg galleries than small beetles (Reid 1962b; McGhehey 1971; Amman 1973). The number of eggs per centimetre of egg gallery length (egg density) is independent of female size except for the smaller beetles that construct shorter egg galleries (McGhehey 1971). In three populations from southern British Columbia, egg density ranged from 2.4 to 4.2 eggs/cm (Richmond 1935; Reid 1962b; McGhehey 1971). Since fewer numbers of eggs are laid at the beginning and at the end of egg galleries, average egg density is less in short versus long egg galleries. Egg density is also affected by the proximity of adjacent egg galleries. The number of eggs per centimetre of gallery increases to a plateau once egg galleries are at least 2.5 cm apart (Amman and Cole 1983).

Survival and development

Temperature and moisture are the two most important abiotic factors affecting brood development and survival (Safranyik 1978). The physiological effects of temperature are important in a) delimiting growth and development, b) setting growth and development rates, c) regulating cold-hardiness, and d) determining survival. Temperature and moisture also affect brood development and survival indirectly through effects on host quality and host resistance. Other important mortality factors are competition for food and space, host quality and host defenses, and natural enemies. The relative importance of these factors varies with the state of the population (i.e., infestation size and age) and brood stage.

Eggs

The minimum and maximum temperatures for egg hatch are near 1.7° and 35°C, respectively (Reid and Gates 1970). However, only a few eggs hatch below 4.4°C. At constant 10°C and 20°C, Amman and Cole (1983) reported average hatching times of 36.6 and 8.4 days, respectively, for beetles from the intermountain region of the western United States. The corresponding values obtained by Safranyik and Whitney (1985) from the central interior of British Columbia, 34.0 and 7.4 days, agree reasonably well with those reported by Amman and Cole (1983), considering the differences in experimental methods and the wide geographic separation of beetle populations used for obtaining eggs.

The time required for mountain pine beetle eggs to hatch decreases with temperature in a curvilinear fashion (Safranyik and Whitney 1985; Logan and Amman 1986). Within the temperature limits for development, the rate of egg hatch per day is a curvilinear function of temperature with a maximum around 24° – 27°C (Safranyik and Whitney 1985; Bentz et al. 1991; Logan and Powell 2001). Under field conditions in southern British Columbia, an average of 118.4 degree-days were required above a threshold temperature of 4.4°C for half of the eggs to hatch (Reid and Gates 1970). The mean daily temperature during the study period was 15.4°C. At constant 15°C, these authors estimated that 127.2 degree-days were

required above 4.4°C for half of the eggs to hatch. Similarly, Safranyik and Whitney (1985) found that 134.0 degree-days were required for half of the eggs to hatch for beetles originating from central British Columbia at the same constant temperature and temperature threshold reported in Reid and Gates (1970). The difference in the reported heat unit requirements for egg hatch based on constant temperatures in the laboratory versus field conditions may be explained in part by a non-linear rate of development above a lower temperature threshold. Differences in the degree-day requirements for egg hatch at constant temperatures may be due to differences in response to temperature among subpopulations.

Eggs of the mountain pine beetle are very susceptible to cold temperatures. Even when conditioned at -5°C, eggs freeze at an average temperature of -18°C whereas eggs not conditioned freeze at -17°C (Reid and Gates 1970). Eggs stored at -5°C for one month suffered 75% mortality. Interestingly, eggs in the first two stages of development were more susceptible to cold temperatures than older stages (Reid and Gates 1970). Since freezing temperatures are the norm in most areas where mountain pine beetles occur, and temperatures lower than the maximum supercooling point (i.e., -18°C) are common, overwintering eggs typically suffer complete mortality.

Conditions associated with the host tree will also affect eggs. Successful embryogenesis and egg hatch requires at least 90% relative humidity beneath the bark (Reid 1969). Furthermore, volatiles originating from defensive resin have only minimal impact (i.e., 3% mortality) on eggs, but coating the eggs with resin causes complete mortality (Reid and Gates 1970). On individual trees Reid (1963) found that up to 32% of the egg galleries were rendered non-productive by resin soaking.

The role of predation, parasitism and disease in the population dynamics of the mountain pine beetle is not well known. In theory, each factor may regulate low populations (McCambridge and Trostle 1972). A large number of predators and parasites are associated with the mountain pine beetle; comprehensive lists are given in DeLeon (1934) and Amman and Cole (1983). Rasmussen (1976) published a field guide to the most abundant insect parasites and predators of the mountain pine beetle in lodgepole pine. Other major references on natural enemies of bark beetles are Bushing (1965), Dahlsten (1982), and Moeck and Safranyik (1984). In general, the abundance of natural enemies varies considerably among stands as well as within and between trees within stands.

Medetera aldrichii Wheeler (Diptera: Dolichopodidae) is considered one of the most effective egg predators of mountain pine beetle as it may destroy up to 50% of eggs in some situations (DeLeon 1935b). Adult flies (Fig. 16a) feed on small insects and mites on the bark surface of trees. Larvae forage within beetle galleries (Fig. 16b). In ponderosa pine, Schmid (1971) found that *M. aldrichii* was most common within the first 10 cm of mountain pine beetle galleries located between 1.5 m and 3 m in height on the bole. The density of *M. aldrichii* larvae averaged 30 to 40 per m² bark, and each larva consumed 15 to 25 mountain pine beetle eggs. However, in a laboratory study of egg mortality in lodgepole pine spanning four seasons, Amman and Cole (1983) found that *M. aldrichii* consumed only 2.5% to 6.5% of mountain pine beetle eggs.

Amman and Cole also found that up to 4.1% of egg mortality was caused by nematode worms, and 0.8%-1.8% was attributed to unidentified fungi. Lesser amounts of mortality were caused by cannibalism, unknown factors, and infertility.

Larvae

Most of the mountain pine beetle life cycle is spent in the larval stage. Consequently, many biotic and abiotic factors have the potential to act alone or in concert to influence survival and development.

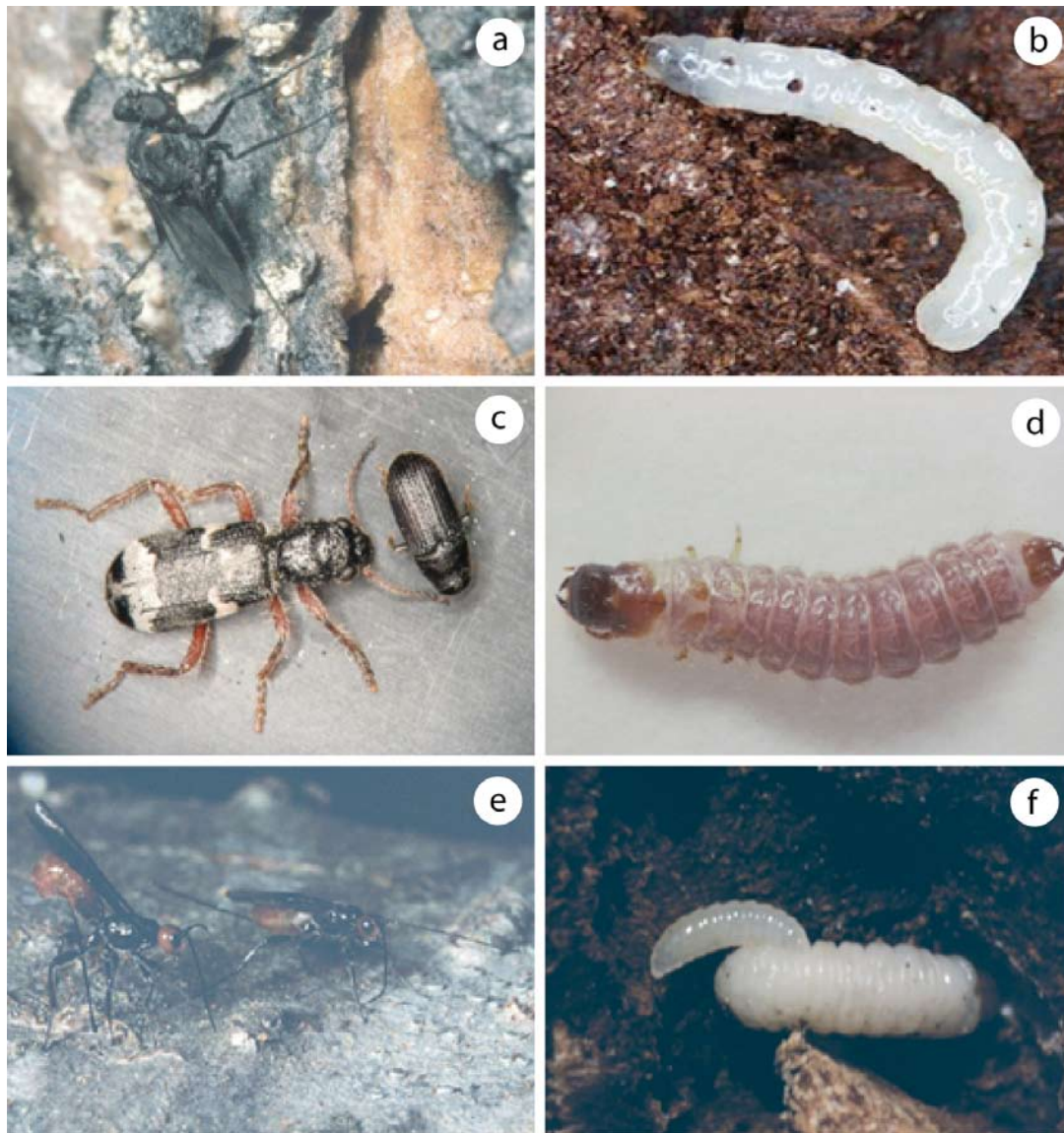


Figure 16. Common predators and parasitoids of the mountain pine beetle: *Medetera aldrichii* Wheeler (Diptera: Dolichopodidae) adult (a) and larva (b); *Thanasimus undatulus* Say (Coleoptera: Cleridae) adult (with a mountain pine beetle) (c) and its larva (d); and *Coeloides dendroctoni* Cushman (Hymenoptera: Braconidae) adults (e) and a larva parasitizing a late instar mountain pine beetle larva (f).

The lowest temperature threshold for larval development is near 2.2°C (McCambridge 1974). However, to ensure populations develop synchronously, the threshold temperature for development increases with successive larval instars (Amman and Cole 1983; Bentz et al. 1991; Logan et al. 1995; Logan and Powell 2001 [see Synchrony and Phenology]). The survival of larvae increases with increasing temperatures to a peak of 24°C, after which survival declines precipitously (Safranyik and Whitney 1985). Beetles are significantly smaller when reared at a constant 25°C compared to those reared at 15°C or 20°C (Amman and Cole 1983; Safranyik and Whitney 1985). At temperatures between 30°C and 35°C larvae will die within 10 days of hatching, still in the first instar.

The average number of degree-days at constant temperatures required for beetle development from egg to adult above a threshold of 5.6°C ranged from 478.3 at 27°C, to 546.6 at 18°C, the lowest temperature at which development was completed (Safranyik and Whitney 1985). As with the egg stage, the differences in degree-day accumulation requirements at different constant temperatures suggest a non-linear development rate above a threshold. Rearing of beetles from the egg to the adult stage was unsuccessful at 10°C and 15°C; at the latter temperature the larvae completed development, turned creamy white, stopped feeding and died 167 – 217 days after the start of incubation. Interestingly, Amman and Cole (1983) were successful in rearing mountain pine beetle from the egg to the adult stage at a constant 15°C, suggesting regional differences in beetle subpopulations.

Competition among mountain pine beetle larvae is the principal density-dependent mortality factor that regulates beetle populations. The significance of intraspecific competition to beetle populations is evidenced by the extremely effective system of anti-aggregation pheromones that has evolved to regulate attack density during colonization. Competition for food and space has a complex effect on brood survival. In general, larval survival is inversely related to attack and egg gallery density. The nature of this relationship is affected by a number of host factors such as tree resistance, diameter, phloem thickness and moisture content. Consequently, under a given set of climatic conditions, low attack densities in non-resistant trees with thick phloem tend to produce high brood per parent ratios (e.g., Reid 1963; Amman and Pace 1976; Berryman 1976).

The effect of larval density on mountain pine beetle fitness is instar dependent. Cole (1973) found that, with increasing larval density, in artificial medium both initial feeding and survival rates increased, and duration between moults of the first two instars decreased. On the other hand, crowding increased the duration of the last two larval instars, and prolonged high larval densities decreased survival to the adult stage. Crowding increases the frequency of encounters, especially among late instar larvae, and frequently results in death from cannibalism or injury (Amman and Cole 1983). Ultimately, the fecundity of surviving females is negatively related to the level of crowding during the larval stages (Cole 1973).

Impacts of phloem thickness are also partly instar dependent. Initially, the rate of mining by larvae in thin phloem is faster than that in thick phloem, and this results in significantly larger individuals (determined by head capsule widths) during the second and third instars (Cole 1973; Amman and Cole 1983). Higher initial feeding rates in thin versus thick

phloem may be due to the need to consume a greater quantity of a less-nutritional substrate to obtain sufficient resources for development. However, by the end of the larval period, individuals developing in thick phloem are much larger than those from thin phloem, due to a combination of overall better nutrition and faster feeding rates during the third and fourth instars.

The production of defensive resin by the tree acts directly on larvae as a physical impediment to feeding, and indirectly by soaking otherwise nutritionally adequate phloem (Shrimpton 1978; Raffa and Berryman 1983a). Defensive resin is also antagonistic to the blue stain fungi (e.g., Smith 1972; Reid et al. 1967) that the beetle depends upon to complete development (see Insect-Host Interactions). Moreover, low larval survival has been associated with high densities of resin blisters in the bark (Berryman 1976) and resin soaking within the egg galleries (Reid 1963). As a consequence of the diminishing impacts of host resistance and increasing impacts of intraspecific interactions with increasing attack density, brood survival is a hump-back function of attack density (Reid 1963; Amman and Pace 1976; Berryman 1976; Raffa and Berryman 1983b [Fig. 17]).

Excessive drying of the phloem and outer sapwood is detrimental to larval feeding and survival. Under very dry conditions the larvae will desiccate and die. The depth of sapwood in even-aged trees tends to be directly related to tree diameter and since the sapwood contains more moisture than the heartwood (Reid 1961), the greater rate of drying of small-diameter trees is assumed to be related to reduced sapwood depth (Amman 1978). Under laboratory conditions, the phloem of young trees can produce large brood densities (Amman and Cole 1983). However, brood production in the field is generally poor, mainly because of the high resin content in the bark of young trees and excessive drying of the sapwood and phloem following attacks.

Interspecific competition is also an important factor affecting the development and survival of mountain pine beetle brood. Over fifty species of scolytid bark beetles breed in the subcortical tissues of lodgepole pine in Canada (Bright 1976). The vast majority of these species do not infest healthy, large-diameter trees, and are therefore referred to as “secondary” species. Depending on host requirements and geographic distribution, only a subset of these species is expected to be present in any given stand of lodgepole pine. Interestingly, in a multi-year study of the interaction of mountain pine beetle with other bark beetle species, the authors (unpublished data) found that throughout central British Columbia endemic mountain pine beetle populations (see Epidemiology) were consistently associated with six or seven secondary species that inhabit the lower bole of lodgepole pine trees (Table 1).

Table 1. Bark beetle (Coleoptera: Scolytidae) species commonly found inhabiting the lower bole of lodgepole pine trees in direct association with endemic mountain pine beetle populations in British Columbia.

Species	Common name
<i>Pseudips mexicanus</i> (Hopkins)	Monterey pine beetle
<i>Ips latidens</i> (LeConte)	-
<i>I. pini</i> (Say)	pine engraver
<i>Hylurgops porosus</i> (LeConte)	-
<i>H. rugipennis</i> (Mannerheim)	-
<i>Dendroctonus murrayanae</i> (Hopkins)	lodgepole pine beetle
<i>D. valens</i> (LeConte)	red turpentine beetle

Secondary bark beetle species may influence both the establishment and survival of mountain pine beetle broods (Safranyik et al. 1999b). For example, the aggregation pheromones utilized by the pine engraver, *Ips pini* Say, reduce the number of attacks by mountain pine beetles, and their larvae compete directly for food and space with mountain pine beetle larvae (Rankin 1988; Safranyik et al. 1996). In general, secondary beetles typically have higher attack densities, and are often bivoltine (i.e., two generations within one year), attacking early in the season before mountain pine beetles emerge, producing a brood that completes development and emerges to attack again, often at the same time mountain pine beetles initiate their attacks. Thus, they can interact with mountain pine beetle in two ways: by pre-empting breeding space and by direct competition for food and space.

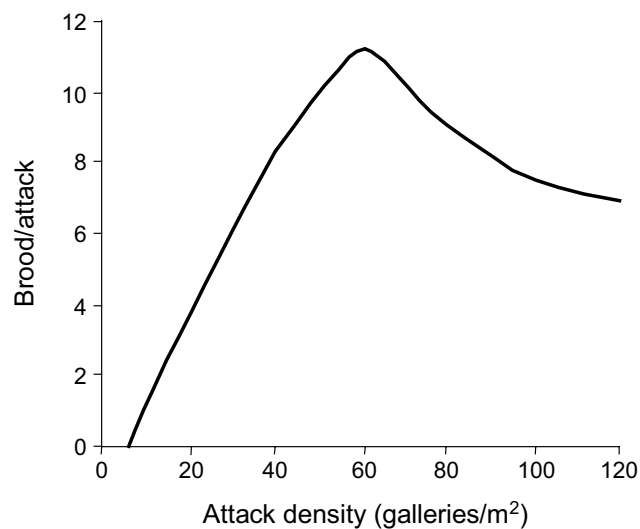


Figure 17. Relationship between brood production (number of pupae formed per attacking female) and attack density. Adapted from Raffa and Berryman (1983b).

Medetera aldrichii is considered the most effective predator of mountain pine beetle larvae (DeLeon 1935b; Amman and Cole 1983). In lodgepole pine in southeastern British Columbia, the highest densities of *M. aldrichii* larvae were found during mountain pine beetle development on the north aspects of trees (Reid 1963) and in the lower 2 m of the bole. *Medetera aldrichii* larvae (Fig. 16b) are able to move through the bark to find their prey, and may kill and feed on several mountain pine beetle larvae during their development (Schmid 1971). In laboratory tests, *M. aldrichii* larvae required 6 to 15 mountain pine beetle larvae to complete development, depending on the size of the beetle prey offered (Nagel and Fitzgerald 1975). *Medetera aldrichii* appears to respond to mountain pine beetle populations in a density-dependent fashion (i.e., predation increases as the density of beetles increases), a behaviour that can potentially increase the impact of predation on population dynamics (see Epidemiology). However, *M. aldrichii* larvae are generalists and will feed on the immature stages of most subcortical insects, including their own (DeLeon 1935b). This behaviour tends to reduce their effectiveness as predators, especially in situations where mountain pine beetle broods are intermingled with those of other subcortical insects.

The clerid beetles (Coleoptera: Cleridae) *Enoclerus sphegeus* Fabricius and *Thanasimus undatulus* Say prey both as adults (Fig. 16c) and larvae (Fig. 16d) on the adults and larvae of various bark beetle species, including the mountain pine beetle. They tend to be more numerous on the north aspect and the lower portions of the bole of lodgepole pine (Reid 1963). Clerid larvae are generalist predators in the bark of infested trees and are able to mine through subcortical tissues to find their prey. In laboratory tests, *E. sphegeus* larvae consumed on average 16 large or 38 small mountain pine beetle larvae during their development (Amman 1970), and larvae of *T. undatulus* larvae consumed an average of 18 large or 35 small mountain pine beetle larvae (Amman 1972c). Clerid larvae are cannibalistic, a behaviour that tends to limit their larval densities (Berryman 1967).

Coeloides dendroctoni Cushman (Hymenoptera: Braconidae) is considered the most important parasite (DeLeon 1935a; Reid 1963) of mountain pine beetle (Fig. 16e,f). *Coeloides dendroctoni* may use either temperature or vibration to locate its host, at which point it pierces the bark with its ovipositor (Fig. 16e) and lays an egg on a larva feeding in the subcortical tissue (Dahlsten 1982). Reid (1963) found *C. dendroctoni* was by far the most abundant parasite attacking mountain pine beetle. It was more numerous on the north and east aspects of lodgepole pine trees, and its density was inversely related to bark thickness. *Coeloides dendroctoni* preferentially parasitizes late instar mountain pine beetle larvae. If beetle larvae develop to this stage and avoid parasitism they have a high probability of reaching the adult stage (DeLeon 1935a). Parasitism appears to be highly spatially variable. DeLeon (1935a) reported average parasitism rates of 4% to 32% from lodgepole pine in eastern Idaho and Montana, whereas Amman (1984) found rates of parasitism between 0.02% and 1.7% in southeastern Idaho and northern Utah. Furthermore, *C. dendroctoni* is more abundant in older, established mountain pine beetle infestations and is relatively scarce in recent, isolated infestations. *Coeloides dendroctoni* has the potential to be a more effective natural enemy than *M. aldrichii* because many of the mountain pine beetle larvae destroyed by the latter in the fall, when prey and predator are most abundant, would have died from other sources prior to

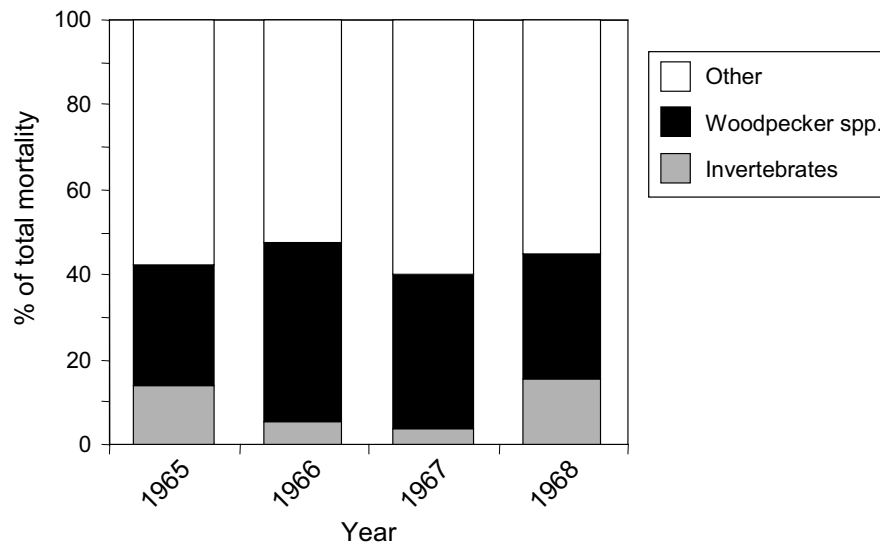


Figure 18. Percentage of total mortality of mountain pine beetle brood caused by invertebrate predators and parasitoids, woodpeckers and other mortality agents over four years in an incipient infestation located in southeastern British Columbia.

reaching the adult stage. Assuming that each parasitoid destroyed one host larva, Reid (1963) reported that parasitism reduced the mountain pine beetle population by 9% in southeastern British Columbia. However, there was no relationship between the density of mountain pine beetle egg galleries and the density of parasites, suggesting that *C. dendroctoni* does not respond to changes in its host abundance in a density dependent manner. Furthermore, peak emergence of *C. dendroctoni* in southeastern British Columbia precedes that of the mountain pine beetle by approximately two weeks (Reid 1963). Hence, there is often a scarcity of late instar mountain pine beetle larvae for parasitism, forcing *C. dendroctoni* to attack advanced larval stages of other bark beetle species such as *Ips pini*. In addition, Amman (1984) suggested that the dispersal capacity of *C. dendroctoni* is much less than that of mountain pine beetle, thereby limiting impacts of parasitism on beetle populations, especially during suboutbreak periods when populations are widely dispersed.

Woodpecker species are considered to be important mortality agents of bark beetles (Dahlsten 1982; Fayt et al. 2005), including the mountain pine beetle (Blackman 1931). They can consume large numbers of larvae, pupae and adults, and they indirectly destroy many more by creating openings in the bark and by chipping away the bark and reducing its thickness thereby promoting larval desiccation (Amman and Cole 1983). Parasitism and predation by the beetle's natural enemies may also increase due to reduced bark thickness as a consequence of woodpecker activity (Otvos 1965). In a four-year study of an incipient-epidemic mountain pine beetle population in southeastern British Columbia, the authors (unpublished data) found that in bark where woodpecker predation was not excluded by wire cages at four heights on the bole, average larval survival was only about half of that in adjacent portions of the bole protected from woodpeckers (Fig. 18). Woodpeckers

concentrate feeding on trees containing high densities of large larvae and tend to avoid trees containing small larvae (Koplin and Baldwin 1970). However, even though it is generally accepted that woodpecker predation may have important impacts on low beetle populations, the magnitude of the impact is inversely related to beetle population size (Berryman 1973; Korol 1985). This inverse density dependence is due, in part, to the territorial behaviour of woodpeckers during nesting season which limits their density within forests.

Pupae

The pupal stage is relatively brief for the mountain pine beetle. Under field conditions, pupation normally requires two to four weeks. Safranyik and Whitney (1985) determined that 100 degree-days above a base temperature of 5.6°C were required to develop to young adults when pupae were reared at constant 24°C. With the exception of host resistance, the natural mortality factors are generally the same as those listed for the larvae. Occasionally, pupae suffer high mortality from desiccation and woodpecker predation. On average, however, mortality in this stage is much reduced compared to the larvae (Amman and Cole 1983).

Adults

At constant temperatures in the laboratory, mountain pine beetle adults matured after 6.4 days at 24°C and 11 days at 18°C. At the higher temperature, this required 118 degree-days, while at the lower temperature 136.5 degree-days were required above 5.6°C for maturation (Safranyik and Whitney 1985), suggesting that the rate of development above a lower threshold may be non-linear just as in the earlier life stages.

In nature, mountain pine beetle populations are consistently female-biased (see Mating and Oviposition), but the extent of this bias varies among populations and among years. Laboratory studies have reported some broods that consist entirely of females (McGhehey 1969). Apparently, factors that cause stress in a population such as crowding, cold exposure, adverse rearing temperatures, and phloem degradation will reduce male survival. It is possible that differential survival of the X and Y sperm are involved, or a lethal cytoplasmic factor that causes the death of male embryos (Lanier and Wood 1968).

A variety of natural enemies are associated with mountain pine beetle adults. Reid (1958c) found seven species of entomophilic nematodes within a beetle population from southeastern British Columbia. Several species inhabited the thorax, abdomen, digestive tract, and the reproductive organs of female beetles. The most common species, *Sphaerularia hasta* Khan (Nematoda: Tylenchida), infested 27.5% of the female adults and caused an average 32.5% reduction in the number of eggs laid (Reid 1958c). Nematodes also cause adult mortality and reduction in dispersal capacity.

Clerid beetles prey on mountain pine beetle adults (Fig. 16c). Adult clerids are attracted by the pheromones emitted by bark beetles during the attack phase (Dahlsten 1982) and so aggregate on trees with abundant prey. This is an effective numerical response by the predator to the prey, but it lasts only as long as the pheromones are emitted. The impact of

predation by adult clerids on adult mountain pine beetle populations is not known. In a laboratory test, Schmid (1970) found that *E. sphegeus* adults killed one mountain pine beetle per individual per day. He estimated that in natural populations of the mountain pine beetle, mortality caused by *E. sphegeus* would be less than 1%.

Occasionally, localized high levels of mountain pine beetle mortality can be caused by diseases (MacCambridge and Trostle 1972) such as that caused by the fungal pathogen *Beauveria bassiana* (Balasmo) Villemin (Euascomycetes: Clavicipitales) (Safranyik et al. 2001). In addition, during dispersal birds may consume many flying beetles. Amman and Cole (1983) reported that within a localized mountain pine beetle infestation, nighthawks (Aves: Caprimulgidae) were collected with an average of 76 beetles/bird in their stomachs. In general, however, the mortality of adult beetles caused by natural enemies does not have a significant effect on population fluctuations.

Epidemiology¹

We recognize four phases in the population cycle of the mountain pine beetle: endemic, incipient-epidemic, epidemic (i.e., outbreak) and post-epidemic (i.e., declining) populations. The endemic and incipient-epidemic phases represent distinct population states regarding interactions with host trees and the assemblage of bole-infesting secondary bark beetle species, whereas the other two population phases mainly represent differences in population size and spatial extent. There is also some suggestion of changes in mountain pine beetle population behaviour among the different phases, as with other species of *Dendroctonus* bark beetles (Wallin and Raffa 2004). However, this aspect of beetle biology is insufficiently understood and needs further research.

Endemic populations

Following the collapse of outbreaks during the post-epidemic phase, and before populations increase as incipient epidemics, the mountain pine beetle is considered to be in the endemic phase. Amman (1984) defined the endemic state as one where populations are so small that they are capable of mass attacking no more than one large-diameter tree within 40.5 ha of forest. In a multi-year study of the dynamics of low-level mountain pine beetle populations across south-central British Columbia, the authors (unpublished data) have determined that endemic populations exist at even lower densities. Indeed, an endemic population can be defined as one with insufficient beetles to overcome even a single large-diameter tree within a stand. Beetles in this population phase are restricted to low-quality host trees with little or no defensive capacity.

¹ Based in part on: Safranyik, L. 2004. Epidemiology. Pages 33-40 in T.L. Shore; J.E. Brooks; J.E. Stone (eds). Proceedings of the mountain pine beetle symposium: challenges and solutions. Canadian Forest Service, Pacific Forestry Centre, Victoria. Information Report BC-X-399. 298 p.

In lodgepole pine, resistance to the mountain pine beetle increases with age, approximately in parallel with increases in current annual increment (CAI) (Safranyik et al. 1974, 1975). Resistance peaks at an age when natural stands attain maximum stocking on all physiographic sites (Horton 1956 [see Fig. 13]). Near the culmination of CAI, on at least the more productive sites, many trees are of sufficient size and density to sustain a large mountain pine beetle population. However, due to high tree resistance and low beetle numbers, these trees are unavailable to endemic populations. The only host trees available to endemic beetles are those largely incapable of a resistance response as a consequence of the stresses associated with among-tree competition (i.e., suppression), pathogens, soil compaction, fluctuations in the water table, or other forms of biotic or abiotic injury. Since the culmination of CAI on fully stocked sites also corresponds to the point at which crown closure begins for lodgepole pine (e.g., Farnden 1996), there is generally a steady supply of low-vigour, suppressed trees as maturing stands begin the process of self-thinning (Yoda et al. 1963). Therefore, after the peak CAI, most lodgepole pine stands will maintain a consistent assemblage of bole-infesting bark beetles, including endemic mountain pine beetles.

Our study of endemic populations has revealed that the mountain pine beetle in this population phase generally infests suppressed trees that have been partially attacked, either during the previous season(s) or earlier in the same season, by other bole-infesting bark beetle species (see Table 1). Within mature lodgepole pine stands, three to six trees/ha/year had mountain pine beetle galleries. Attacks occurred at very low densities (two or three per tree), and the mountain pine beetle galleries were either intermingled with those of co-attacking secondary species or occurred in strips within the uncolonized portions of the boles of trees attacked in previous years (unpublished data). Subsequent to mountain pine beetle attack, the infested trees frequently sustained additional attacks during the same year, (and in the subsequent years if sufficient green phloem persisted) by one or more of the secondary bark beetle species listed in Table 1. Interspecific competition appears to be an important mortality factor during this population phase of the mountain pine beetle and may be largely responsible for the regulation of population fluctuations. The activity of secondary beetles may affect endemic mountain pine beetle populations in several ways. Exploitation of the limited resource of low-vigour trees through attacks during previous seasons or earlier in the same season will preempt mountain pine beetle breeding space. Furthermore, since many of the bole-infesting bark beetles are bivoltine, their second broods often compete directly with mountain pine beetle for phloem.

Based upon the above discussion, an endemic population can be characterized as follows.

- The diameter of attacked trees is less than the stand average (although occasional large-diameter trees are attacked following sudden, near-lethal stress such as lightning or windthrow).
- Attack densities are very low; often only two or three galleries per tree.
- Attacks are preceded in the current or previous season(s) by attacks from secondary, bole-infesting bark beetle species (see Table 1).

- Currently attacked trees are not located near brood trees.
- Yearly tree mortality is less than yearly volume growth within a stand.

Another important characteristic of endemic populations is that they are in a dynamic balance with their environment so that, over a number of generations, there is no significant change in population size. For populations to maintain this balance (i.e., to remain more or less static) in time and space for a number of generations, they must suffer very high levels of generation mortality. Given an average number of eggs per female (E) and an average female ratio (R), the relationship between generation mortality (M) and potential change in population size (P) is as follows:

$$P = ER(1 - M) \quad [1]$$

where M is expressed as a proportion.

To maintain static population levels among generations, $P = 1$. Therefore, the corresponding generation mortality $M = 1 - 1/ER$. Since female mountain pine beetles lay on average 60 eggs, about two-thirds of which will be females (Reid 1962b), the beetle population has to suffer a generation mortality in the order of $M = 97.5\%$ to remain static (Fig. 19).

Under endemic conditions a large number of factors may interact to limit beetle populations from increasing. However, given that endemic beetle populations are relatively small, host availability (the scarcity and patchy distribution of suitable trees to attack), host quality and interspecific competition are thought to be the most important factors. Since endemic populations exist mainly in suppressed and otherwise weakened trees, stand hygiene (i.e., the removal of suppressed and damaged trees) may be an effective means of limiting the localized build-up of mountain pine beetle populations.

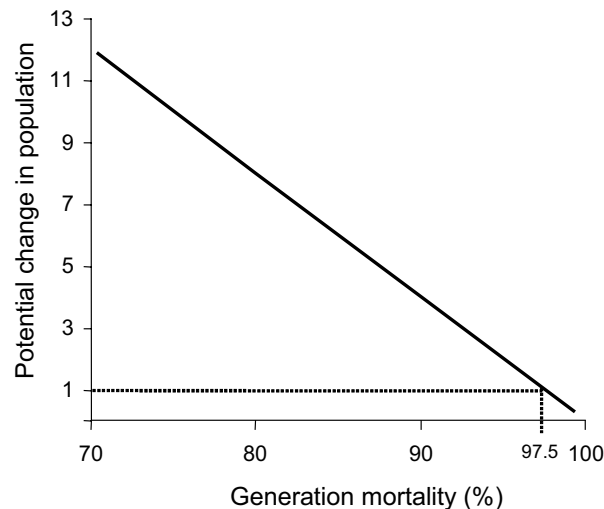


Figure 19. Relationship between the yearly potential change in populations and generation mortality of mountain pine beetle populations, assuming that populations are two-thirds females with a mean fecundity of 60 eggs/female. The dotted line indicates the level of generation mortality (97.5%) required for populations to remain static (i.e., potential rate of change = 1).

Incipient-epidemic populations

We define this phase as one where mountain pine beetle populations have grown to a minimum size sufficient to successfully mass attack a single large-diameter tree within a stand. Because large-diameter trees tend to be the most resistant within stands (Shrimpton 1973a), the main factors that permit the populations to escape the endemic phase are those that cause 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 a period of drought, or it could be a permanent consequence of senility, disease or damage. A number of consecutive years with warm and dry weather during the flight and dispersal periods, combined with mild winters, has been associated with sustained increases in beetle populations (e.g., Safranyik et al. 1974, 1975). 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.

Berryman (1982b) defined the minimum beetle population size necessary for colonizing the larger-diameter components in a stand as the epidemic threshold. The concept of the epidemic threshold in relation to beetle population size and stand resistance is illustrated in Figure 20. In most situations, incipient-epidemic populations are the beginning stages of epidemics. However, where stands suffer from temporary weakening, such as short-term drought in younger stands, incipient populations usually decline back to the endemic state once the stands have recovered (Fig. 20). In addition, during the early stages of the incipient-epidemic phase, attack densities may be relatively low, allowing overlapping attacks by secondary bark beetle species such as *I. pini* (Hopping 1961; Wood 1982; Amman and Safranyik 1985). Reduced brood production associated with interspecific interactions may also return a mountain pine beetle population to the endemic state. Similarly, increased impacts by natural enemies, especially woodpeckers, may act to hold localized mountain pine beetles below the epidemic threshold.

The tenuous nature of the incipient-epidemic phase is illustrated in Figure 21. For a mountain pine beetle population with a generation mortality sufficient to maintain a static population (i.e., 0.975; see Fig. 19), the probability of extinction, as defined by Bartlett (1956), remains extremely high unless populations are reasonably large (Fig. 21). However, if conditions are ideal for mountain pine beetle survival and generation mortality declines, for example to 0.850 [equivalent to a yearly six-fold increase in populations (Fig. 19)], the probability of extinction diminishes to zero even with very small populations (Fig. 21).

Incipient-epidemic populations are distinct from endemic populations in several ways. Based upon the pattern of trees infested, they have the following characteristics.

- Most of the infested trees have larger diameters.
- Clumps of infested trees are scattered and confined to parts of individual stands.
- The groups of infested trees vary considerably in size and number from year to year but tend to grow over time.

- Perhaps as a consequence of localized pockets of tree stress, groups of infested trees are frequently associated with draws and gullies, edges of swamps or other places with wide fluctuation in the water table, places where lodgepole pine is growing among patches of aspen (possibly indicating the presence of root disease), and areas on dry, south-facing and west-facing slopes.

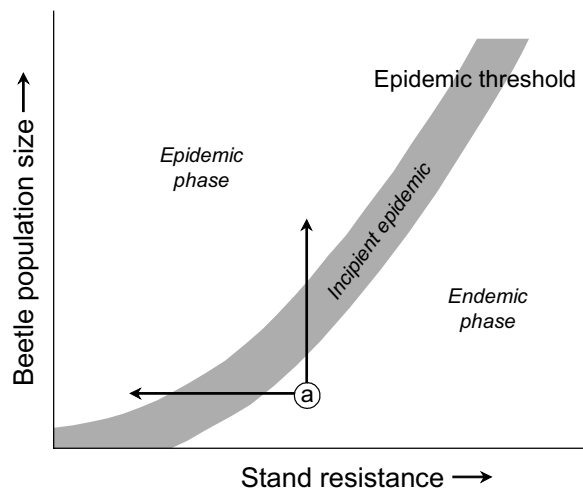


Figure 20. Conceptual representation of the threshold nature of mountain pine beetle population states. Populations in the endemic phase (a) may cross the threshold to the epidemic phase through reductions in stand resistance and/or increases in beetle numbers (as indicated by arrows). Beetles may reach the intermediate incipient-epidemic phase (shaded area) and return to the endemic state if reduced stand resistance is ephemeral and/or the magnitude of the increase in beetle numbers is insufficient to maintain an increasing population. Modified from Berryman (1982b).

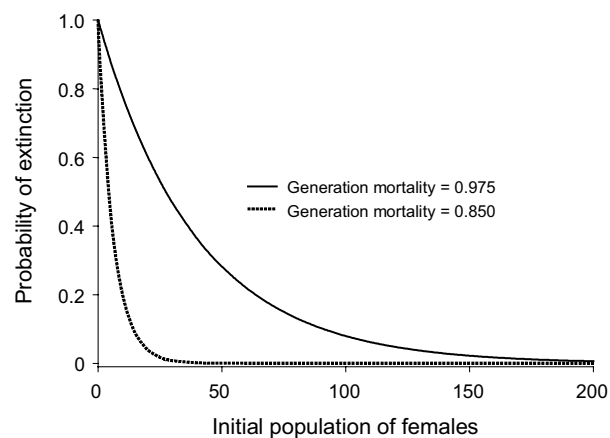


Figure 21. Probability of extinction (Bartlett 1956) for a mountain pine beetle population versus the initial population of females where generation mortality is either 0.975 (solid line) or 0.850 (dotted line). Extinction probability was calculated as $(D/B)^F$, where D = death rate, B = birth rate; and F = initial female population (Bartlett 1956). See also Fig. 19.

During and following the development of incipient-epidemic populations, there is a strong positive linear relationship between mortality and tree diameter. Expressed in terms of the number of trees killed in a diameter class (i.e., dbh) in a given area (N_k), the relationship between mortality and dbh (D_c) is as follows:

$$N_k = 0, D_c < a/r \quad [2]$$

$$N_k = N_c(rD_c - a), a/r \leq D_c \leq (1 + a)/r \quad [3]$$

$$N_k = N_c, D_c > (1 + a)/r \quad [4]$$

where N_c is the number of trees in dbh class D_c , a is a constant such that the minimum dbh for killed trees is a/r , and r is the mortality rate per unit dbh above a/r . In this form the relationship indicates that tree mortality is a function of both tree diameter and the number of live trees in that dbh class. Interestingly, the same relationship can be derived based on an assumption of random search by the attacking beetles and the probability of landing being proportional to the silhouette (i.e., dbh) of trees above a minimum size (Safranyik et al. 2004).

Generally, incipient-epidemic populations grow relatively slowly at first. Indeed, averaged over a number of generations the rate of increase may not exceed two. As a consequence, there may not be much noticeable change in infestation levels for up to five or more years. Eventually, however, as long as populations do not fall back below the epidemic threshold there will be a sustained yearly growth in beetle population size with corresponding increases in size and number of infested spots. Spot infestations will coalesce into larger patches and new infested spots may develop in several adjacent stands (see Fig. 6). This situation marks the beginning of the onset of epidemic-level infestations.

Epidemic populations

As a consequence of the growth and expansion of local incipient-epidemic populations combined with long-range dispersal, epidemic populations exist at the landscape level. If large areas of susceptible host, such as mature lodgepole pine, coincide with sustained favourable weather conditions for beetle establishment, development, and survival, outbreaks may spread over many thousands of hectares.

Epidemic populations have the following characteristics.

- They are resilient to proportionally large losses in their numbers. This generally means that the larger the population size (and the infested area) the less likelihood of collapse from adverse factors such as unseasonably cold temperatures.
- Generation mortality is usually in the range of 80% to 95%, corresponding to potential rates of population increase of approximately two- to eightfold each year (see Fig. 19). The usual annual rate of increase, however, is two- to fourfold taken over the entire area of the epidemic.
- Infestations are widespread and exist at the landscape level.
- There are usually large annual increases in both infested areas and numbers of infested trees.

Outbreaks tend to be synchronized over much of the distribution of the mountain pine beetle. This may be due to the Moran effect (Moran 1953; Royama 1992). 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 climate and weather that function over large areas.

The following factors are the main determinants of yearly changes in population and damage levels during outbreaks: i) size of the parent beetle population; ii) stand characteristics such as species composition, density, age and diameter distribution; iii) the spatial distribution of stands of different susceptibility; iv) weather events; and v) intraspecific competition. Natural enemies are thought to be of minor importance to epidemic populations due to their inability to respond in a density-dependent manner. Similarly, interspecific competition has little impact compared with the endemic and incipient-epidemic phases because much of the infested bark area is fully colonized by the mountain pine beetle (Berryman 1976).

During epidemics, tree mortality is usually proportional to tree diameter above a certain minimum value. The minimum dbh where little or no mortality occur varies somewhat with stand characteristics and infestation intensity, but is usually close to 10 cm (Safranyik et al. 1974). The expected rate of mortality above this minimum diameter is in the range of 1.5% to 4.0% with each centimeter increase in dbh (Fig. 22). As a consequence of this pattern of mortality, trees in the larger diameter classes are often severely depleted. Although some stands may sustain nearly complete mortality, average mortality in mature stands over the landscape will be much less, normally in the range of 30% to 45% of trees. However, because proportionately more of the larger-diameter trees are killed, the volume of killed trees will be proportionately much greater. At the landscape level, the relative severity of mortality in the various stands will generally reflect tree and stand susceptibility as defined in Shore and Safranyik (1992).

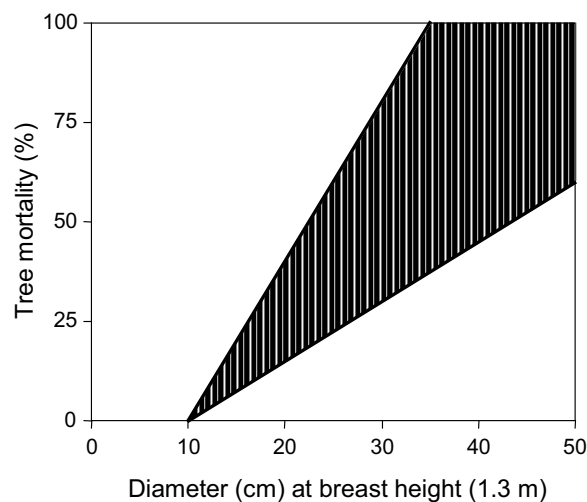


Figure 22. Relationship between tree mortality within stands and diameter above a threshold of 10 cm during a mountain pine beetle epidemic. Above the diameter threshold, the rate of mortality ranges from 1.5% (lower line) to 4% (upper line) with each centimetre increase in diameter.

Outbreak populations collapse primarily from one or a combination of the following two factors: i) unseasonably cold weather conditions during the late fall to early spring period; ii) the large-diameter susceptible host components of stands have been killed. In the final stages of population decline, increased mortality from natural enemies, inter- and intraspecific competition may also have an impact.

Post-epidemic populations

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 as a consequence of lethal low temperatures, the residual beetle population generally breeds in the same type of trees that were attacked prior to the decline. However, as there are far fewer beetles, many trees may only be partially attacked. As well, the rate of accumulation of attacks may be reduced. Consequently, brood survival will be reduced due to the expression of host resistance resulting from an insufficient mass attack. Another consequence of reduced beetle numbers is that interspecific competition for food and space (Safranyik et al. 1999b), as well as predation and parasitism, once again may become important factors affecting populations. By contrast, when the collapse of epidemics is primarily due to local depletion of suitable hosts, subsequent generations of beetles are forced to breed in trees of reduced nutritional quality or increased resistance and will likely suffer mortalities of similar magnitude as those occurring in endemic populations.

During outbreaks, large populations of some secondary bark beetle species such as *I. pini* will build up in portions of the bole not utilized by mountain pine beetle [e.g., high on the stem where the phloem becomes thin (Amman and Safranyik 1985)]. For one to three years following the collapse of mountain pine beetle outbreaks, these secondary species may kill large numbers of pine trees, mainly in the lower diameter classes (Safranyik et al. 1974).

In western Canada, the average duration of epidemics has been about 10 years. Most persist for more than five years, while the longest recorded epidemic continued for about 18 years (Safranyik et al. 1974). Based on the assumptions that (i) mean outbreak duration in the region is 10 years, (ii) minimum duration is five years, (iii) outbreak-terminating events follow a geometric temporal distribution, and (iv) the future will repeat the past, predictions of the probability of outbreak collapse as a function of years since initiation are possible. Based on a fixed expected probability of outbreak collapse in year i , for years 6 to 18 given that it has not collapsed prior to year i , then:

$$Y_i = \sum_{j=1}^n P(1 - P)^{(i-j)} \quad [5]$$

where Y_i = the cumulative distribution of the probability of outbreak collapse as a function of the number of years since the start of the outbreak ($Y_i = 0$ when $i \leq 5$); $n = i - 5$; $P =$ expected (average) probability of outbreak collapse ($1/(10-5) = 0.20$) for years 6 – 18. If the

expected probability of collapse increases with years after year 6, then the equation changes to become:

$$Y_i = \sum_{j=1}^n \left[\left\{ \prod_{k=1}^j (1 - P_{k-1}) \right\} P_j \right] \quad [6]$$

where P_j = the probability of outbreak collapse in year j given that it has not occurred in previous years, and the symbol Π designates a mathematical product. P_j is calculated as the product of the average probability of outbreak collapse (P in equation 5) and the ratio $(m+1-i)/(m-i)$, where m = maximum observed outbreak duration (i.e., 18 years).

Figure 23 is a graphical representation of the two models. If the probability of epidemic collapse increases with time since outbreak initiation (equation 6), then the probability of outbreak termination (Y_i) after 10 and 15 years is 75% and 98%, respectively. These probabilities are approximately 12% higher than the corresponding estimates of Y_i based on a fixed probability of outbreak collapse (equation 5; Fig. 23). While these two models are useful for projecting the potential impacts of outbreaks, it should be noted that changing climatic conditions may alter the course of future epidemics (Carroll et al. 2004).

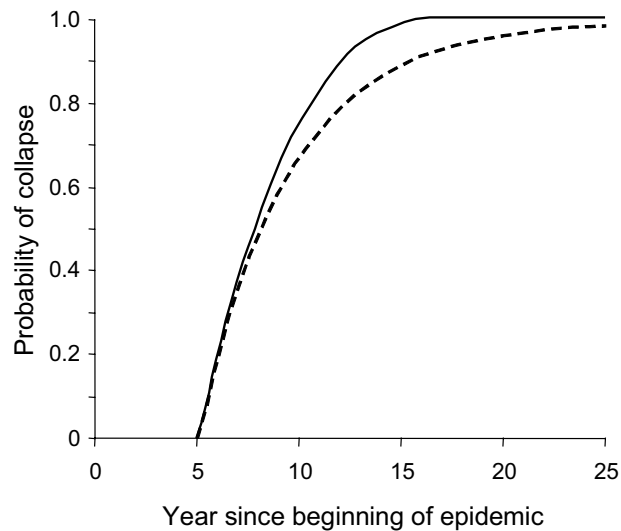


Figure 23. Predicted probability of epidemic collapse as a function of years since outbreak initiation based upon an increasing probability of collapse (solid line) and a fixed probability of collapse (dashed line). See text for details.

Population regulation

Regulation is a stabilizing process characterized by negative feedback and is caused by factors whose intensity of action is related to population density (e.g., Royama 1992). These are called density-dependent factors. The effects of food (availability, quantity, quality), habitat and parasitism/predation often (but not always) are density-dependent factors. Weather and edaphic conditions are examples of density-independent factors. Regulation in the sense described above does not necessarily prevent population eruptions; population density is determined by the interaction of density-dependent and density-independent factors (see Royama 1992).

Amman and Cole (1983) and Amman (1984) showed that for mountain pine beetle populations from the southern Rocky Mountains, the density-independent effects of temperature extremes caused the greatest amount of mortality overall. Phloem drying, a factor that becomes increasingly important with increasing brood density, was the second most important factor in epidemic and post-epidemic infestations. Of the insect's natural enemies, *Medetera aldrichii* (Fig. 16a,b) was the only one that showed a consistent density-dependent response over time. Mortality from woodpeckers showed a weak density-dependent response, especially in pre-epidemic infestations when the birds concentrated on the few available infested trees. In general, the relative effects of mortality factors varied by the size of trees and the state of the mountain pine beetle infestation.

It is generally accepted that, for a localized mountain pine beetle population, host availability is the primary density-dependent factor affecting the epidemic population state. Indeed, even at the landscape level, in the absence of a widespread density-independent mortality event such as extreme unseasonable cold, epidemic populations will persist until they deplete the host resource (e.g., Safranyik et al. 1975). As epidemic beetle populations increase, the largest trees in a stand will be attacked first. With each successive generation, as the large-diameter hosts are depleted, beetles are forced into smaller and smaller trees and the resultant increasingly deleterious effects of intraspecific competition will ultimately cause populations to collapse. For example, high attack densities in small-diameter trees leads to increased mortality due to phloem drying (Amman and Cole 1983). Moreover, the thinner, less nutritious phloem of increasingly smaller host trees leads to smaller adult females and lower fecundity (Amman and Pace 1976; Amman and Cole 1983).

Host availability is also the primary factor regulating endemic mountain pine beetle populations. Locally, there may be many potential host trees, but because of host resistance only those with severely impaired vitalities are available to endemic populations. These trees are often in short supply and are widely scattered over the landscape. Hence, mortality during dispersal and host finding is likely one of the main factors determining the rates of population change in endemic populations.

In a recent study of endemic mountain pine beetle populations, the authors (unpublished data) have found that, in the absence of significant emigration from neighbouring populations, interactions among competitors, host resistance and the mountain pine beetle

may be the primary factor limiting the transition from the endemic to incipient-epidemic state. In pine forests, bole-infesting secondary bark beetles have specialized to attack suppressed and damaged trees. In contrast, mountain pine beetle fitness is low in these trees due to their thin phloem. However, endemic populations comprise too few beetles to mass attack a healthy, thick-phloem tree, and therefore, are restricted to suboptimal trees in direct competition with secondary beetles. As discussed above, secondary beetles can restrict endemic mountain pine beetles through both exploitation (i.e., preempting potential breeding space) and interference (i.e., direct competitive interactions) competition. The form of this interaction is shown in Figure 24a. Stress events, such as among-tree competition, or biotic or abiotic damage, will reduce the vigour of some trees in a stand, thereby increasing the number of trees susceptible to bark beetles. This will have a positive influence on the amount of food available to both secondary and endemic mountain pine beetles. The increased food available to secondary bark beetles will increase their brood production, which in turn will exploit the resource (thereby reducing their own food availability). At the same time, the increased resource will have a positive influence on food availability to mountain pine beetle brood (who also reduce their own food availability); however, the rapid and effective exploitation of these trees by secondary beetles will reduce the food available to mountain pine beetle (Fig. 24a), thereby restricting their numbers.

It requires only a subtle shift for this interaction to change and allow mountain pine beetles to escape to the incipient-epidemic phase (Fig. 24b). If the stress within a stand increases (as a result of drought, for example), then the number of susceptible trees and the amount of food available to the bole-infesting bark beetle assemblage, including the mountain pine beetle, will increase. If the increase is sufficient for the mountain pine beetle population to gain access to an average, large-diameter tree within a stand, it may breach the endemic-epidemic threshold and enter the incipient-epidemic phase (Fig. 20). In general, the secondary bark beetle assemblage cannot tolerate tree resistance to the same extent as the mountain pine beetle. Thus, the mountain pine beetle can escape the constraint of interspecific competition that limits endemic populations. Furthermore, the beetle no longer strictly depends on a stress event to gain access to hosts. Provided the stand has sufficient large-diameter trees and weather conditions remain amenable to beetle survival, the dramatic increase in populations associated with brood production in larger trees (Fig. 25) effectively means that in the incipient-epidemic phase most trees in a stand are susceptible to attack. Thus, a short-term positive feedback loop is formed (Fig. 24b), and populations may grow to the epidemic phase.

The relationship with secondary beetles changes dramatically with the transition from the endemic to the incipient-epidemic state. Primary attacks of healthy trees by the mountain pine beetle often increase the amount of food available to secondary species (Fig. 24b), and those secondary species will attack unexploited portions of the phloem of dying trees early the next season. Thus, mountain pine beetle populations may regulate the bole-infesting secondary bark beetle assemblage during the incipient-epidemic and epidemic phases.

An epidemic forms as localized infestations coalesce over the landscape. This entails emigration of mountain pine beetles from the localized points of increase into neighbouring stands, thereby facilitating the endemic – incipient epidemic transition of resident populations. During the epidemic phase, since the mountain pine beetle is the first to initiate attacks in relatively resistant trees, it is able to largely escape competitive interactions with the rest of the bole-infesting bark beetle assemblage (Fig. 24c). However, the rapid increase in populations often quickly depletes the host resource and the positive feedback loop that developed in the incipient-epidemic phase begins to locally break down (Fig. 24c).

Within individual stands, the collapse of populations during the post epidemic phase is precipitated largely by the depletion of susceptible trees. In addition, it is common for large populations of secondary bark beetle species that have built up in the unexploited portions of mountain pine beetle-killed trees during the epidemic phase to once again exert significant competitive pressure and exacerbate the collapse (Fig. 24d). The renewed interspecific interactions manifest as both interference competition where secondary beetle species, notably *Ips pini* (Safranyik et al. 1999b), attack amongst the declining density of mountain pine beetles, and exploitation competition where the elevated secondary populations are capable of attacking any residual healthy larger-diameter trees remaining in the stand. At the landscape level, epidemics will continue until the losses from mortality factors within trees and from dispersal exceed beetle production in the available trees.

There is compelling evidence that endemic mountain pine beetle populations are limited by interactions among the secondary bark beetle assemblage and host tree resistance. In a four-year study in which every stem within six mature lodgepole pine stands (three at each of two sites; mean (\pm SE) stand size = 14.9 ± 0.96 ha) in south-central British Columbia was assessed at four-week intervals for the presence of bole-infesting bark beetles (see Table 1), three stands transitioned from endemic to incipient-epidemic phases as defined above, without detectable mountain pine beetle emigration (unpublished data). In each case, the escape by mountain pine beetle populations from the endemic state was preceded by a drought event followed by one or two years of elevated secondary bark beetle activity (Fig. 25). The increase in attacks by the bole-infesting bark beetle assemblage (including endemic mountain pine beetles) as a consequence of a localized increase in stress facilitated an increase in the endemic mountain pine beetle past the endemic-epidemic threshold (see Figs. 20 and 24b).

The escape from competitive interactions with the secondary bole-infesting bark beetle assemblage is characterized in Figure 26 (unpublished data). During the endemic phase, beetles colonized trees in diameter classes not significantly different than the stand averages (19.9 – 21.9 cm), but as the assemblage of beetles increased in stands (Fig. 25), and the mountain pine beetle populations entered the incipient-epidemic phase, the diameter of successfully attacked trees increased by nearly 40% (Fig. 26a). In gaining access to the relatively resistant, larger-diameter trees within a stand, the mountain pine beetle effectively eludes the remainder of the bole-infesting beetle assemblage. Indeed, during the endemic to incipient epidemic transition, the percentage of trees colonized by the mountain pine beetle that were previously attacked by other bark beetle species declined from approximately 70% to less than 5% (Fig. 26b).

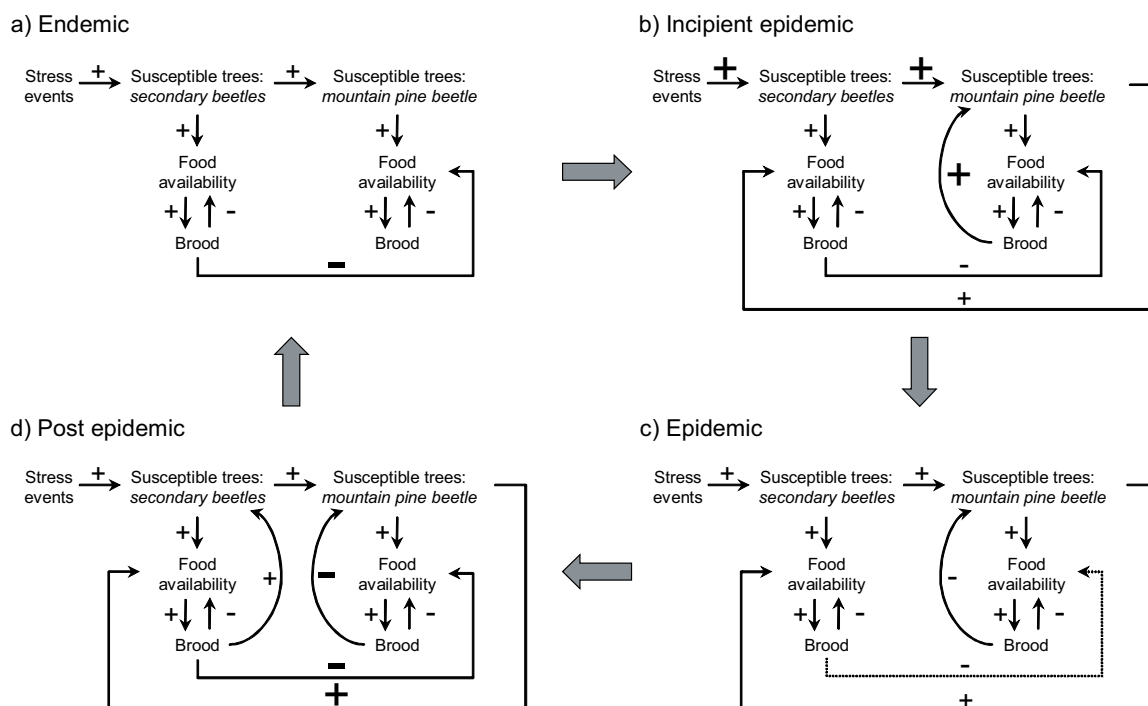


Figure 24. A schematic representation of the interaction among lodgepole pine, secondary bark beetle species, and the mountain pine beetle as its populations cycle through the endemic (a), incipient-epidemic (b), epidemic (c), and post-epidemic (d) phases. Arrows accompanied by ‘+’ and ‘-’ indicate positive and negative effects, respectively, whereas the size of the symbols represent the strength of the interaction. Arrows with a dotted line represent a very weak or insignificant interaction. See text for details.

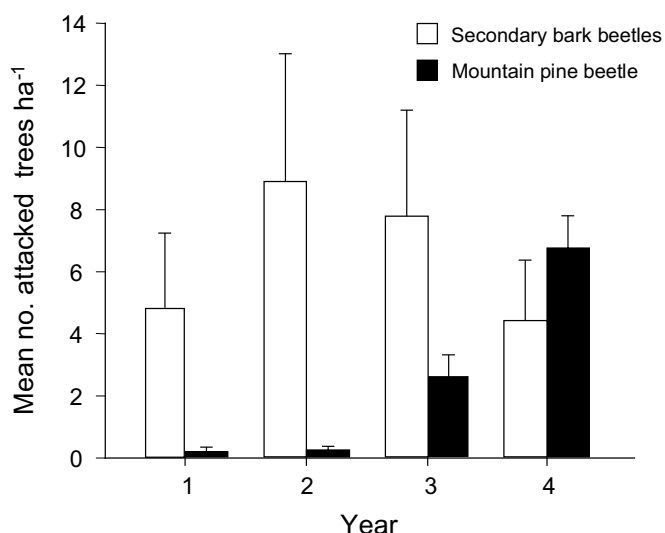


Figure 25. Mean (\pm standard error) number of trees per hectare either mass attacked by the mountain pine beetle (black bars) or infested by secondary bark beetle species (white bars) in three mature lodgepole pine stands in southern British Columbia over four years as mountain pine beetle populations increased from the endemic to the incipient-epidemic state. See text for description of population states.

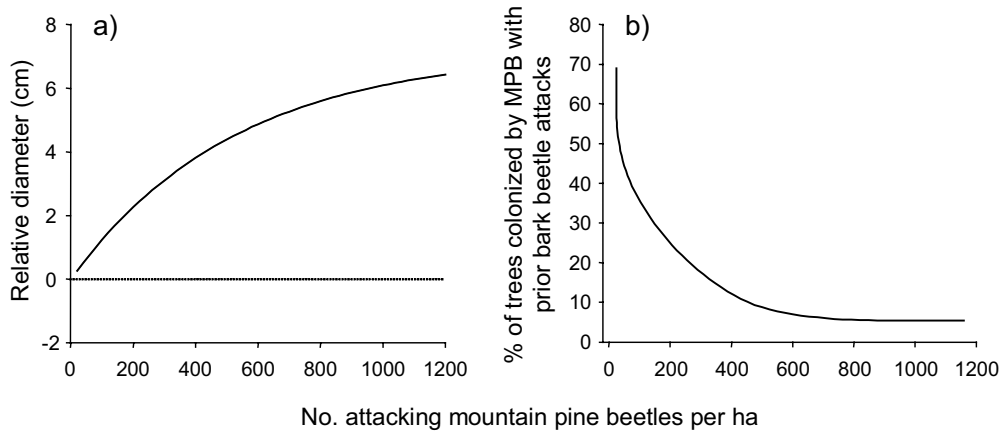


Figure 26. Relationships between the relative diameter (attacked – stand average) of trees attacked by mountain pine beetle (MPB) (a), and the percentage of trees it colonized that were attacked previously (in the same season, or in previous years) by other bole-infesting bark beetle species (b), versus the number of attacking mountain pine beetles per hectare in three mature lodgepole pine stands in southern British Columbia.

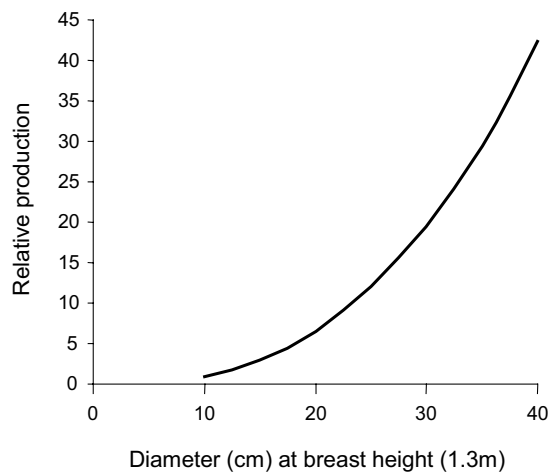


Figure 27. Mountain pine beetle brood production in lodgepole pine trees of different diameters in relation to a 10-cm-diameter tree. Based on Safranyik et al. (1975) and Safranyik (1988).

The critical nature of the endemic to incipient epidemic transition to mountain pine beetle populations can be seen in Figure 27. Until the beetle can gain access to large-diameter trees, the potential rate of increase is very small. In fact, roughly 40 times the number of beetles will emerge from a 40-cm tree when compared with a 10-cm tree (Fig. 27). The constraints imposed by interspecific competition for suppressed and damaged trees may have selected for the “aggressive” attack of healthy, resistant trees by mountain pine beetle.

Summary and conclusions

The potential for mountain pine beetle populations to establish, persist and ultimately increase to epidemic levels in lodgepole pine forests depends on the coincidence of large amounts of susceptible hosts on the landscape, several years with weather that is conducive to beetle survival, and the complex interaction of an intricate suite of life-history traits. The critical aspects of mountain pine beetle life history are:

- An efficient host-selection behaviour that enables beetles to discover even sparsely distributed patches of suitable host trees;
- A significant dispersal capacity that enables beetles to move over short (i.e., hundreds of metres) and long (i.e., hundreds of kilometres) distances;
- A highly evolved mutualistic relationship with ophiostomoid “blue stain” fungi that facilitates access to trees that are otherwise too resistant to successfully colonize;
- A semiochemical communication system that mediates “mass attacks” of highly resistant host trees while at the same time minimizing intraspecific competition by regulation of attack density;
- Stage-specific developmental thresholds that ensure synchrony of development with the growing season, increase the chance that the most cold tolerant stages (the larvae) will overwinter, and lead to temporally coincident emergence of adults to facilitate mass attacks; and
- Subpopulation-based development rates to ensure synchronous univoltine development over a large part of the distributional range.

Based upon the nature of their interactions with host trees and the assemblage of bole-infesting secondary bark beetle species, there are four distinct phases in the population cycle of the mountain pine beetle: endemic, incipient-epidemic, epidemic (i.e., outbreak) and post-epidemic (i.e., declining) populations. Endemic populations are defined as those with insufficient beetles to overcome a single large-diameter tree within a stand. A complex of factors interact to cause sufficient generation mortality in endemic populations ($\approx 97\%$) such that, on average, their yearly rate of increase equals unity (i.e., populations are stable). Because endemic beetles are restricted to suppressed or damaged trees in direct competition with an assemblage of “secondary” bark beetle species that have evolved as specialists on such a resource, interspecific competition is one of the primary factors limiting endemic populations. As a consequence of increasing stress within lodgepole pine stands, secondary beetles and mountain pine beetles may increase in concert such that the latter may escape the endemic phase and attack a large-diameter, high-quality host tree. This is the incipient-epidemic phase which may expand to the epidemic phase if conditions remain conducive to beetle survival and there are sufficient large-diameter trees within stands. Access to large-diameter trees is critical to mountain pine beetle populations; brood production is more than 40 times greater in a 40-cm versus a 10-cm-diameter tree. Epidemic populations occur on the landscape and, due to their sheer size, extent and potential rate of increase (two - to eightfold, yearly), they are highly resilient to losses. In the absence of a widespread extreme

weather event, epidemics will normally continue until most of the large-diameter trees on the landscape are depleted, at which point intraspecific interactions within a host resource of diminishing quality will cause populations to collapse. During the post-epidemic phase, large populations of some secondary bark beetle species such as *Ips pini* will build up in portions of the bole not utilized by mountain pine beetle and for several years following the collapse of mountain pine beetle outbreaks, they may kill large numbers of pine trees, mainly in the lower diameter classes.

From our review of the biology and epidemiology of the mountain pine beetle, several management implications emerge.

- 1) Given the large contiguous forests of lodgepole pine that dominate much of northwestern North America, and evidence for a warming climate (see Carroll et al. 2004), future large-scale mountain pine beetle outbreaks are highly probable and will necessitate new, efficient control strategies and tactics.
- 2) Mountain pine beetle populations have a significant capacity to erupt and rapidly coalesce over vast landscapes. Consequently, effective control programs must be based on early detection and implementation, and a continuous commitment of resources.
- 3) Since past forest management has shifted the age-class structure of most pine forests in western Canada into the range where they are highly susceptible to mountain pine beetle (Taylor and Carroll 2004), the most viable means of mitigating future impacts in the long term is to shift the management focus from the beetle to strategies for managing lodgepole pine age-classes, host vigour and stand resistance on the landscape.

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