

The bionomics of the mountain pine beetle in lodgepole pine forests: establishing a context

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Abstract

Due to the significant impacts of mountain pine beetle (*Dendroctonus ponderosae* Hopk.) epidemics on the pine forests of western North America, there exists an extensive body of literature devoted to its bionomics. This paper reviews the critical aspects of mountain pine beetle biology and ecology that enable its eruptive population fluctuations in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) forests: dispersal and colonization; insect-host interactions; cold tolerance; and synchrony and phenology. The potential for mountain pine beetle populations to establish, persist and ultimately increase to outbreak levels is a function of the beetle's capacity to locate, colonize and reproduce within highly resistant host trees situated in thermal environments conducive to overwintering survival and with sufficient heat accumulation to maintain a synchronous univoltine life cycle. Management strategies and tactics intended to mitigate the impact of outbreaks must be based on an understanding of the effects these constraints have on populations and the subsequent adaptations that the mountain pine beetle has evolved to overcome them.

Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopk.) is a native insect that occurs in pine forests over much of western North America, extending from northern Mexico to northwestern British Columbia (BC) and from the Pacific Ocean east to the Black Hills of South Dakota (Wood 1982). Normally mountain pine beetle populations are innocuous, and only a few scattered infested trees are to be found within a forest. However, during outbreaks, which occur at irregular intervals and may persist for periods of 5 to 20 years, trees may be killed over vast areas (Safranyik 1988). In recent years, the mountain pine beetle has caused extensive mortality over millions of hectares of forests in central BC (Ebata 2004). In stands managed for commercial production, the direct economic losses during such an outbreak are usually greater than that indicated by the volume loss because most mortality is among the larger-diameter trees (Safranyik et al. 1974). In addition to extensive timber losses, mountain pine beetle epidemics may increase fuel loading, hasten succession to the climax forest type, affect watershed quality, wildlife composition, and recreational values (Safranyik et al. 1974; McGregor 1985).

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Due to the impacts of the mountain pine beetle on forest resource values, many aspects of its biology and population dynamics have been studied during the last 60 years. Consequently, there exists an extensive body of literature devoted to this insect. This paper comprises a review of mountain pine beetle bionomics. It is not intended to be exhaustive, but is instead meant to be a comprehensive discussion of aspects of mountain pine beetle ecology that form the basis of its temporal and spatial dynamics in pine forests. Furthermore, even though virtually all species of pine within its range are suitable hosts for the beetle (Furniss and Schenk 1969; Smith et al. 1981; Wood 1982), due to the size, intensity and commercial impact of epidemics, this review will concentrate on mountain pine beetle in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) forests.

Predicting the mountain pine beetle's impacts on the landscape and implementing effective management strategies to mitigate losses during an outbreak can only happen if those efforts are built upon a solid understanding of the beetle's bionomics. The potential for mountain pine beetle populations to establish, persist and ultimately increase to epidemic levels in lodgepole pine forests depends on the capacity for beetles to locate and colonize suitable host trees in environments with favourable climatic conditions. This paper discusses the critical aspects of mountain pine beetle bionomics required for outbreak development: dispersal and colonization, insect-host interactions, cold tolerance, and synchrony and phenology.

Dispersal and colonization

Dispersal

Although dispersal is arguably one of the most important aspects of mountain pine beetle ecology, it is perhaps the least understood. The dispersal phase begins with emergence and ends as beetles orient toward new host trees. Dispersal flights may be short range (i.e., within a single stand), or long range (i.e., among stands). At the population level, these types of dispersal lead to either the growth of local infestations (i.e., spot growth), or the proliferation of new ones (i.e., spot proliferation), respectively (Safranyik et al. 1992; Safranyik, 2004).

Prior to emergence, young beetles complete maturation by feeding on the inner bark and on spores of fungi and other microorganisms which line the walls of their pupal chambers. This enables the flight muscles to increase in size (Reid 1958), and the mycangia (specialized compartments on the maxillae) to become charged with spores, thereby ensuring transport of necessary fungi and microorganisms to new trees (Whitney and Farris 1970; Safranyik et al. 1975). Upon completion of maturation feeding, temperature becomes the primary determinant of the onset of emergence and the initiation/duration of the dispersal period. Emergence occurs only when ambient temperatures exceed 16°C (Reid 1962a; Schmid 1972; Billings and Gara 1975) and declines above 30°C (Gray et al. 1972; Rasmussen 1974). Most beetles emerge during the mid-afternoon when temperatures reach approximately 25°C (Fig. 1).

From year to year, the peak of emergence may vary by as much as 1 month, but normally varies by less than 10 days (Reid 1962a; Safranyik 1978). Throughout most of BC, peak emergence usually occurs 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 and/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 humidity. Once temperatures exceed 35°C, beetles begin to respond negatively to light (Shepherd 1966), and above 38°C flight is severely restricted (McCambridge 1971).

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 velocity, is approximately 2 ms^{-1} (Rudinsky 1963).

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 will disperse out of a stand (Safranyik et al. 1992). The tendency for beetles immediately following emergence to be non-responsive to aggregation pheromones suggests that a flight period is required before they adopt a 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 meters 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 (Safranyik et al. 1989, 1992). Beetles that do not disperse from the stand in which they develop usually locate suitable host trees within 2 days of emergence, but are capable of searching for several days (Safranyik et al. 1992).

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 incipient population and would likely be much higher during an outbreak when locally available host trees have been depleted. Given that beetles fly during warm, fair-weather periods 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 kilometers from potential host trees, indicating that long-range dispersal likely occurs during outbreaks and may be an important factor in the spread of epidemics.

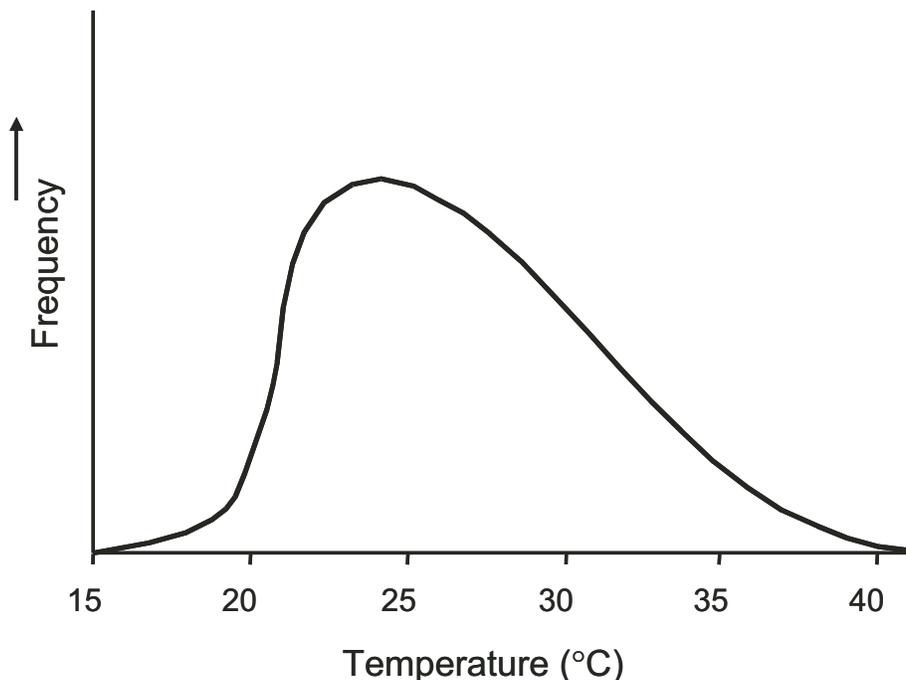


Figure 1. Frequency of emergence of mature mountain pine beetle in relation to temperature. Adapted from McCambridge (1971).

Colonization

Colonization involves establishment of initial attacks on host trees by pioneer beetles followed by aggregation and mass attacks of these trees in response to a combination of volatiles produced by the host tree and the beetle.

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 large, dark silhouettes (Shepherd 1966) and vertically oriented cylinders (Billings et al. 1976) are attractive to beetles. By contrast, Hynum and Berryman (1980) 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.

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., Pureswaran and Borden 2003), there is evidence that dispersing adults orient to lodgepole pine trees suffering from injury or disease (Gara et al. 1984). 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 (see Borden et al. 1987 and references therein). As pioneer females penetrate the bark they release the pheromone trans-verbenol which acts in combination with myrcene, a tree volatile, to attract mainly male beetles. Responding males release exo-brevicomin and later frontalin, which in combination with trans-verbenol and myrcene attracts mainly females. Autoxidation of another tree volatile, α -pinene, and microbial conversion of trans-verbenol (and cis-verbenol) result in production of the anti-aggregation pheromone verbenone. As the beetles approach optimal colonization density on a tree [approximately 60 attacks per m² of bark (Raffa and Berryman 1983a)], verbenone in combination with large amounts of exo-brevicomin and frontalin results in close-range redirection of responding beetles to nearby trees.

The process of mass attack on an individual tree is normally completed in 1-2 days. The subsequent redirection of beetles to nearby trees results in clusters of dead trees (i.e., a spot infestation).

Insect-host interactions

In the course of a mass attack, female beetles begin constructing galleries in the phloem and males join them once the gallery has been initiated. Following mating, females extend the galleries vertically and plug the entrance hole with boring dust. Males often assist females at this stage, but sometimes leave the gallery shortly after mating. Typically 60 – 80 eggs are laid singly in niches (approximately 2 eggs/cm) along the margins of the gallery (e.g., Safranyik et al. 1974). However, oviposition will cease if the moisture contents of the inner bark and outer sapwood drop below approximately 105% and 60% oven dry weight, respectively (Reid 1962b). If this occurs, the female will re-emerge to make a second flight and attack. Consequently, there may be significant differences in the number of eggs per gallery between trees in the same infestation. Eggs hatch within about 2 weeks and larvae mine the phloem circumferentially, developing through four instars. Broods normally overwinter as larvae and complete their development in the spring.

The mountain pine beetle preferentially attacks large-diameter trees. This is because characteristics of the stem that are related to tree diameter are the primary determinants of a tree's potential to produce beetles once it has been successfully colonized. For example, attack densities are higher on trees with rough versus smooth bark as females prefer to initiate galleries in bark crevices (Safranyik 1971). In addition, trees with thick bark tend to produce more brood than thin-bark trees due to the protection it provides from natural enemies and temperature extremes (Reid 1963; Safranyik et al. 1974). Similarly, the

number of surviving progeny is positively related to phloem thickness (Amman 1972; Amman and Cole 1983), bark surface area (Reid 1963; Cole and Amman 1969) and sapwood moisture retention (Reid 1963) due to the greater quantity and quality of resources available for brood development. Bark roughness, thickness and surface area, phloem thickness and sapwood moisture retention all increase as trees increase in diameter (e.g., Safranyik et al. 1975; Shrimpton and Thomson 1985). In practical terms, this means that on average lodgepole pine trees ≤ 25 cm in diameter are beetle sinks (i.e., more beetles attack than emerge), whereas trees > 25 cm 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 is conditional upon the death of its host tree. This intense selection pressure has resulted in the evolution of a complex array of defenses that enable resistance by lodgepole pine to 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 resins 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). 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 monoterpene and phenolic compounds (Raffa and Berryman 1982b; 1983a). If the induced response is rapid and extensive, the beetles and associated microorganisms will be confined and killed in a lesion of dead tissue.

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 1983a; 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 the close association between the mountain pine beetle and several microorganisms. Beetles usually carry a number of different organisms into a tree, but two blue stain fungi, *Ophiostoma clavigerum* and *O. montium*, are consistently present (Whitney and Farris 1970; Six and Paine 1998; Six 2003). Spores of the fungi are inoculated into trees as beetles bore through the bark. These spores germinate quickly and penetrate living cells in both phloem and xylem (Safranyik et al. 1975; Ballard et al. 1982, 1984; Solheim 1995) causing desiccation and disruption of transpiration (Mathre 1964), effectively terminating resin production by the tree. The relationship between the mountain pine beetle and its associated blue stain fungi is a symbiotic one; the fungi benefit as they are transported from tree to tree, and the beetles benefit through the pathogenic activity of the fungi, physical conditioning of the phloem environment for larvae, and necessary contributions the fungi make to the beetle's diet (reviewed by Paine et al. 1997; Six and Klepzig 2004).

At the stand level, resistance by 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 and decline rapidly with age (Safranyik et al. 1974) (Fig. 2). Initiation of the drop in resistance roughly corresponds to the point at which, in fully stocked stands, current annual increment peaks and basal area growth culminates (Safranyik et al. 1974, 1975; Raffa and Berryman 1982b). 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 (Safranyik, 2004). As a general rule, by the time stands reach 80 – 100 years, they are considered to be highly susceptible to mountain pine beetle.

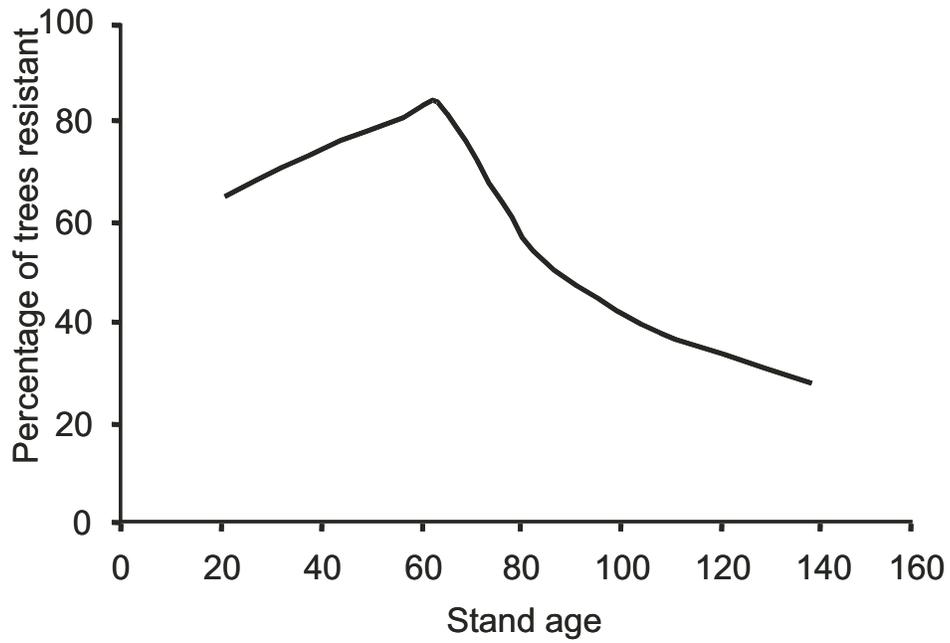


Figure 2. Change in the frequency of lodgepole pines resistant to colonization by blue stain fungi in relation to stand age. (Redrawn from Safranyik et al. 1974.)

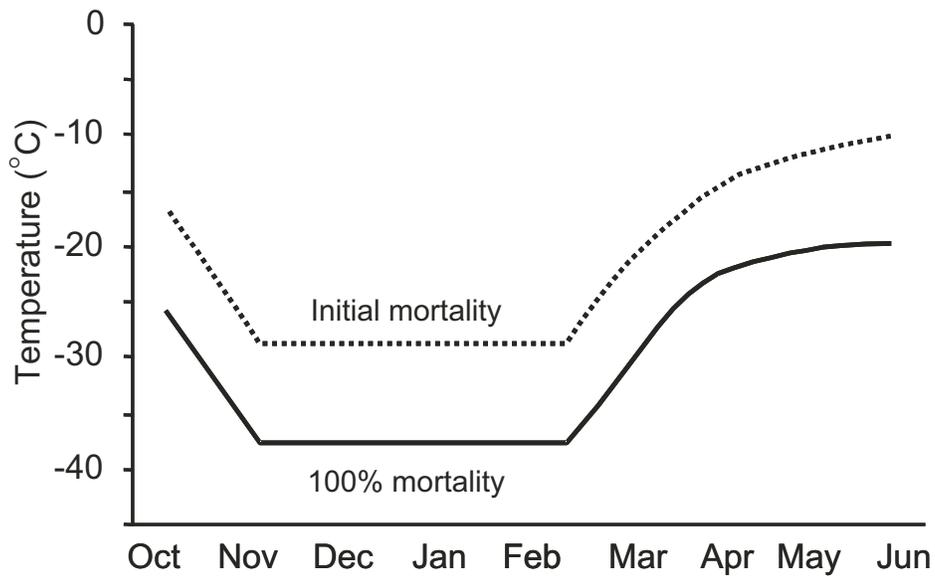


Figure 3. Tolerance limits of third- and fourth-instar mountain pine beetle larvae to 2.5 hours exposure to low temperatures. (Adapted from Wygant 1940.)

Cold tolerance

Exposure to 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., blood) as temperatures decline during autumn (Somme 1964; Bentz and Mullins 1999). Tolerance to cold varies with life stage. Eggs are least tolerant, followed by pupae, adults then larvae (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°C and -34°C , and adults between -23°C and -34°C . Larvae are the most cold-tolerant stage, and tolerance increases as larvae mature (Amman 1973; Safranyik et al. 1974; Langor 1989; Safranyik and Linton 1998; but see Bentz and Mullin 1999). Lethal low temperatures manifest between -23° and -29°C for first instars, -23° and -34°C for second instars, and -29° and -40°C for both third- 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). 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 in a population 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 middle of March, then nearly 100% mortality can be expected (see Fig. 3). Interestingly, in 1984 and 1985 a major outbreak in the Chilcotin region of British Columbia collapsed due to the occurrence of a series of days during which temperatures dropped to below -30°C in late October and early November, respectively (Safranyik and Linton 1991).

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). In addition, the rate of decline of subcortical temperatures is slower for large- 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, 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

One generation per year is the most common life cycle for mountain pine beetle populations throughout their range (Safranyik 1978). Adults disperse, attack and colonize new trees in mid- to late summer thereby enabling their broods to develop to third- or fourth-instar larvae, the most cold-tolerant life stages, before the onset of winter. However, variations in the life cycle can occur with year-to-year variations in weather. For example, during an unusually warm summer adults may emerge and attack several weeks earlier than average. Often beetles from this flight will re-emerge later in the season and infest a second tree (Reid 1962a). Similarly, as a consequence of unusually mild winters, a high proportion of parent beetles may survive and emerge prior to the emergence of their progeny (Amman and Cole 1983), usually during late May and early June. These beetles often construct egg galleries in the green phloem of trees that were strip-attacked, resistant, or attacked late in the season of the previous year (Rasmussen 1974). Attacks that occur early or late in the season have little chance of contributing to infestations because of high mortality due to the poor synchrony between the occurrence of cold tolerant life stages and the onset

of winter, and the overall lack of coincidence with the general mountain pine beetle population (Amman 1973; Safranyik 1978).

Unlike many insects in seasonal environments, the mountain pine beetle does not have a diapause 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. However, the high mortality associated with asynchrony has selected for adaptations that (i) ensure adult emergence is temporally coincident, thereby maximizing chances for successful mass attacks, and (ii) phenologically timed to enable broods to mature to cold tolerant life stages before winter (Logan and Bentz 1999; Logan and Powell 2001).

Temporally coincident adult emergence is facilitated 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 at high elevations and near the northern edges of the distributional range, heat accumulation is often insufficient for completion of the typical univoltine life cycle and mountain pine beetle populations become semivoltine. Stretching the life cycle over 2 years results in severe mortality consequences since the beetles will be forced to overwinter twice, often in cold-susceptible stages (Amman 1973; Safranyik 1978). Moreover, a 2-year life cycle slows the beetles’ 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 endemic levels. By contrast, in semivoltine populations climate becomes a dominant factor affecting both the distribution and abundance of mountain pine beetle (Safranyik 1978).

Conclusions

The potential for mountain pine beetle populations to establish, persist and ultimately increase to outbreak levels in lodgepole pine forests depends on the capacity for beetles to locate, colonize and reproduce within highly resistant host trees situated in thermal environments conducive to overwintering survival and with sufficient heat accumulation to maintain a synchronous univoltine life cycle. Understanding the effects these constraints have on populations and the subsequent adaptations that the mountain pine beetle has evolved to overcome them is the critical foundation of a successful management program intended to minimize the impacts of epidemics.

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