Mountain Pine Beetle Population Dynamics:
Insights from empirical evidence and modeling

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1 Literature review on the spatial modeling of Mountain Pine Beetles (report) for NRC project # 8.19
“Modeling Spatio-temporal Patterns of MPB Infestations”
INTRODUCTION

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is an aggressive bark-beetle that occurs naturally throughout much of western North America (Logan & Powell 2001). Beetles breed in the phloem tissue of recently dead host trees and, given sufficient beetle densities, coordinate attacks that can overwhelm the defenses of even the healthiest trees. While able to breed in many species of pine, mountain pine beetles are most often found in stands of lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosae*). Insects pests are the largest cause of forest disturbance in terms of both area affected and economic impact (Logan *et al.* 2003). Mountain pine beetle outbreaks have become more intense during the last few decades, and have spread to new areas (Logan & Powell 2001; Carroll & Safranyik 2003). For example, mountain pine beetle infestations in Canada have escalated into the largest insect epidemic in the history of the province of British Columbia, covering millions of hectares (Ebata 2004), and are rapidly spreading into the province of Alberta (Ono 2003).

Control and prevention of outbreaks requires an understanding of the mechanisms that determine population dynamics and dispersal. For over half a century, researchers have studied beetle phenology (Amman & Cole 1983; Amman & Bartos 1991; Bentz *et al.* 1991), behavior (Ryker & Rudinsky 1976), outbreak development (Bentz *et al.* 1993; Logan & Bentz 1999), host defenses (Reid & Gates 1970; Raffa & Berryman 1982b) and factors determining stand and individual tree susceptibility (Bartos & Amman 1989; Elkin & Reid 2004). Several models have been developed to estimate the probability of attack (Berryman 1978; Mitchell & Preisler 1991; Powell *et al.* 1996; Powell *et al.* 2000; Heavilin *et al.* 2005). However, the ability to reliably predict where and when outbreaks will occur remains a problem.

In this report, we review the ecological and behavioral mechanisms that influence the population dynamics and dispersal of the mountain pine beetle. We review the statistical and mechanistic models that have been developed for the mountain pine beetle, and assess the successes and failures of each. Through this contrast between empirical studies and modeling efforts, we identify important voids in our current ecological understanding, suggest areas where the application of statistical models could provide greater insight, and propose an approach to model development that will hopefully better
predict when and where outbreaks may occur, as well as further our understanding of the ecological processes that are germane to infestations.

MOUNTAIN PINE BEETLE ECOLOGY

General Life Cycle
Mountain pine beetles are typically univoltine, completing a single generation each year. Recently developed adults emerge from their host trees in mid to late summer to search for and attack new hosts (Figure 1). Attacking beetles bore through the outer bark of potential hosts into the phloem tissue. Healthy trees can resist small numbers of attacks by producing resin that slows down or stops beetles from constructing galleries in the phloem tissue (Raffa & Berryman 1983). In response, attacking beetles emit aggregation pheromones that can recruit additional beetles into a mass attack on the focal tree. If sufficient beetles are available, resin defenses will be overwhelmed and beetles successfully construct galleries (Raffa & Berryman 1983). To avoid intraspecific competition, attack density is thought to be regulated by the production of anti-aggregation pheromones and a reduction in the emission of aggregation pheromones (Raffa & Berryman 1983; Borden et al. 1987), both of which signal the depletion of host defenses (Geiszler et al. 1980). When a focal tree is saturated with anti-aggregation pheromones, newly arriving beetles switch to nearby trees (Mitchell & Preisler 1991).

Once host defenses have been overwhelmed, beetles construct vertical galleries in the phloem tissue to lay eggs. Mountain pine beetles infect the host with an aggressive fungal symbiont that helps to resist host defenses. Males speed up gallery construction by moving frass out of the way of the female into bottom of the gallery (Reid 1958). Males die in the galleries soon after mating (Reid 1958), but females may re-emerge in fall for a second flight and create a second gallery (Reid 1962). The recently laid eggs quickly develop into larvae (Bentz et al. 1991). Larvae create feeding galleries at right angles to the egg gallery and collectively girdle the tree. Beetle populations often over-winter as third or fourth instar larvae, and resume development in the spring (figure 1). Pupation occurs in early spring (Reid 1962) and teneral adults mature by feeding under the bark for 3-4 weeks (Raffa 1988) before emerging as fully developed adults in late July or August.
(Amman 1973). The third and fourth instars, as well as the pupae, require higher temperatures (>15°C) for development than eggs, first or second instar, providing an inherent mechanism for synchronizing larval instar molts and adult emergence. This is because higher temperature thresholds in the third and fourth instars prevent development to advanced life-stages less cold tolerant and allow late-hatching eggs to catch up (Bentz et al. 1991). Coincident adult emergence is important for successful mass attacks.

To better understand these ecological processes, the mountain pine beetle life-cycle can be divided into two phases: a within-tree reproductive phase and an among-tree dispersal phase. The within-tree phase determines the density of newly emerging adults that result from the previous years attacks. The among-tree phase governs how these newly emerging adults will disperse and aggregate to attack new hosts.

**Within-Tree Phase**

The engraved galleries that remain on the host reveal a wealth of ecological information about the mountain pine beetles. They provide a rare opportunity to directly observe the rates of reproduction and mortality that determine population growth. Commonly collected data include the number of successful attacks, the number of eggs laid, the rate of development through the stages, the causes of mortality, and the number of new adults that emerge the following season. Based on this information, it is known that the density of emerging beetles is largely governed by attack density, host characteristics, and temperature (Safranyik 1978; Raffa & Berryman 1983; Berryman et al. 1985; Raffa 2001).

**Attack density**

The density of attacking beetles has both a positive and negative effect on the density of new adults that emerge the following year. The positive influence results from the need to overwhelm host tree defenses. At low attack densities, a healthy tree can successfully repel all attacks (Raffa & Berryman 1983; Mulock & Christiansen 1986). As the attack density (attacks per area of bark) increases, the proportion of attacks that successfully produce offspring also increases (Raffa & Berryman 1983; Elkin & Reid 2004). When averaged over all trees in a stand, the shape of this relationship is a smooth monotonically
saturating function (Raffa & Berryman 1983; Elkin & Reid 2004); a pattern observed across a number of aggressive bark-beettle species (Berryman 1974) (Figure 2a). However, it is also known that the minimum density required to overwhelm a host tree increases with the vigor of the host (Mulock & Christiansen 1986), which implies that each host of a different vigor has a separate relationship between attack density and proportion of successful attacks. As a result, the relationships reported for the average of all trees in a stand represent the average of many curves reflecting both the underlying process of host defense and the heterogeneity of host vigor within the stand.

A common field method used to study bark beetles is to set out fresh log bolts (cut trees with ends sealed in wax) and observe the pattern of beetle attacks. Beetles respond to these logs in a similar manner as live trees, but without having to contend with host defenses. In the absence of tree defenses there is an almost linear decline in the number of new adults produced per attack as attack density increases (Cole 1962; Berryman 1974; Raffa & Berryman 1983; Amman & Pasek 1986) (Figure 2b). This negative density-dependence begins at even the lowest of possible attack densities (Raffa 2001); indicating that, in the absence of tree defenses, the maximum per capita growth rates are attained by a single attack. At high attack densities, the strength of the negative density-dependence can be sufficient to reduce the per capita emergence rate to below one (Cole 1962; Raffa & Berryman 1983). This likely results from a combination of reduced egg laying rates at higher gallery densities and increased mortality from greater intraspecific competition (Cole 1962).

The combined effects of both positive and negative density-dependence on reproductive success creates a unique tension for aggressive bark beetles. Any increase in beetle density required to overcome host defenses translates into a direct reduction in the per-capita reproductive success. There is good evidence to suggest that the positive and negative density-dependent mechanisms operate independently of one another, such that the number of new adults emerging from each attack can be described by the simple product of per-capita reproductive success and proportion of successful attacks (Berryman 1974; Raffa & Berryman 1983; Raffa 2001) (Figure 2b). The advantage from using this perspective is that the influence of other factors, such as temperature and host
vigor, on overall reproductive success is readily understood by considering their independent effects on each of the two density-dependent mechanisms.

Estimates of attack densities are usually based on the average over a tree (Raffa & Berryman 1983). If host defenses have been completely overwhelmed, such that beetles have fully colonized the tree, then the average density accurately reflects the local attack densities within the tree. However, *strip-attacks* are common in infected stands, where only localized spots on a tree have been successfully attacked (Raffa & Berryman 1983; Mulock & Christiansen 1986; Bentz *et al.* 1996). These localized attacks successfully produce new adult beetles, but do not kill the host tree (also referred to as *strip-kills*). Averaging the attack densities over the entire bark area of a strip-attacked tree would underestimate the true attack densities that succeeded in overwhelming host defenses. The factors behind the development of strip-attacked trees versus fully-attacked trees may be related to the local availability of beetles. The within-tree distribution of attacks is clumped when the average attack density on the tree is low, but becomes random as the average attack density on the tree increases (Raffa & Berryman 1983). The change in distribution suggests that attacks are focused within local areas on a tree, and that fully-attacked hosts may be the result of multiple strip-attacks. This perspective may be important when considering the endemic state of a beetle population. If there are insufficient beetles to attack an entire tree, the population could persist by concentrating attacks on local spots. Since strip-attacked trees do not die, they will not be evident in aerial surveys.

*Host characteristics*

Tree characteristics can have a large influence on the reproductive success of bark beetles. Larger trees have a greater surface area of bark and thicker phloem. Thicker phloem provides a greater volume of food that can be utilized by the growing beetle larvae, which in turn supports greater egg densities and more emerging adults independent of the initial attack density (Amman & Cole 1983; Amman & Pasek 1986). As a result, larger trees give rise to more beetles emerging on both an absolute and per-unit-area scale (Reid 1963). Thin-phloemed trees cannot support large densities of beetles (Berryman 1976). Within a tree, phloem thickness decreases with increased height above
the ground, and determines the surface area of the bole that can be colonized by bark beetles (Langor 1989). It has also been suggested that phloem thickness and surface area may account for much of the differences in MPB reproductive success among host species (Langor 1989).

The greatest challenge for aggressive bark beetles is to overcome host defenses and gain access to the phloem habitat. Pine trees produce a range of chemical and physical products that are thought to provide defense against bark beetles (Reid et al. 1967; Berryman 1969, 1972; Dunn & Lorio 1992). However, the primary defense mechanism is resin. Defenses are initiated as soon as burrowing begins because the attacking beetles cut into special ducts, causing resin to flow out of the wound. If the flow is sufficient, it can flush an attacker out of the entrance hole. If the attacking beetle is not flushed out, flowing resin can plug the entrance hole and prevent the emission of aggregation pheromones (Raffa & Berryman 1983). Hosts also initiate a secondary resin response by producing oleoresin flow in the galleries under construction. If the host tree has sufficient energy and resources, this secondary response can kill all of the freshly laid eggs (Reid & Gates 1970; Christiansen et al. 1987). As discussed above, the successful defense against attack depends on both the density of attacking beetles and host vigor.

Larger trees are less vigorous than smaller trees, when vigor is measured as the stem growth per leaf area (Shrimpton & Thompson 1982; Larsson et al. 1983). A number of studies have show that more vigorous trees are more resistant to attack, requiring a greater density of beetles to overwhelm tree defenses (Waring & Pitman 1983; Mulock & Christiansen 1986; Christiansen et al. 1987). From the perspective of the attacking beetle, host vigor is perceived through resin flow (Raffa & Berryman 1983; Dunn & Lorio 1992; Lorio et al. 1995). Trees with greater vigor have greater reserves of carbohydrates and can produce greater amounts of resin (Christiansen et al. 1987). Support for the relationship between the ability of a host to defend against attacking beetles and the reserves of energy to produce resin is evident in the temporal patterns of resin flow. Resin flow declines rapidly in hosts that become completely overwhelmed, whereas resin flow remains high in hosts that successfully prevent attacks (Raffa & Berryman 1983; Lorio et al. 1995).
Temperature

Temperature has a strong influence on both survival and development in the mountain pine beetle. Winter temperatures cause significant mortality, ranging from 20% during moderate winters to 100% during very cold winters (Amman 1973; Amman & Cole 1983; Amman 1984; Langor 1989). In fact, it has been argued that the northern expansion of the mountain pine beetle range is prevented by temperature induced mortality at a latitude where the average minimum temperatures is less than -40ºC (Safranyik 1978). However, the ability to survive cold winters is not shared equally among the different life-stages. Laval stages have the greatest cold tolerance, in particular the 3rd and 4th stage (Amman 1973), which can survive temperatures of -34ºC (Safranyik 1978; Bentz & Mullins 1999). In contrast, the egg, pupae and adult stages are particularly vulnerable to temperature and do not appear to survive winters colder than ~ -18ºC (Reid 1962; Reid & Gates 1970; Amman 1973; Safranyik 1978). The result is that winter mortality depends not only on temperature, but also on the timing between the minimum temperatures and the stage of beetle development.

Development rates in all insects are strongly tied to temperature. Provided that food is sufficient, development through each stage of the mountain pine beetle can be reliably predicted by the number of degree-days (Reid & Gates 1970; Bentz et al. 1991). The implication is that lower than average temperatures will extend the length of time it takes to complete one generation, and higher than average temperatures will reduce it. At the extremes, temperature could determine whether a population is bivoltine, univoltine or semivoltine (Logan & Powell 2001). Empirical support for this idea can be found across elevations. Mountain pine beetle populations at high elevations often require two years to complete a single generation, whereas populations at lower elevations require only one (Amman 1973).

A more subtle influence of temperature on beetle development is the control over which stage will be forced to over-winter. Cooler summer temperatures may not be sufficient for eggs to develop into larvae before winter sets in, preventing the population from surviving because of the low cold tolerance for eggs (Amman & Cole 1983). At lower elevations, Amman (1973) found that populations developed into the 2nd or 3rd
instar larvae prior to the onset of winter. In contrast, at higher elevations where the
temperature is colder, development was much slower and most populations entered
winter as eggs. The result was significantly greater mortality at the higher elevations. In
addition, larvae that grew at warmer temperatures were able to develop longer galleries,
which means that they attained a larger mass before the winter set in than larvae at cooler
temperatures, which is thought to increase survival at colder temperatures (Amman
1973). The reverse may also be true. Warmer summer temperatures may cause the
population to develop through the larval stage into pupae and adults before winter sets in
(Reid 1962). Since these stages also have low cold tolerance, this could cause elevated
mortality rates.

**Among Tree Phase**
The attack phase of the mountain pine beetle is probably the most famous part of the life-
cycle—yet it is also the least understood. This phase is characterized by individual
dispersal from recently depleted hosts, followed by strong aggregation that can
overwhelm the defenses of even the most vigorous trees. Pheromones are generated by
beetles during the process of attacking a host. Aggregation is coordinated by the
chemotactic response of individuals to these pheromones. Reproductive success depends
significantly on the ability to recruit sufficient adults into mass-attacks. However, as
discussed above, too great of an attack density will also reduce reproductive success
because of larval competition within the phloem. From the perspective of the bark-
beetles, the optimal attack density is the minimum required to overwhelm host defenses.
The pheromone system appears to be well tuned to generate these optimal attack
densities.

*Non-pheromone directed dispersal*
There are two situations when beetles move without the influence of pheromones; when
they are insensitive to pheromones because of recent emergence and when they are the
‘pioneer’ beetles emerging into an environment without other attacking beetles. Newly
emerging adults require a period of flight exercise before they respond to pheromones
cues (Borden *et al.* 1986; Raffa *et al.* 1993). While the length of time for this flight period
is not well understood in natural stands, it may be sufficient to disperse greater than 50m
(Borden 1993; Carroll & Safranyik 2004).

The term *pioneer* beetles refers to the first wave of beetles that emerge in a flight
season. Pioneer beetles disperse into an environment without any guidance from
pheromone cues. Such movement appears to be a random search for suitable hosts
(Safrinyik *et al.* 1974; Burnell 1977; Turchin & Theony 1993), perhaps influenced by a
preference for larger trees (Cole & Amman 1969). Dispersal of these pioneer beetles can
be on the order of several hundred meters (Turchin & Theony 1993). Unfortunately, there
is little data to determine how much beetles are assessing potential hosts during this
dispersal phase, or how they respond to other physical factors such as wind direction and
slope. Once beetles have landed on a tree, they must decide whether or not to initiate
gallery construction. Beetles assess host quality by chewing into the bark (Raffa &
Berryman 1982a). If the host is not perceived to be suitable, then beetles continue flight.
The behavior of these pioneer beetles can have a large impact on the spatial dynamics of
an infestation because these beetles will establish the first pheromone plumes that will
focus aggregation.

**Pheromone directed dispersal**

As with all aggressive bark-beetles, mountain pine beetles show a strong chemotactic
response to pheromones. Two broad classes of pheromones have been identified; those
that aggregate and those that repulse (Purswaran *et al.* 2000; Raffa 2001). While a
number of the chemicals responsible for the aggregate and anti-aggregate behavior have
been identified (Purswaran *et al.* 2000), it is not possible to quantify the spatial or
temporal pattern of these chemicals in a natural stand. As a result, the proposed
mechanisms behind the pheromone system are based on the temporal patterns of beetle
attacks in relation to the host response.

The temporal sequence of attacks on a focal host is characterized by a rapid
increase in the number of beetles landing, followed by a rapid decrease, within four to
five days (Raffa & Berryman 1983; Bentz *et al.* 1996). We distinguish the two phases of
the sequence because it has been proposed that each are the result of different
mechanisms. The initial aggregation is the result of aggregation pheromones that are
derived from the host materials (reviewed in Raffa 2001). If subsequent attacks to the
host are experimentally prevented (Raffa & Berryman 1983), or the host is able to resist
attack (Lorio et al. 1995) then attraction to the host can go on for a very long time,
sometimes for the entire flight period. It has suggested that this is because pheromones
are specifically derived from resin. As long as the host can produce resin defenses,
beetles will have a substrate from which to produce pheromones (Raffa & Berryman
1983; Borden et al. 1987). The advantage to this perspective is that when a host has been
overwhelmed, resin flow stops and the aggregation pheromones are no longer produced
(Raffa 2001). This simple mechanism does not require any sophisticated behavior from
the beetles, but may successfully prevent the over-colonization of the host.

While some researchers believe that the end of the host attack is initiated by a
decline in aggregation pheromones (Raffa & Berryman 1983; Raffa 2001), others believe
that it is initiated by anti-aggregation pheromones (Bentz et al. 1996; Pureswaran et al.
2000; Borden et al. 2003). Anti-aggregation pheromones are produced by both male and
females, but it has been hypothesized that some of these are only produce by males in
response to crowded conditions (Pureswaran et al. 2000). In many ways, the debate
between the two alternative mechanisms may not be important because the mechanisms
have a similar effect. However, a real distinction has to do with the perception of
crowding. If anti-aggregate pheromones are responsible for terminating the attack, then
there is the possibility that local crowding may not be tightly coupled to the state of the
host, allowing for sub-optimal colonization strategies.

When a focal tree is well under attack, secondary attacks begin to appear on the
surrounding trees (Bentz et al. 1996). It was once thought that this was a result of spill-
over because the focal tree had been completely colonized (Geiszler & Gara 1978).
However, temporal observations have revealed that secondary attacks appear long before
the focal tree is fully colonized (Bentz et al. 1996), suggesting that secondary attacks are
pheromone driven rather than directly driven by attack densities on the focal tree. The
pattern of secondary host attacks surrounding the focal tree appears to be random
(Geiszler & Gara 1978).
Host interference

As discussed above, the primary defense response of hosts is to produce resin, which inhibits gallery construction by the attacking beetles (Reid et al. 1967; Raffa & Berryman 1982b; Raffa & Berryman 1983). If beetles succeed in developing galleries, resin flow can seal the entrance hole and prevent the emission of pheromones (Raffa & Berryman 1983). It has been proposed that the interference of pheromone production by resin may be critical for outbreaks because it provides an opportunity for vigorous trees to avoid aggregated attacks, even when sufficient beetles are available (Raffa & Berryman 1983; Raffa 2001). While not discussed, this hypothesis also implies that hosts with high vigor would likely only come under mass-attack if there were enough random landings, by either pioneer or secondary attacks, to reduce resin flow sufficiently and allow pheromone emission.

Long range dispersal

The dispersal mechanisms discussed above are the most common behavior in mountain pine beetle infestations. However, a small proportion of the population may undergo long range dispersal, primarily above the tree canopy. Beetles have been observed to travel distances of up to 20-30kms during long distance dispersal (Safranyik 1978). It is not known if such dispersal is the result of being carried on wind currents (Furniss & Furniss 1972) or from sustained flight (Safranyik 1978).

Competition with non-aggressive bark beetles

Secondary bark beetles, such as the pine engraver (Ips pini), are less successful at attacking live hosts. Most often, these beetles colonize trees that are weak or have been killed by aggressive species such as the mountain pine beetle. These secondary bark beetles often respond to aggregation pheromones emitted by aggressive beetle species (Raffa 2001), which provides the potential for strong interspecific competition. For example, secondary bark beetles that colonized hosts attacked by spruce beetles caused reduced brood densities through interspecific competition (Poland & Borden 1998). However, field studies reveal that pine engravers colonize marginal areas on trees attacked by mountain pine beetles, reducing interspecific competition (Safranyik et al.)
It is not clear whether interspecific competition has an important role in regulating mountain pine beetle dynamics.

MODEL INSIGHTS

A number of models have been developed for mountain pine beetle infestations. This effort has covered a wide range of approaches from simple strategic models (Heavilin et al. 2005) to complex simulation models (Safranyik et al. 1999), from a focus on dispersal (Preisler 1993) to a focus on population growth (Berryman 1979), and from statistical models (Mitchell & Preisler 1991) to predictive models (Powell et al. 1996).

Our primary goal is to understand the factors that contribute to population outbreaks in the mountain pine beetle, and thus increase our ability to predict where and when outbreaks occur, as well as the resulting spatial-temporal dynamics. Thus, we focus our review efforts on the modeling work that has attempted to understand either the spatial or temporal patterns of beetle dynamics.

Statistical models

The most obvious effect of aggressive bark beetles is their impact on the host tree. As a result, numerous studies have recorded the number of beetle-killed trees over space and time. While some of these are at a spatial-scale of the individual host tree (hereafter referred to as stand-level), the longest time-series that cover the widest areas are at a spatial-scale of the forest (hereafter referred to as landscape-level) where the observations are often simply the presence or absence of beetle-attacked trees somewhere in the stand. Data on host mortality is only one component of the beetle-host interaction. However, it can provide valuable insight into which factors have the greatest spatial and temporal correlation with patterns of attacked trees.

At the stand-level, the detailed observations on attacking beetles suggest that attack success depends on a complex set of processes involving behavioral aggregation and host vigor. The qualitative prediction is that larger and older trees, which are less vigorous, will be successfully attacked at lower densities than smaller and younger trees. While there is ample qualitative supported for this in stand-level data (Waring & Pitman 1983; Mulock & Christiansen 1986; Christiansen et al. 1987), quantitative statistical models of
spatial attack patterns can provide further insight (Mitchell & Preisler 1991; Preisler 1993; Preisler & Mitchell 1993). These analyses use auto-logistic regression methods to model the probability of host attack as a function of host size, age, vigor, and proximity to other attacked trees. They found that host size and vigor have a significant influence on the probability of attack. Larger trees are attacked more often than smaller ones, particularly when host vigor is low. The analyses have also found a significant influence of proximity to attacked trees. Small trees were attacked more often if they were near other attacked trees, suggesting that spatially explicit processes may be important for understanding attack patterns. The results do not appear to be influenced by changing beetle densities (Mitchell & Preisler 1991).

Spatial heterogeneity in factors such as average temperature, elevation or forest management practices are larger at the landscape-level than at the stand-level, providing an opportunity to study how such factors correlate with the probability of attack. While much landscape-level data exists for the mountain pine beetle, statistical models of landscape-level attack patterns have only been applied to the southern pine beetle (Gumpertz et al. 2000; Zhu et al. 2004). These studies also used auto-logistic regression methods to study the correlation between landscape-level patterns of environmental factors and the spatial-temporal autocorrelation of attack patterns. The analyses found that the probability of host attack by the southern pine beetle correlates with spatial proximity to previous attacks, host factors such as size, and environmental factors such as temperature.

**Mechanistic models**

Early models of the mountain pine beetle focused on the population dynamics without explicitly considering space (Berryman 1978, 1979). The models incorporate such things as host size, age and vigor, as well as beetle density (Raffa & Berryman 1986; Berryman et al. 1989). Beetle dynamics are determined by the ability to successfully attack the available hosts using the well established relationships for host resistance and beetle reproduction. Beetles are assumed to only attack trees whose defenses can be successfully overwhelmed by the current density. These models often include many details, such as the influence of temperature, stage-specific mortality, and management
practices such as pheromone traps and forest thinning (Raffa & Berryman 1986; Safranyik et al. 1999). The primary conclusion from these models is that the population growth rate is bimodal as a function of beetle density (Figure 3). Population growth is positive at low densities of beetles, but becomes negative at intermediate densities because larval competition is intense and vigorous trees remain inaccessible until population densities are higher (Raffa & Berryman 1986). If beetle densities can increase above this point, then the population growth is again positive, reflecting the ability of the population to attack vigorous trees. The conclusion from these models is that outbreaks result from environmental factors (e.g. drought) that cause host vigor to decrease and allow endemic densities of beetles to successfully attack the usually inaccessible high quality hosts (Raffa & Berryman 1986).

The outbreak model proposed by Berryman (1979) (Figure 3) has some parallels with other insect outbreak models. For example, the now classic spruce budworm outbreak models can display the same three equilibria; stable endemic state, unstable transition and stable outbreak state (Ludwig et al. 1978). However, the ecological mechanisms behind these models are different. While resource limitation limits the outbreak states of both models, the endemic state of the spruce budworm model is maintained by predation whereas in the endemic state of the mountain pine beetle model it is maintained by host vigor. A more subtle difference is the time scale for resource regeneration. Trees regenerate at a much slower rate than they are killed during beetle outbreaks. Numerical simulations that explicitly account for this (Raffa & Berryman 1986) reveal that there is no stable outbreak state. Rather, the beetle population erupts rapidly depleting the available hosts, and then crashes to a level lower than the endemic state. As the forest regenerates, the beetle population returns to the endemic state abundance. Simulations such as this indicate that population growth is likely not well described by beetle density alone.

Recent work has expanded the detailed models of Raffa & Berryman (1986) to include spatially explicit dispersal (Powell et al. 1996; White & Powell 1997; Logan et al. 1998; Powell et al. 2000). The relationships that govern the local beetle-host interactions are very similar, but the pheromone system is explicitly modeled. Pheromone synthesis is assumed to depend on resin capacity, as related to host vigor, and diffuses
through the stand (Powell et al. 1996). Beetle dispersal can have both random movement as well as the strong chemotactic pheromone response. These models predict a similar transition from endemic to epidemic beetle infestations, which the authors refer to as *phase transitions* (White & Powell 1997). Furthermore, a similar relationship is found between host vigor and beetle density, where the focal trees are generally weaker in the endemic state than in outbreak states. The conclusion from these models is that outbreaks can be caused by the chance spatial arrangement of weak trees, which leads to a locally high density of emerging beetles and the initiation of large-scale infestations (White & Powell 1997).

Most models of mountain pine beetles have focused on the emergence and propagation of infestations through a forest on time scales that are fast enough to ignore stand regeneration. However, since mountain pine beetles have been part of a natural cycle of disturbance and regeneration with their hosts for centuries (Logan & Powell 2001), the ecological interactions at the stand scale must also allow for coexistence at the landscape scale. Heavilin *et al.* (2005) developed a landscape-level model that provides for forest regeneration as well as considering how infestations spread over spatial scales larger than a stand. The tree component of the model is stage-structured to allow for heterogeneity in host vigor, and beetle population dynamics are determined by the number of attacked trees from the previous year. Beetle dispersal is continuous across space, but does not allow for aggregation behavior. While such a model is useful for understanding how outbreaks progress, it will likely fail to capture the dynamics of the endemic population. Endemic populations may exist in strip-attacks, which do not kill the host. Thus, at low densities, it is unlikely that the beetle population could be approximated by the number of dead trees.

**CONCLUSIONS**

A great deal of effort has focused on understanding the basic ecology of mountain pine beetles. Since reproductive effort, development and mortality are relatively easy to observe, this effort has resulted in a unique depth of ecological understanding. For example, much is known about how live hosts defend against attacks, how temperature interacts both directly and indirectly with development and survival, what attack densities
are required to overwhelm hosts of different vigor, how intraspecific competition reduces reproductive success, how pheromones are produced, and how chemotactic behavior allows for aggregated mass-attacks. Yet, we have been largely unsuccessful at predicting when and where infestation outbreaks will develop. In the paragraphs below, we discuss areas where further empirical information and modeling efforts would be most beneficial.

While many parts of the mountain pine beetle life-cycle are well understood, there are some key processes where little is known. Most of these have to do with dispersal. The behavior of pioneer beetles is not well understood in terms of both direction and dispersal distance. Since these beetles are the first to sample available hosts and initiate attacks, the resulting spatial dynamics of an infestation may largely depend on how beetles respond in an environment without pheromone cues. Furthermore, a finer quantitative assessment of how beetles respond to pheromone cues in natural stands would increase our understanding of aggregation behavior, in particular how it relates to secondary attacks.

The second area where further data are important is the attack pattern at all levels of infestations. For example, few data exist on the endemic state of the beetle population. While some studies have recorded the occurrence of strip-attacks, there is little data to assess how important these are for the persistence of endemic populations. An alternative is that the endemic population only exists as spot infestations that appear in aerial surveys as clumps of dead trees (Borden 1993). Since strip-attacks can only be detected by targeted ground surveys, such data would help distinguish between the importance of the local endemic population versus long distance dispersal for initiating outbreaks observed by aerial surveys. Observations on the spatial distribution of attacks, both successful and unsuccessful, would also provide important independent data for model validation.

Statistical analyses of the attack patterns within a stand reveal that proximity to attacked trees has a large influence on the probability of being attacked. This provides important insight into the patterns that emerge from the complex interaction between beetle behavior and pheromone production. Similarly, spatial-temporal landscape-level analyses, which have been conducted other aggressive bark-beetles, can identify the environmental factors and host characteristics that have the strongest correlation with the probability of infestation. Applying these landscape-level analyses to the mountain pine
beetle data would be invaluable to help guide model development. The statistical methods discussed above all focus on the probability of host mortality (binary data), ignoring the density of beetles. When sufficient data are available, a significant improvement would be to develop these models for non-binary data such as beetle density.

We feel that the inability to predict infestation outbreaks is largely because beetle dynamics are an emergent property from a number of interacting and sometimes complex processes. There is no doubt that mathematical models provide the only means to understand how outbreaks emerge from these interacting processes, but such predictions may be sensitive to how the models are developed and parameterized. Previous modeling efforts suggest that a minimal model needs to explicitly model both the within-tree reproductive phase and the among-tree dispersal phase. We believe that key to creating a robust and meaningful model of mountain pine beetle infestations depends a careful balance of strategic development guided by independent validation.

References Cited


Raffa, K.F. & Berryman, A.A. 1982b. Physiological Differences between Lodgepole Pines Resistant and Susceptible to the Mountain Pine-Beetle (Coleoptera,


Figure 1. Mountain pine beetle life-cycle. Much of the life-cycle is spent in the phloem habitat, with the exception of when adults emerge and disperse to attack new hosts (hatched area). Eggs are laid in freshly excavated galleries and develop through four larval stages that feed on the phloem tissue. Beetles often over-winter in the larger larval stages, and pupate in late spring. Adults further develop in the phloem tissue and emerge during the brief flight period.
Figure 2. The effect of attack density on intraspecific competition and overcoming host defenses (from Raffa & Berryman 1983). a) the proportion of successful attacks increases with attack density, reflecting the ability of higher beetle densities to overwhelm host defenses. b) the decline in per capita reproduction begins at very low attack densities (dashed line) when host defenses are artificially prevented. The natural distribution of per capita reproduction as a function of attack density reflects the combined effects of intraspecific competition and host resistance (solid line).
Figure 3. Population growth rate as a function of population density (from Berryman 1979). It is postulated that the population dynamics of the mountain pine beetle has three equilibria. The first is stable ($N_1$), representing the endemic population state, the second ($N_2$) is unstable, and the third ($N_3$) is stable representing the outbreak state. Growth at the endemic state is controlled by host vigor, and growth at the outbreak state is controlled by resource limitation.