

Spatial and Temporal Attack Dynamics of the Mountain Pine Beetle: Implications for Management

BARBARA J. BENTZ¹, JESSE A. LOGAN¹, AND JAMES A. POWELL²

¹USDA Forest Service, Intermountain Research Station, Logan UT and Department of Forest Resources, Utah State University, Logan, UT, USA

²Department of Mathematics and Statistics, Utah State University, Logan, UT, USA

ABSTRACT Colonization of a host tree by the mountain pine beetle, MPB (*Dendroctonus ponderosae* Hopkins, Coleoptera: Scolytidae), involves a complex, synergistic interaction between host-produced chemicals and beetle-produced pheromones. This system of chemical communication enables a massive aggregation of beetles on a single resource, thereby ensuring host death and subsequent beetle population survival. Because a single host tree is a limited food and breeding resource, MPB populations have evolved mechanism(s) for termination of colonization on a tree at optimal beetle densities, with a concomitant shift of attacks to nearby trees. Several hypothesis attempt to explain this pheromone-mediated phenomena. In an effort to more fully understand the entire colonization process, including the switch of attacks among trees, we observed the daily spatial and temporal attack process of MPB (non-epidemic) attacking lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann). Our results from this preliminary study suggest that beetles switch attacks to a new host tree before the original focus tree is fully colonized, and that verbenone, an anti-aggregating pheromone, may be acting within a tree rather than between trees. Results from this and additional on-going studies are being used for parameterization of a spatially explicit model of MPB dispersal. Alternative hypotheses for MPB colonization and management implications are discussed.

KEY WORDS mountain pine beetle, verbenone, switching, spatial, lodgepole pine

MANY SPECIES OF bark beetles in the genus *Dendroctonus* (Coleoptera: Scolytidae) use kairomones and pheromones in the processes of host selection, attack, and colonization (Borden 1982, Wood 1972). Female *D. ponderosae* Hopkins (MPB), which in this species are usually responsible for initiating a new attack, bore into the bark and through a chemically mediated synergistic reaction with host chemicals, release *trans*-verbenol. *Trans*-verbenol is an aggregative pheromone attracting both sexes (Pitman et al. 1968, Hughes 1973, Pitman 1971). At higher concentrations of *trans*-verbenol, higher proportions of males are attracted (Renwick and Vite 1970). Males produce *exo*-brevicomin which at low concentrations primarily attracts females (Conn et al. 1983). Both inhibition (Borden et al. 1987, Rudinsky et al. 1974) and attraction (Shore et al. 1992) of beetles at higher concentrations of *exo*-brevicomin have been observed. This system of chemical communication enables a massive aggregation of individuals on a single "focus" tree which, for species such as MPB, is selectively advantageous in overcoming host defensive mechanisms. As with most herbivores, however, there is an optimal density range of individuals on an exhaustible food resource (Berryman et al. 1985). If beetle densities on a single tree are too high, mortality can result from within-tree competition for limited breeding and feeding space.

Several hypothesis attempt to explain the termination of colonization on a single tree

at optimal beetle densities. The first assumes that anti-aggregative or inhibitory pheromones such as verbenone and *exo*-brevicommin deter incoming beetles, thereby terminating additional attacks and ensuring that beetle attack density does not exceed the threshold for optimum brood survival (Borden et al. 1987). Verbenone is a semiochemical produced by MPB (Rudinsky et al. 1974), through autoxidation of host terpenes, and by enzymatic conversion by yeasts (Hunt and Borden 1989). Based on this hypothesis, as verbenone is released, the majority of beetles are dispersed at some distance, switching attacks from the focus tree to adjacent recipient trees (Gieszler et al. 1980).

A second hypothesis emphasizes the role of host resistance, citing cessation of resin exudation as the primary cause for termination of colonization on a particular tree (Renwick and Vite 1970, Raffa and Berryman 1983). As with the first hypothesis, attacks switch to adjacent trees once the focus tree becomes fully utilized--the difference lying in the roles of inhibitory pheromones and host-tree resins. In the second hypothesis, inhibitory pheromones are one component of a series of territorial behaviors which, in conjunction with a decrease in resin exudation, enable individual colonizers to maximize reproductive potential (Raffa and Berryman 1982, 1983). From this perspective, inhibitory pheromones are perceived and function at the local scale, while attacks switch to neighboring trees because the focus tree has become fully colonized and resin exudation ceases. A third hypothesis, labeled the "threshold model", assumes that as a tree is mass attacked, the high concentration of *trans*-verbenol being emitted in the local area causes incoming beetles to attack neighboring trees which are enveloped in the pheromone cloud (Coster and Gara 1968, Gara and Coster 1968, see Geisler et al. 1980). A threshold level of *trans*-verbenol is necessary to cause landing and attack on adjacent trees.

The presence of inhibitory pheromones in the genus *Dendroctonus* is known (Hunt et al. 1989, Libbey et al. 1985, Pitman et al. 1969, Ryker and Yandell 1983, Rudinsky et al. 1974). However, our lack of knowledge about the explicit function of these pheromones in MPB community ecology is exhibited by confounding results in past research endeavors (see Amman and Lindgren 1995 for a review). It is unclear whether inhibitory pheromones such as verbenone have a shielding effect around the tree under attack and are the main cause of switching, or if their function is to regulate attacks once beetles are on or very near the tree surface, playing a more localized role in the switching process. If indeed verbenone has a shielding effect, unknown parameters include the size of the shielding plume, and timing of its influence. The main objective of this study was to collect information on the spatial and temporal sequence of the MPB switching process. Original motivation for the study was to obtain quantitative information for parameterization of a mathematical model of MPB dispersal which includes chemical ecology and spatial interaction between beetles and host trees (Powell et al. 1996). Data at the fine spatial and temporal resolution necessary for deriving model parameters was unavailable in published literature. In this study we did not measure pheromone emission, but rather the effect of these pheromones on beetle behavior.

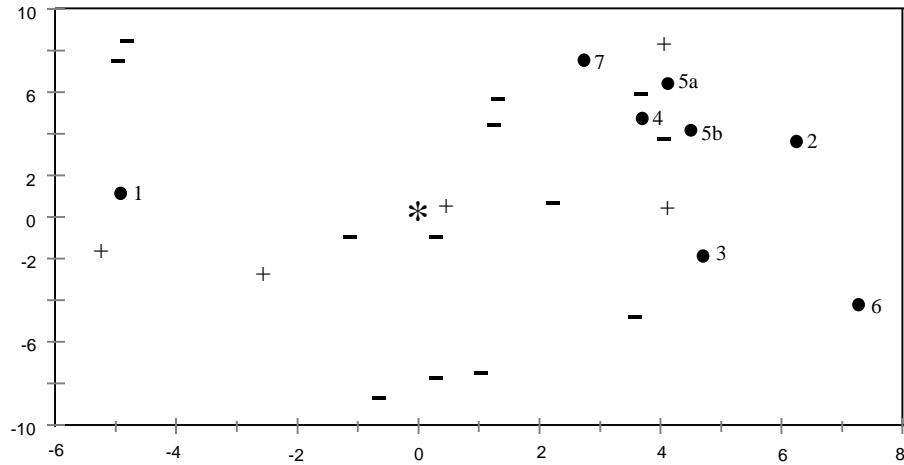


Figure 1. Spatial map (in meters) of all trees in Plot 1. ☆ is the baited tree at plot center, ⊙ are successfully attacked trees, with the number representing the day in the attack sequence, ⊕ are strip-attacked trees, and ⊙ are live trees at the end of the attack period. Size of circle indicates relative dbh of each tree.

Methods

Three plots in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) stands in the Gold Creek drainage of the Sawtooth National Recreation Area were selected. Species composition in the drainage is approximately 80% lodgepole pine and 20% Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). Currently there is a sub-epidemic MPB population which has been slowly building during the last 4-5 years. All plots were at an elevation of approximately 2073 meters, and at least 100 meters apart. On August 6, 1995, an MPB pheromone tree bait¹ was placed on the north side of a single tree in each plot. Based on emergence data from a nearby experiment (Bentz unpublished data), beetle flight in the area had just begun. The bait was left on each focus tree for 24 hours, then removed. All trees within a radial distance of 10 meters (20 meter diameter) from the focus tree were monitored for beetle attacks until August 18 at which time colonization of trees within the plots had, for the most part, stopped. Attacks

were tallied twice per day (approximately 8:00 am and 5:00 pm), by height on the bole (0-1.2 meters, 1.2-1.8 meters, and 1.8-2.4 meters) and aspect of the bole (N, E, S, W) where the attack was located. An attack was counted once the nesting hole was initiated and resin or frass was noticed, and consequently landing rates were not included.

Each entry was marked with a colored push pin, and later tallied. Because our intent was to monitor the 'natural' attack process of MPB on lodgepole pine, those trees attacked while the bait was on the focus tree were removed from data analysis. A stem map was developed for each plot including diameter of each tree at 1.5 meters above the ground (dbh) (Fig. 1). Only results for plot 1 are included here.

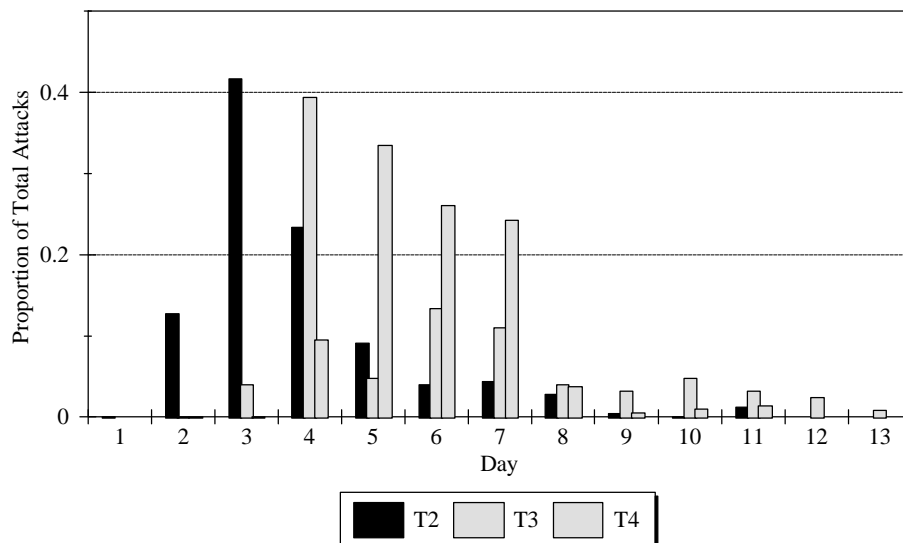


Figure 2. Proportion of total attacks on lower 2.4 meters of bole of 3 successfully attacked trees, by day of attack. Day 1 is August 6, 1995.

Results and Discussion

The first hypothesis for switching suggests that the production of inhibitory pheromones during the latter stages of colonization deter incoming beetles and therefore cause a switch to adjacent trees. If this is true, then inhibitory pheromones would be perceived prior to beetles landing on the focus tree, with a switch of attacks to adjacent trees once the original focus tree was fully colonized. At the point of full optimization of the focus

tree, inhibitory pheromones would produce a shield, resulting in no additional attacks on that tree. Our results do not support this hypothesis. On the day of peak attack density on Tree 2, new attacks occurred on Tree 3. The following day, at peak attack density of Tree 3, Tree 4 was initially attacked (Fig. 2). The next day, at peak attack density on T4, T5a and T5b were attacked (Fig. 3). In all cases, on the day when attacks switched to another tree, the proportion of attacks on the current focus tree was less than 45% (Figs. 2, 3). These results suggest that attacks are redirected to a new tree prior to full utilization of the current tree under attack. McCambridge (1967) also observed that trees adjacent to the focus tree came under attack by MPB before the initial focus tree had been fully mass attacked. Anderbrandt et al. (1988) observed a similar pattern with *Ips typographus* Linnaeus. Others (Geiszler et al 1980), however, reported that the switch to a new tree occurred after the original focus tree had been fully mass attacked.

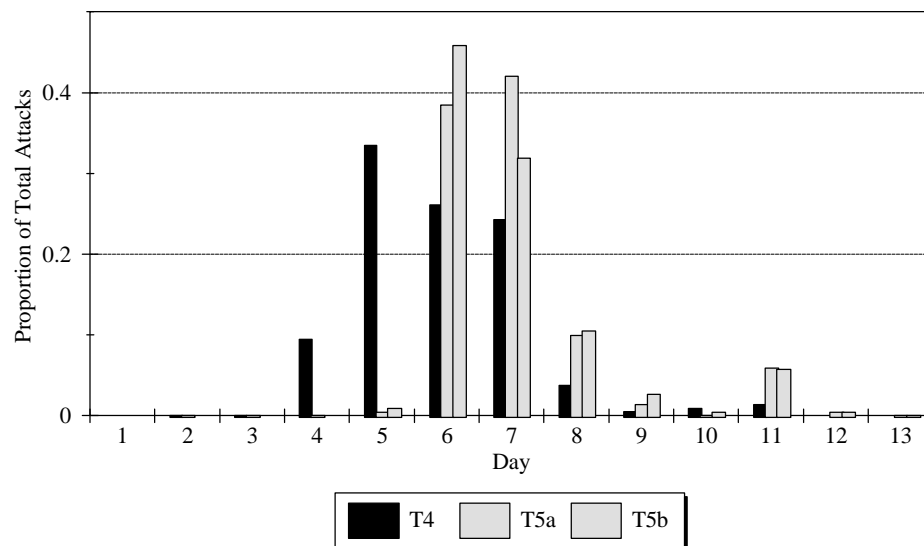


Figure 3. Proportion of total attacks on lower 2.4 meters of bole of 3 successfully attacked trees, by day of attack. Day 1 is August 6, 1995.

The basis of the second hypothesis is that resin exudation would cease when the original focus tree was fully colonized. At this time, attraction to that tree would be terminated due to an absence of the tree-produced precursor, α -pinene, necessary for beetle production of *trans*-verbenol. Without production of the aggregating pheromone *trans*-verbenol, additional attacks would not occur on the focus tree once the switch to adjacent trees begins. Again, our results do not support this hypothesis for switching of attacks. Beetles continued to attack the original focus tree after adjacent trees came under attack (Figs. 2, 3).

The basis for the third hypothesis is that given a threshold number of attacking beetles on a focus tree, the level of *trans*-verbenol being produced would be great enough to envelope surrounding trees in the aggregating plume. All trees within the aggregation pheromone plume would be attractive and experience attacks. Therefore, additional landing and attacks could occur on the focus tree even after attacks were initiated on adjacent trees. The larger the focus tree the greater number of attacks, and hence the larger the size of the aggregating pheromone plume. Data from our preliminary study support this hypothesis for switching of attacks. We observed that attacks on nearby trees were initiated while the focus tree was also still being attacked.

We use the term "switch" to represent a shift in attacks on consecutive days between a focus tree and surrounding trees. In our study, switch in attacks from a focus tree to nearby trees typically occurred the second day of attack, and at time of peak daily attack density on the focus tree (Figs. 2, 3). This coincides with the time of maximum production of *trans*-verbenol which peaks for individual beetles at about 24 hours of feeding (Pitman and Vite 1969). However, female MPB which had fed in lodgepole pine bolts for 24 hours also contained significant amounts of verbenone (Hunt and Borden 1989). Therefore, the large concentrations of both aggregation and inhibitory pheromones in the first few days of attack on a tree may cause MPB to be attracted to the focus tree, and both space out on the bole and participate in the tree-switching mechanism (Bedard et al 1980, Birgersson and Bergstrom 1988). The function of inhibitory pheromones such as verbenone in this tree-switching mechanism is unclear, however.

Based on results in our study, shift in attacks to a new host occurred before the focus tree was fully colonized, although each tree continued to be attacked at a decreasing daily rate for 5-6 days. If beetles were responding to verbenone before landing on a tree as suggested by Bertram and Paine (1994), the range of perception in our study plot was smaller than the distance between the two closest trees attacked within a day (< 1 meter). If verbenone was providing an inhibitory plume around a tree, most attacks on that focus tree would cease, signaling a fully utilized resource, although additional attacks may occur due to variability in the response threshold of individual beetles. However, because attacks shifted to a new tree while less than 50% of total attacks had occurred on the focus tree, verbenone (and other inhibitory pheromones) could be functioning at a more local scale, perhaps around a particular entrance hole as was suggested previously (Raffa and Berryman 1983, Renwick and Vite 1970). While large amounts of aggregating pheromones are still being produced, verbenone may provide a means to reduce competition within a tree, while some other component of the pheromone system is the primary cause of attack switch to a new tree. Our results indicate that a shift in attacks to a new tree occurred on the day of greatest attack rate on a nearby tree. If we assume that time of greatest attack rate on a particular tree coincides with peak *trans*-verbenol emission from that tree, switch in attacks to a new tree could be

explained by a spill-over effect. This would occur when the concentration of aggregation pheromone was large enough to envelope surrounding trees, resulting in random attacks on trees enveloped by the plume, setting up a new focus tree. The new focus tree then has an increase in number of attacks, while attacks on the old focus tree declines due to a reduction in attacks and concomitant *trans*-verbenol production (Pitman and Vite 1969). These results were seen in our data, whereby number of attacks on recipient trees the first day of switching was always less than number of attacks on the focus tree that same day, although the following day, attacks on recipient tree were greater than previous focus tree (Figs. 2, 3). Although we do not know the size of aggregation pheromone plumes, our data does suggest that the inhibitory, or anti-aggregation plume being released is smaller than the distance between two consecutively attacked trees spaced less than 1 meter apart.

Implications for Management

Techniques for identifying bark beetle semiochemicals were first developed in the 1960's (Silverstein et al. 1967). A plethora of field and laboratory trials for measuring the response of beetles to these semiochemicals have occurred since that time. Because opportunities for exploitation of beetle pheromones for forest management purposes are numerous, the temptation for researchers in this field to hastily launch into applied programs has been great. However, if the immense natural complexity of these semiochemicals is not fully understood, effectiveness of field applications may be inconsistent and often times unsuccessful (Borden 1995). This has been the case with attempts at applying synthetically produced verbenone for protecting stands of trees from attack by the mountain pine beetle (Amman et al. 1989, Amman et al. 1991, Amman and Lindgren 1995, Bentz et al. 1989, Gibson et al 1991, Lindgren and Borden 1993, Lindgren et al. 1989, Lister et al. 1990, Shore et al. 1992). The inconsistent results from year to year and between host types and geographic regions could be due to a number of reasons (Borden 1995) including: 1) technical problems with deployment of the pheromone, 2) effects of microclimate, 3) changes in behavior and/or genetic makeup with changes in the insect population phase (Amman 1993) and 4) inadequate knowledge of the functional role of inhibitory pheromones in MPB population dynamics.

Because verbenone is used by so many species of aggressive bark beetles, and a large portion is produced by microorganisms in decaying wood, it may be a signal to beetles that the immediate substrate, either an entire tree or a localized space on a tree, is no longer suitable for colonization (Borden et al. 1987, Leufven and Birgersson 1987). The question remains whether MPB are responding to verbenone prior to or after landing on the tree. Our results suggest that verbenone may be acting within a tree rather than between trees, and that it does not provide a very large inhibitory shield around the tree under attack. This is a different functional role for verbenone in MPB chemical ecology than the role researchers previously had in mind when applying synthetic capsules in field trials. To this date, synthetic verbenone has been applied either aerially or by stapling single capsules on trees spaced throughout an MPB infested stand. These experiments were aimed at deploying a certain dose of verbenone per hectare. Conversely, if the functional role of verbenone is to space beetles on a tree rather than between trees, alternative verbenone applications will need to be field tested.

Researchers have been tantalized by the hope that synthetically produced pheromones

might be the answer to management of epidemic phase MPB populations. However, we need to step back and conduct additional research at the behavioral level to more fully understand the sequence of the colonization process, and the spatial and temporal influence of inhibitory pheromone(s) in MPB population dynamics. Inconsistent results in attempts to apply inhibitory pheromones in a management scenario attest to a current deficiency in our knowledge of their role in MPB chemical ecology.

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