

Mountain Pine Beetle Dispersal: The Spatial–Temporal Interaction of Infestations

Colin Robertson, Trisalyn A. Nelson, and Barry Boots

Abstract: An understanding of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) dispersal during an outbreak is important for modeling future infestations and aiding management decisions. Data on the spatial pattern of red and green attacked trees were used to characterize the spatial–temporal nature of dispersal. Research goals were to detect evidence of dispersal based on the distance and direction between red and green attacked tree clusters, determine how dispersal changes at different stages of infestation, and to detect landscape variables influencing the observed dispersal patterns. Key variables explored were Biogeoclimatic Ecosystem Classification (BEC), topography, and the local population of susceptible hosts. Dispersal distances of 30 meters and 50 meters were consistently observed among different data subsets. Findings suggest that short-range dispersal often occurs despite an available population of susceptible hosts, and as the infestation grows in intensity, the abundance of dispersing beetles causes spot infestations to coalesce. *FOR. SCI.* 53(3):395–405.

Keywords: infestation spread, lodgepole pine, red attack, green attack

THE MOUNTAIN PINE BEETLE (*Dendroctonus ponderosae* Hopkins) epidemic currently having an impact on British Columbia's central interior forests is the largest on record (Westfall 2004). Although the mountain pine beetle is native to British Columbia and is a natural part of forest disturbance, a combination of warm winter temperatures and an abundance of mature lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) stands have created optimal conditions for the development of outbreak mountain pine beetle populations (Taylor et al. 2006).

An understanding of mountain pine beetle behavior is essential to forest managers tasked with preparing for and managing attacks. Mountain pine beetles have been extensively researched, and a large body of knowledge exists on their biological and ecological processes. However, dispersal is thought to be one of the least understood aspects of mountain pine beetle ecology (Carroll and Safranyik 2004).

There are believed to be two main methods of mountain pine beetle dispersal; short-range and long-range. Long-range dispersal is thought to occur when beetles are transported above the forest canopy and carried long distances by wind. This enables the development of new infestations at long distances from previously attacked areas, and explains the observation of beetles in unsuitable habitats (Furniss and Furniss 1972). The dominant dispersal method is thought to be short-range, often called within-stand dispersal, which occurs below the canopy as beetles emerge and seek out a suitable nearby host tree (Safranyik et al. 1989). Once colonization is established, more beetles are attracted through pheromone communication, and subsequent beetles

switch to new trees once the initial host approaches optimal attack density.

In British Columbia, beetles usually disperse once a year (during synchronized univoltine cycles), in late summer (Logan and Powell 2001). Peak emergence and dispersal occurs during the afternoon, usually within a 2–3-hour window when air temperatures exceed 20°C, with optimal emergence occurring between upper and lower bounds of 22 and 32°C, respectively (Safranyik et al. 1989). At optimum temperatures, the rate of hourly emergence is also affected by other environmental factors such as cloud cover, precipitation, and light intensity. Above 30°C, daily and hourly emergence rates decline (Safranyik et al. 1992).

Large mature trees are better hosts for beetle reproduction and development, and as such, beetles attack large trees disproportionately (Safranyik et al. 1974). Although the benefit of attacking large trees is understood, there remains debate as to how emergent mountain pine beetles select larger trees. For instance, it is unknown if beetles visually seek out trees with large silhouettes (Shepherd 1966), or if beetles land at random and larger trees are affected disproportionately during outbreaks due to their larger surface area (Burnell 1977). The end result is that infestations target large-diameter pine, and because tree diameter is directly related to brood production, infestation of large trees (>25.4 cm dbh) contributes to a growth in beetle populations and tree mortality the following year (Safranyik et al. 1974, Cole and Amman 1980).

The pattern of tree selection and infestation has been hypothesized to change over the course of an outbreak. Mortality of the largest-diameter trees is thought to peak

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early in the infestation, and progressively smaller trees are infested over time (Klein et al. 1978, Cole and Amman 1980, Nelson et al. 2006). This theory suggests that colonization of large trees is necessary to establish an outbreak, and thereafter smaller-diameter pines are equally susceptible to infestation (Cole and Amman 1980). In other words, the size of trees infested in a stand relates to the duration of beetle activity. In an investigation of spot infestations, Borden (1993) found that the ratio of newly infested (green) trees to previously infested (red) trees did not indicate that susceptible large-diameter trees were infested in relation to their proximity to previously infested trees, concluding that it was just as common for beetles to disperse past susceptible trees into new areas as it was for them to infest the closest susceptible tree. This is further supported by a mark-recapture experiment, where a small percentage of beetles was observed to disperse past suitable hosts and were captured over 200 meters from the point of release (Safranyik et al. 1992).

Mitchell and Preisler (1991) investigated the stand scale spatial pattern of infested lodgepole pine and found that large trees were preferentially selected and essential for the establishment and maintenance of a successful infestation. They also found that the proportion of large and small trees being infested did not change significantly over the course of the infestation. These findings agree with others that the “switching” attack dynamic dictates the growth of spot infestations within a year (Geiszler et al. 1980). However, between years, beetles are likely to fly to new locations, often past susceptible host trees (Safranyik et al. 1989, Borden 1993).

The question of why beetles do not attack the nearest host trees is central to understanding short-range spatial dynamics of dispersal. One likely explanation is that beetles require a period of flight exercise before becoming responsive to pheromones (Shepherd 1966, Borden et al. 1986). This is a known behavior of other species of bark beetle. For example, Douglas-fir beetles (*Dendroctonus pseudotsugae* Hopkins), were found to require 30 and 90 minutes of flight exercise before responding to pheromone-laden frass (Bennett and Borden 1971). One hypothesis relates this type of dispersal behavior to lipid content, where the most physiologically fit (lipid-rich) Douglas-fir beetles disperse widely until responding to pheromones, while the least physiologically fit (lipid-deficient) beetles attack the nearest host trees, with little to no dispersal period (Atkins 1969, Borden et al. 1986). It is reasonable to suggest that at some level, mountain pine beetle responsiveness to pheromone signals could vary with physiological state, which in large part is determined by environmental factors such as host phloem thickness, crown volume, and temperature (Safranyik et al. 1974). Physiological variations in dispersal behavior could also influence the factors guiding the primary attraction of pioneer beetles to potential host trees. It would therefore be expected for the dispersal mechanisms guiding the growth of infestations to vary both geographically and temporally.

Mark-recapture studies have provided a wealth of information about the characteristics of mountain pine beetle dispersal ecology at the stand level. Spatial pattern analysis has also provided information about dispersal and infesta-

tion spread over time (Mitchell and Preisler 1991, Preisler and Mitchell 1993), yet knowledge gaps remain between dispersal ecology and infestation patterns of mountain pine beetles. This article takes an exploratory approach to characterizing dispersal processes by investigating patterns in the spatial interactions of red attack and green attack clusters of mountain pine beetle-infested trees. By investigating landscape conditions at locations where spatial patterns are indicative of short-range dispersal, a better understanding of the conditions influencing dispersal processes may be generated.

Study Area and Data

Field data used in this analysis were collected in 2003 and 2004 for locations in and around the Morice Timber Supply Area (TSA) (Figure 1). The Morice TSA is part of the Nadina Forest District, located in west central British Columbia (54°24'N, 126°38'W). The Cascade Mountains flank its western border, and Tweedsmuir Provincial Park runs along its southern border. The terrain is generally rolling hills in the north and east, and mountainous in the southwest. Major water features include Babine Lake as well as the Bulkly, Morice, and Nadina Rivers. The dominant species is lodgepole pine, which covers over 50% of the forested land base, followed by hybrid white spruce, a cross of white spruce (*Picea glauca* [Moench] Voss), and Engelmann spruce (*Picea engelmanni* Parry ex Engelm.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). There are five biogeoclimatic ecosystem classification (BEC) zones in the Morice, the largest being subboreal spruce.

The current mountain pine beetle infestation has been active in the Morice TSA since the early 1990s. Mountain pine beetle heli-global positioning systems (GPS) estimated approximately 55,000 red trees in 2002, approximately 80,000 red trees in 2003, and over 230,000 red trees in 2004. The impacts of exponential growth in infestation are evident in much of the analysis conducted in this article.

Data used in the analysis were collected in the field for plots centered on infestation clusters identified during helicopter surveys of mountain pine beetle infestations. In helicopter surveys, a helicopter-mounted GPS is used by an operator to record the spatial location of a group of attacked trees and an estimate of the number of infested trees. Infestations are detected from the air by means of visible discoloration in crown foliage. Typically, by the year after infestation, crown foliage has turned yellow-brown or red. Clusters of such trees are identified during helicopter surveys and a GPS is used to map cluster centroids as points (Nelson et al. 2006). In Morice, red foliage indicates infestations that occurred 1 to 2 years before surveying, whereas nonvisible foliage change or green attack indicates infestations that occurred in the year of the survey.

Field data were collected for 669 plots centered on infestations identified during heli-GPS surveys (Figure 2). Thus, field plots were located where infested trees were visible and the infestation at least 1 year old. Each circular plot had an 8 meter radius (~200 m²) and was located at least 100 meters from any other plot centroid. In each plot, an inventory of all trees was taken. Trees were categorized

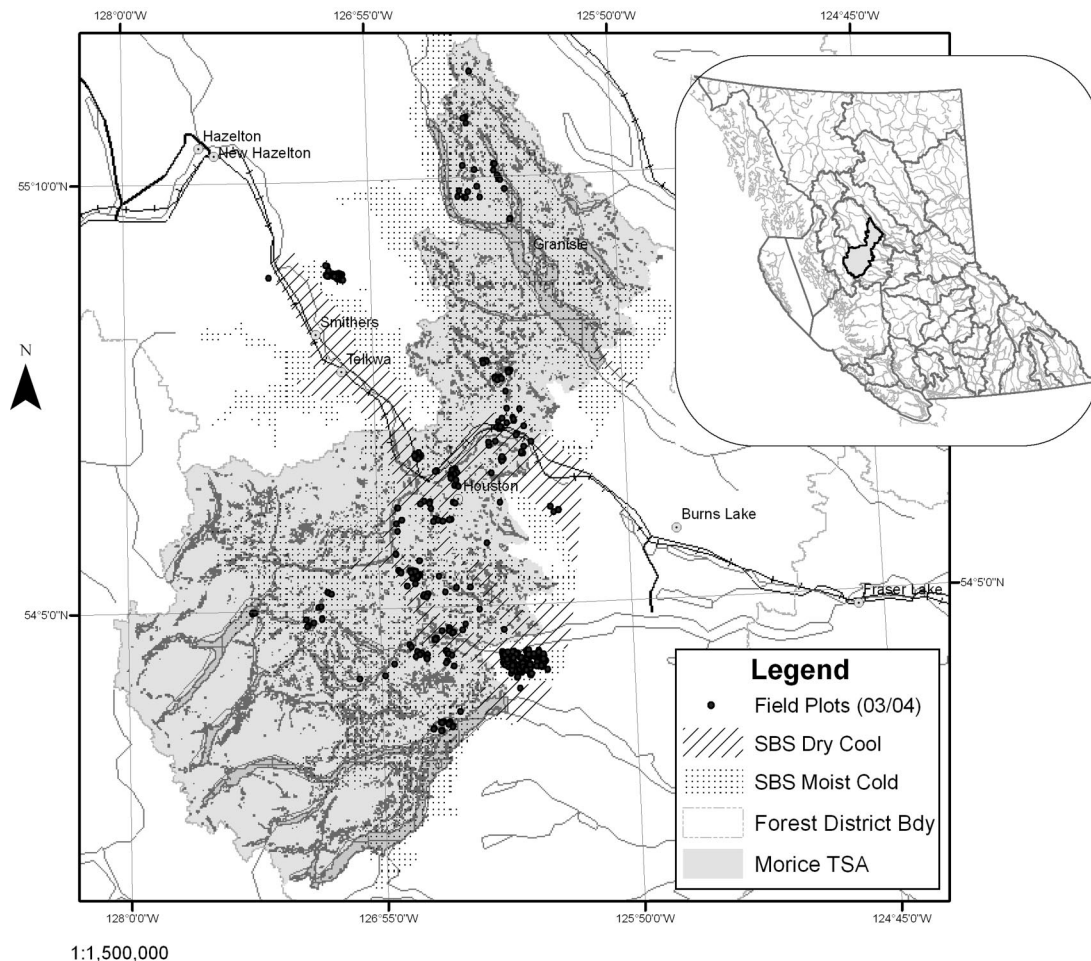


Figure 1. Map of the study area. The Morice TSA, centered on Houston, British Columbia (54°24'N, 126°38'W).

as healthy pine, green attack, red attack (infested 1 to 2 years previously), gray attack (infested > 2 years previously), and nonpine species. Almost all plots (97.5%) had healthy pine trees. Throughout this article the term “green trees” refers to trees that have been recently infested. Red and gray attacked trees were identified in the field by the presence of foliage discoloration and signs of beetle attack. Green trees were identified in the field by examination of tree boles for evidence of mountain pine beetle attack, such as entrance holes, boring dust, and pitch tubes, combined with a lack of foliage discoloration. If the green or red trees in the plot were part of a cluster that extended beyond the circumference of the plot, the green and red trees outside of the plot that were part of the clusters were also recorded. For each category, trees were counted and the average dbh and tree height estimated. At each plot location, a search was made for green trees within a 100-m radius of the plot centroid. If any were found, the distance and direction from the plot centroid to the center of the nearest green infested trees were approximated and the number of green trees estimated.

Supplementary data used in this analysis included forest inventory polygons (FIP), vegetation resource inventory (VRI), biogeoclimatic ecosystem classification (BEC), and a digital elevation model (DEM). British Columbia forest inventory data are generated by aerial photo interpretation at

an approximate scale of 1:15,000. FIP data are an inventory data set last updated for the Morice TSA in the mid-1990s. VRI is the replacement inventory program and was used for plots located outside of the Morice TSA (updated in 2001). For each plot site index, an expression of forest site quality based on stand age and height, was extracted from forest inventory data (Stearns-Smith 2001).

The BEC system classifies landscapes based on climatic and site characteristics. Zones represent large geographic areas under the influence of the same regional climate and subzones represent geographically related ecosystems (Eng and Meidinger 1999). Subzones are the basic unit, represented as vector polygons. The BEC data used in this analysis were mapped at a scale of 1:20,000 in 2003. The main BEC zone in the Morice TSA area is subboreal spruce. Figure 1 shows where different subzones are located within the study area. The subzones used in the analysis were the dry cool subzone (275,000 ha) and the moist cold subzone (970,000 ha), as these were the most prevalent and were coincident with locations of field survey sites.

Elevation base data in the form of a digital elevation model were used for all topographic analysis. This data set has a spatial resolution of 25 meters, and conforms to provincial base-mapping DEM specifications (Province of British Columbia 1996).

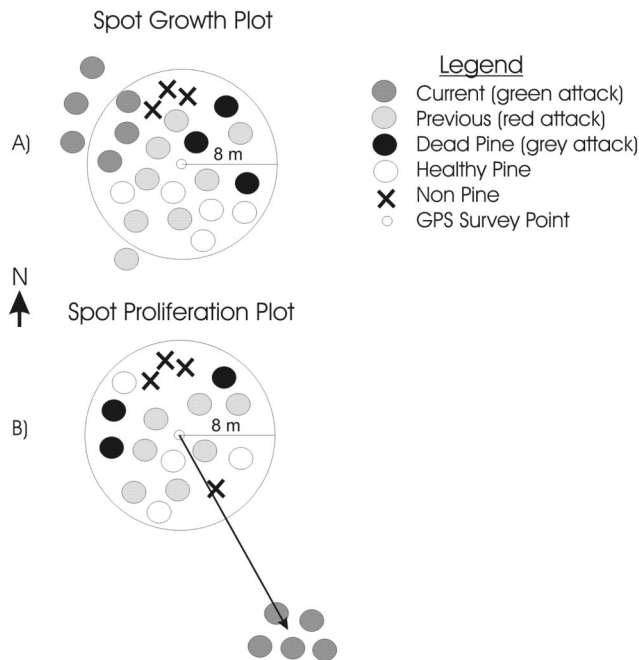


Figure 2. Example of typical field data. Each plot is circular, with a radius of 8 m, centered on an infestation identified during helicopter surveys. All trees within the plot were inventoried. Additionally, an area within a 100-m radius of the plot centroid was surveyed. When green attack trees were identified in this search, the distance and direction to the center of the nearest green attack trees from the plot centroid were estimated.

Methods

The link between the spatial pattern of infestation and dispersal is based on previous research (Safranyik et al. 1992, Safranyik 2004), which identified three movement patterns for dispersing beetles: spot infestation growth, spot infestation proliferation, and movement between infestation spots. Spot infestation growth occurs when beetles at a given location attack other trees at the same location. Spot infestation proliferation occurs when beetles from one spot disperse to initiate an infestation at a new location. Movement between spots is the interaction from one infested spot to another infested spot. In the field data, red trees are typically infested 1 to 2 years earlier than infested trees that are green. Spot growth is assumed to occur when green trees are found within the plot but not found in the 100-meter search outside the plot, whereas spot proliferation is defined as occurring where a cluster of green trees is found in the 100-meter search. Given the nature of the field data, we are unable to identify movement between spot infestations. The 8-meter threshold used to differentiate between spot growth and proliferation is somewhat arbitrary, however, as will be demonstrated in the Results; dispersal distances associated with proliferating sites tend to be at least 20 m. Therefore, this analysis is robust to small variations in this definition.

A key assumption of this methodology is that green trees were attacked by beetles from the nearest field plot. Although we cannot be certain of this interaction, it is interesting to note that, even though there are many more heli-GPS survey locations than field plots, over 90% of infested green trees are closer to a field plot than to other infested locations identified during the heli-GPS survey. Addition-

ally, as field plots are located a minimum of 100 meters from each other, spatial interaction between field plots is unlikely.

The spatial patterns of green and red trees, as they relate to beetle dispersal, were investigated in two phases of analysis described below. For each phase, patterns of spot growth and proliferation were differentiated. Selected forest characteristics were explored for sites of growth and proliferation. These were the mean number of susceptible host trees (healthy pine with diameter greater than 10 cm), stem density, site index, the dbh of red attacked trees in the plot, and mean elevation. Statistical comparisons were performed using the nonparametric Mann-Whitney Test (Burt and Barber 1996, p. 338–344), and each mean value is reported with its coefficient of variation. Statistical significance levels $\alpha = 0.05$ and $0.10 > \alpha \geq 0.05$ are reported separately.

Phase 1—General Trends

The first phase of investigation focused on characterizing the general spatial interaction between red and green infestations. Plots were partitioned based on the presence or absence of green trees, and forest characteristics were compared for each subset. For plots with green attacked trees, the proportion with spot growth and proliferation were determined and forest characteristics of spot growth and proliferation plots also compared. Where proliferation occurred, trends in the distance and direction between red and green trees were characterized. To test for significant differences in directional trends the Rayleigh test was used (Swan and Sandilands 1995).

To detect whether topography affected the spatial patterns of dispersal and spread, elevations associated with spot proliferation and growth were examined. For plots exhibiting spot proliferation, the estimated distance and direction between red and green infestations were used to estimate the location of the center of green infested trees. The elevations of the centers of the red and green infestations were extracted and variations compared.

Phase 2—Biogeoclimatic Trends

Previous research indicates that beetle dispersal patterns may differ under various environmental and climatic conditions. For instance, infestation spread and dispersal have been observed to vary geographically (Cole and Amman 1980), and have been inversely related to elevation (Amman et al. 1973). To investigate the impact of broad scale environmental and climatic conditions on dispersal movement patterns, trends associated with BEC subzones were explored. Field plots were partitioned into the two dominant BEC subzones found in the study region (subboreal spruce dry cool and subboreal spruce moist cold). For each subzone, plots were partitioned based on the presence or absence of green trees and forest conditions compared. For plots with green trees, the frequency of spot growth and proliferation were explored. For plots indicative of spot proliferation, the distance and direction between red and green infestations were characterized. Additional analysis

was conducted to investigate the forest characteristics of plots experiencing spot proliferation and spot growth.

Results

Phase 1—General Trends

Mountain pine beetles were active in the study area in both 2003 and 2004. In both years, green trees were found at a majority of plots (Table 1). In 2003, 66% of plots had green trees found, which increased to 92% in 2004. This rapid increase is representative of the broader trend toward exponential increase in infestation levels in 2004. Plots lacking green trees were found at locations where conditions for mountain pine beetles were of relatively low suitability; higher elevation, and lower stem density (Table 1). Additionally, there were fewer remaining susceptible hosts at these locations. Plots with green trees in 2003 had on average 3.4 more susceptible hosts than plots without green infested trees. The difference in the number of susceptible hosts between plots with and without green attack trees increased to 4.4 in 2004. The lower number of remaining susceptible host trees at locations devoid of green trees may be due to the lower population of pine in general rather than a result of previous infestations. In 2003 plots with green trees, there was an average total of 10.4 lodgepole pine trees, and for plots lacking green trees, the average number of lodgepole pine was 6.7. Similar counts were found in 2004 (10.0 and 5.4).

In 2003 and 2004 combined, 75% (499/669) of plots had green trees within a 100-m radius of the plot centroid. As we are interested in the interaction between red and green trees, only plots having green attacked trees were analyzed further. Spot proliferation was more common than spot growth, occurring in 60% (298/499) of plots. The distribution of distances for 2003 and 2004 are presented collectively, as annual trends were similar. For plots identified as experiencing spot proliferation, the most common distances between red and green tree clusters were approximately 50 m, 30 m, and 20 m (Figure 3). However, the mean distances were different between years, with a significantly higher mean distance between red and green trees in 2004 than in 2003 (Table 2).

For plots experiencing spot proliferation, the directions from red to green infestations indicate different trends between years. In 2003, the majority of green infested trees were found northward (47% were north, northeast, or northwest) of the red trees (Figure 4). The modal direction from red to green trees was northeast (17%) and a Rayleigh test

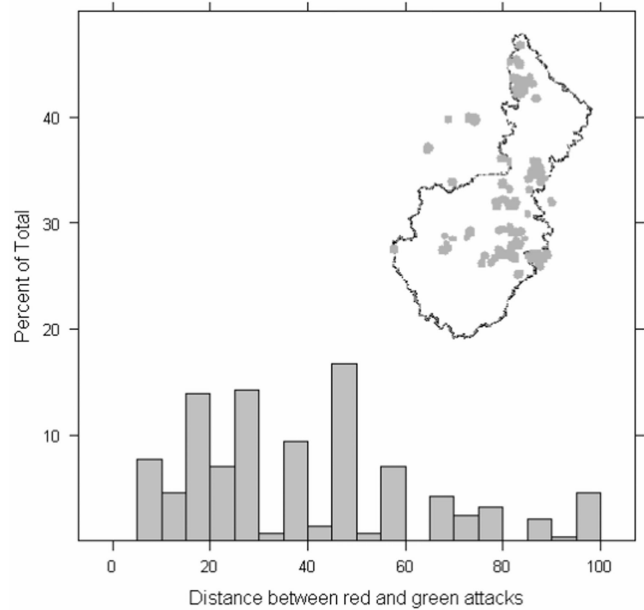


Figure 3. Interaction of mountain pine beetle-infested trees: distance (m) from center of red attack to center of green attack for plots with spot proliferation, 2003/2004 ($n = 298$). Plots located near Houston, British Columbia. Map in upper right corner of figure shows the locations of plots.

indicated the presence of a directional trend ($\theta = 17.9^\circ$, $P = 0.01$). In 2004, the modal direction of attack was south, with 21% of green attack clusters located due south of red clusters, and 30% of sites being southward of red trees. However, there was not a significant directional trend ($\theta = 177.8^\circ$, $P = 0.35$) in 2004, probably due to a more varied distribution of directions (few observations were southwest or southeast). Generalizing directional trends associated with dispersal is difficult, as they likely relate to site-specific factors such as wind speed, wind direction, and the spatial distribution of suitable hosts.

Changes in elevation between red and green trees at plots experiencing spot proliferation were as follows: in 133 (45%) observations the green attack were lower than the red, in 121 (41%) observations the green attack were higher than the red, and in 44 (15%) observations were at the same elevation. Slope revealed little information with no difference in range and mean between red and green attacks for both years. This is likely due to the small distances observed. The direction newly dispersing beetles take may be more related to wind than local topography.

The mean characteristics of plots experiencing spot

Table 1. Plot characteristics for all sites, by presence (G)/absence (NG) of green attacked trees (coefficient of variation). Plots located near Houston, British Columbia

Partition	<i>n</i>	Mean susceptible hosts remaining in plot	Mean stem density (#/ha)	Mean site index	Mean dbh of red attacked plot trees (cm)	Mean elevation (m)
2003 G	289 (66%)	6.6 (0.85)*	690 (0.56)*	16.4 (0.17)*	36 (0.15)	881 (0.11)*
2003 NG	151 (34%)	3.2 (1.27)*	504 (0.72)*	15.2 (23)*	36 (0.17)	916 (0.12)*
2004 G	210 (92%)	5.6 (0.73)*	567 (0.41)*	16.1 (0.16)	35 (0.17)	914 (0.12)*
2004 NG	19 (8%)	1.2 (1.38)*	426 (0.60)*	15.7 (0.21)	34 (0.28)	970 (0.13)*

* Statistically significant ($\alpha = 0.05$) between G and NG for a given year.

Table 2. Plot characteristics for sites with green attacked trees (coefficient of variation)

Partition	<i>n</i>	Mean susceptible hosts remaining in plot	Mean stem density (#/ha)	Mean site index	Mean dbh of red attacked plot trees (cm)	Mean distance (m)	Mean elevation (m)
2003 SP	181 (63%)	7.1 (0.76)	726 (0.51)*	16.4 (0.15)	36 (0.15) [†]	41.56 (0.67)*	873 (0.10)*
2003 SG	108 (37%)	6.7 (0.88)	630 (0.65)*	16.4 (20)	35 (0.15) [†]		896 (0.11)*
2004 SP	117 (56%)	5.6 (0.62)	546 (0.43)*	16.1 (0.15)	35 (0.19)	59.44 (1.16)*	911 (0.14)
2004 SG	93 (44%)	5.8 (0.80)	597 (0.38)*	16.2 (0.17)	36 (0.18)		919 (0.11)

SP, spot proliferation; SG, spot growth. Plots located near Houston, British Columbia.

* Statistically significant ($\alpha = 0.05$) between SP and SG for a given year and for mean distance between years.

[†] Statistically significant ($0.10 > \alpha \geq 0.05$) between SP and SG for a given year and for mean distance between years.

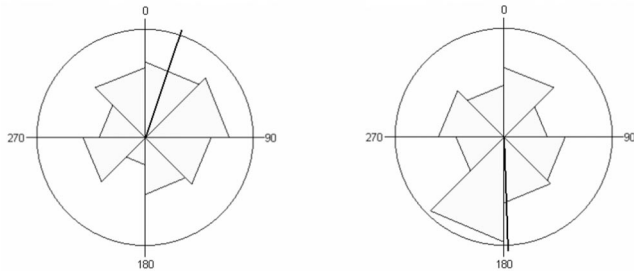


Figure 4. Directional interaction of mountain pine beetle-infested trees: relative frequency distribution of directions from red to green attacks for plots with spot proliferation for 2003 (left, *n* = 181) and 2004 (right, *n* = 117). Plots located near Houston, British Columbia.

growth and proliferation are presented in Table 2. In 2003, proliferating plots were associated with lower elevations and denser plots than plots experiencing only spot growth. Different trends are noted in 2004, when denser plots were associated with spot growth. It is interesting to note that on average, 2004 plots were found at higher elevations than plots surveyed in 2003 (Figure 5). As well, 2004 plots were less dense and had fewer remaining susceptible hosts than plots surveyed in 2003 (Table 2).

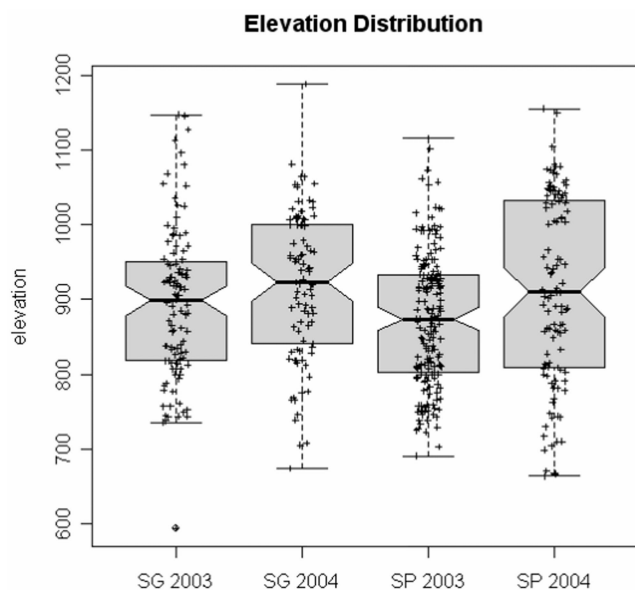


Figure 5. Topographical distribution of mountain pine beetle-infested trees: elevation (m) at spot proliferation (SP) and spot growth (SG) plot locations, 2003/2004. Plots located near Houston, British Columbia.

Phase 2—Biogeoclimatic Trends

More plots were located in the moist cold than dry cool subzone (Table 3). Plots where green trees were absent were found predominantly at higher elevations, where susceptible hosts were sparse. As with the general trends, plots with green infested trees have on average more susceptible hosts. As well, stem densities and site indexes are higher, although the 2004 dry cool subzone is an exception to this trend. In Morice, pine trees grow at elevations ranging from 600 to 1,400 meters and mountain pine beetle have been observed over this elevation range (Nelson and Boots 2005). In the moist cold subzone, trends between the presence of green trees and elevation indicate that at higher elevations forest conditions are increasingly less suitable for mountain pine beetles. When plots in the dry cool subzone are partitioned by presence or absence of green trees, differences in elevation are negligible for 2003, and in 2004 almost all plot locations had green trees present (Table 3).

Relative to dry cool subzone plots, moist cold subzone plots are associated with lower site indexes and higher elevations (Table 4). In general, they appear to be a less suitable habitat for mountain pine beetles. In 2003, the moist cold subzone had, on average, fewer susceptible hosts and lower stem density, and in 2004 attacked trees had a smaller average dbh than trees in the dry cool subzones in the same years. From 2003 to 2004, the number of susceptible hosts was fewer in both BEC zones and stem densities of all plots declined. In the moist cold subzone, a greater proportion (46% and 47% for 2003 and 2004, respectively) of plots experienced only spot growth compared with locations in the dry cool subzone (26% and 37%) (Table 5).

In both subzones spot proliferation was more common than spot growth. Figure 6 shows relative frequency distributions for distances between red and green attack in the dry cool and moist cold subzones over both years. The most dominant difference is the proportion of dry cool sites that experienced spot proliferation. Actual distances are similarly distributed as other data subsets, with frequent observations of 50 meters and 30 meters between red and green attack. Also, distances were more variable in the moist cold subzone when compared to the dry cool subzone.

In 2003, in the moist cold subzone, spot proliferation (54%) was only slightly more common than spot growth (46%). Where spot proliferation occurred, plots were significantly denser, had more remaining susceptible hosts, and larger diameters of red attacked trees than plots where spot growth occurred (Table 5). In the dry cool subzone, spot

Table 3. Plot characteristics in biogeoclimatic subzones, by presence (G) / absence (NG) of green attacked trees - (coefficient of variation). Plots located near Houston, British Columbia

Partition	<i>n</i>	Mean susceptible hosts remaining in plot	Mean stem density (#/ha)	Mean site index	Mean dbh of red attacked plot trees (cm)	Mean elevation (m)
2003 MC-G	159 (36%)	6.0 (0.75)*	625 (0.58)*	16.1 (0.17)*	36 (0.14)*	927 (0.09)**
2003 MC-NG	101 (23%)	3.2 (1.32)*	505 (0.71)*	14.7 (0.26)*	37 (0.18)*	940 (0.10)**
2003 DK-G	122 (28%)	8.2 (0.81)*	797 (0.51)*	16.8 (0.17)*	36 (0.16)	815 (0.07)
2003 DK-NG	37 (8%)	3.7 (1.09)*	546 (0.73)*	16.4 (0.13)*	35 (0.19)	813 (0.07)
2004 MC-G	142 (62%)	5.6 (0.75)*	567 (0.44)*	15.8 (0.18)	35 (0.18)	972 (0.08)*
2004 MC-NG	17 (7%)	0.7 (1.27)*	400 (0.64)*	15.3 (0.22)	35 (0.16)	995 (0.10)*
2004 DK-G	67 (29%)	5.6 (0.68)	578 (0.34)	16.9 (0.11)	37 (0.16)	788 (0.09)
2004 DK-NG [†]	2 (1%)	5.0 (0.20)	650 (0.08)	19.3 (0.09)	23 (0.06)	754 (0.02)

* Statistically significant ($\alpha = 0.05$) between G and NG for a given year.

** Statistically significant ($0.10 > \alpha \geq 0.05$) between G and NG for a given year.

[†] Sample size too small for comparison.

Table 4. Plot characteristics in biogeoclimatic subzones for sites with green attacked trees (coefficient of variation)

Partition	<i>n</i>	Mean susceptible hosts remaining in plot	Mean stem density (#/ha)	Mean site index	Mean dbh of red attacked plot trees (cm)	Mean elevation (m)
2003 MC	159 (55%)	6.0 (0.75)*	625 (0.58)*	16.1 (17)*	36 (0.14)	927 (0.09)*
2003 DK	122 (42%)	8.2 (0.81)*	797 (0.51)*	16.8 (0.17)*	36 (0.17)	815 (0.07)*
2004 MC	142 (68%)	5.6 (0.75)	567 (0.44)	15.8 (0.18)*	35 (0.20)*	972 (0.08)*
2004 DK	67 (32%)	5.6 (0.68)	578 (0.34)	16.9 (0.11)*	37 (0.15)*	788 (0.09)*

Plots located near Houston, British Columbia. MC, subboreal spruce moist cold biogeoclimatic subzone; DK, subboreal spruce dry cool biogeoclimatic subzone.

* Statistically significant ($\alpha = 0.05$) between MC and DK for a given year.

Table 5. Plot characteristics in biogeoclimatic subzones, by spot proliferation and spot growth (coefficient of variation)

Partition	<i>n</i>	Mean susceptible hosts remaining in plot	Mean stem density (#/ha)	Mean site index	Mean dbh of red attacked plot trees (cm)	Mean distance (m)	Mean elevation (m)
2003 MC SP	86 (54%)	6.6 (0.70)*	694 (0.54)*	15.8 (0.18)	37 (0.13) [†]	44.80 (0.74)	927 (0.08)
2003 MC SG	73 (46%)	5.4 (0.79)*	545 (0.60)*	16.4 (0.16)	35 (0.14) [†]		927 (0.08)
2003 DK SP	90 (74%)	8.0 (0.76) [†]	775 (0.47)	17.0 (0.12) [†]	36 (0.16)	39.88 (0.54)	813 (0.07)
2003 DK SG	32 (26%)	10.0 (0.78) [†]	859 (0.57)	16.4 (0.28) [†]	35 (0.18)		822 (0.07)
2004 MC SP	75 (53%)	5.9 (0.63)	543 (0.48) [†]	15.5 (0.17)	34 (0.21)	64.10 (1.28)	983 (0.08)*
2004 MC SG	67 (47%)	5.6 (0.83)	591 (0.40) [†]	16.0 (0.19)	35 (0.19)		959 (0.07)*
2004 DK SP	42 (63%)	5.0 (0.60)	552 (0.34) [†]	17.0 (0.11) [†]	36 (0.14)	51.19 (0.62)	781 (0.10)*
2004 DK SG	25 (37%)	6.5 (0.73)	622 (0.32) [†]	16.8 (0.11) [†]	38 (0.16)		801 (0.07)*

Plots located near Houston, British Columbia. MC, subboreal spruce moist cold biogeoclimatic subzone; DK, subboreal spruce dry cool biogeoclimatic subzone.

* Statistically significant ($\alpha = 0.05$) between SP and SG for a given BEC subzone, for a given year.

[†] Statistically significant ($0.10 > \alpha \geq 0.05$) between SP and SG for a given BEC subzone, for a given year.

proliferation was more common (74%), and proliferation plots generally had fewer remaining susceptible hosts and higher site index than the spot growth plots.

In 2004, there were generally fewer remaining susceptible hosts and lower plot densities than in 2003. In the moist cold subzone, spot proliferation occurred at 53% of plots, while in the dry cool subzone, proliferation occurred at 63% of locations (Table 5). For moist cold proliferation plots, stem density was lower and elevation higher than growth plots. For dry cool proliferation plots, plot differences were lower stem density, higher site index, and lower elevation than dry cool growth plots (Table 5). Only elevation trends were significant at the 0.05 significance level.

In Table 6, the average dbh of red, green, and healthy trees are presented for data separated by biogeoclimatic subzone and movement pattern. While there is some vari-

ability in trends between 2003 and 2004 and between BEC subzones, red trees consistently had the largest diameters and healthy trees had the smallest. Over time, mountain pine beetles were infesting smaller trees. There were more significant differences, and thus a more pronounced preference for large trees in the moist cold subzone.

Discussion and Conclusions

The clearest trend observed in this analysis is the large proportion of plots (60%) where spot proliferation occurred, despite a local population of susceptible host trees within the plot. This is evidence that beetles are dispersing past suitable hosts to new locations. This pattern has previously been observed in mark-recapture studies (Safranyik et al. 1992, 1989) and investigations of spot infestations over

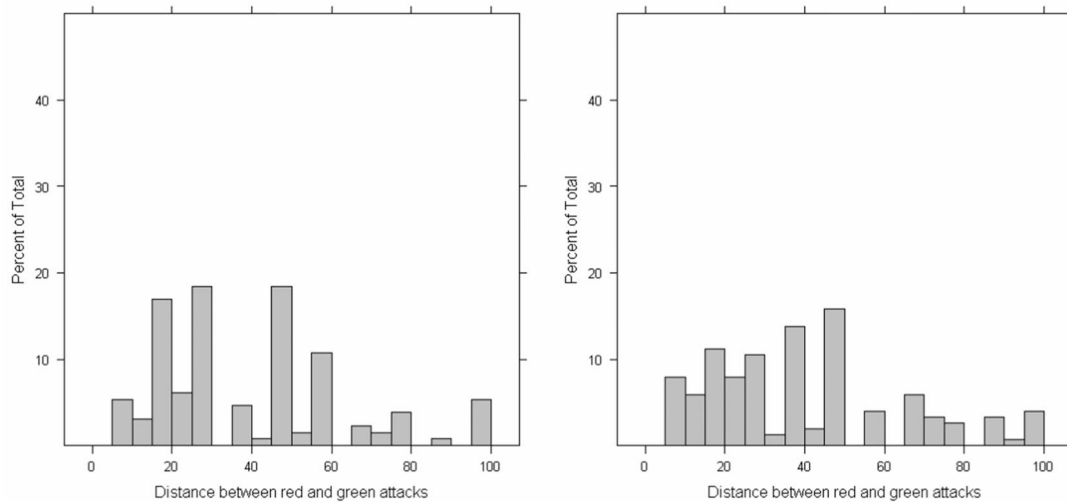


Figure 6. Interaction of mountain pine beetle-infested trees: distance (m) to green attack for plots with spot proliferation for subboreal spruce dry cool (left, $n = 132$) and subboreal spruce moist cold (right, $n = 161$) subzones (2003/2004). Plots located near Houston, British Columbia.

Table 6. Variations in the size of trees attacked through time for biogeoclimatic subzones (coefficient of variation)

Partition	n Plots	Mean red dbh (cm)	Mean green dbh (cm)	Mean healthy dbh (cm)
2003 DK SP	85/59/73	36 (0.16)	35 (0.17)*	29 (0.26)*
2003 DK SG	28/32/28	35 (0.18)	33 (0.22)	32 (0.21)
2003 MC SP	75/46/62	37 (0.13)*	34 (0.18)*	31 (0.19)*
2003 MC SG	69/72/45	35 (0.15)	34 (0.18)*	31 (0.16)*
2004 DK SP	41/37/27	36 (0.15)	36 (0.17)*	30 (0.26)*
2004 DK SG	25/25/13	38 (0.17)	37 (0.16)*	27 (0.25)*
2004 MC SP	68/58/51	35 (0.17)*	33 (0.17)*	29 (0.23)*
2004 MC SG	65/67/37	35 (0.19)*	34 (0.21)*	27 (0.26)*

Plots located near Houston, British Columbia. MC, subboreal spruce moist cold biogeoclimatic subzone; DK, subboreal spruce dry cool biogeoclimatic subzone.

* Statistically significant ($\alpha = 0.05$) between adjacent classes for a given BEC subzone, for a given year. No comparisons made between red and healthy dbh.

time (Borden 1993). At proliferating spots, distances were not distributed linearly (Figure 3), with distances of 30 meters and 50 meters most common.

Beetles seem to have been dispersing past susceptible hosts up to distances of at least 100 meters, and most often at distances of 50 meters (Table 2). This differs from findings of previous studies (Safranyik et al. 1992), which found the number of captured beetles to decline exponentially with distance from the point of release. One possible explanation for this difference is methodological. Inferring dispersal from the locations of previous and currently infested trees requires an assumption that the spatial interaction of red and green tree clusters is representative of the movement patterns of dispersing beetles. As well, the distances used in this analysis are estimates. Alternatively, mark-recapture studies assume that trap catches are representative of the attack habits of dispersing beetles. The distinction in these assumptions may explain the variation in observed distributions of dispersal distances. Additionally, in reality all beetles will disperse, yet in this analysis only dispersal greater than 8 m was characterized as spot proliferation.

Variations in dispersal characteristics of mountain pine beetles induced by environmentally determined factors

could also significantly alter the observed patterns of infestation. Environmental differences between locations of previous mark-recapture experiments (Williams Lake, BC—Safranyik et al. 1989, Safranyik et al. 1992) and the current investigation (Morice area, BC) could also explain observed variations in dispersal processes, as well as differences in geography.

Results suggest that spot proliferation typically indicative of short-range dispersal is not solely determined by the presence or absence of nearby host trees. Beetles appear to have been dispersing to new locations despite the number of susceptible hosts nearby (Tables 2 and 5). This is indicated by plots that have remaining susceptible trees and are either absent of green attack or the site of spot proliferation. There does appear to be a pattern to the dispersal of beetles past suitable hosts. Overall, plots experiencing proliferation in 2003 were characterized by higher densities, more optimal climate conditions, and more remaining susceptible hosts (Table 2). This may suggest that there is a site condition threshold, where habitat suitability increases the likelihood of spatially extensive infestation spread to a certain point, and at locations where habitat is less suitable, dispersal to new areas becomes less common, and existing spots are

more thoroughly infested. However, as the beetle population rises, for instance to the intense levels observed in 2004, the beetles become less selective of site conditions.

Results also indicate that denser plots having more susceptible hosts have less likelihood of complete infestation, or rather, take a longer time for full infestation, as more beetles are required to kill the additional trees (Table 1). As areas become more thoroughly infested, fewer susceptible hosts remain, and fewer areas are devoid of mass attacked trees.

In 2004, a huge rise in the number of green attacked trees may have caused infested areas to coalesce. Lower amounts of remaining susceptible hosts per plot (Table 4) and lower average dbh for healthy pine (Table 6) suggest that previously infested areas were being re-attacked. Typically, mountain pine beetles do not infest all susceptible hosts in an area in 1 year (Mitchell and Preisler 1991), and it appears that depleted stands were further attacked when beetle populations became large. This indicates that large infestation patches develop as the dominant movement pattern of dispersing beetles shifts from spot proliferation to movement between infested spots.

In Table 6, the differences between green attack and healthy remaining pine indicate a stronger relationship between mortality and dbh in 2004 than in 2003. The differences between green and healthy pine diameters in 2004 are greater than the corresponding differences in 2003. If we consider this trend in the context of population dynamics, we can see how it may reveal a shift in the state of the local mountain pine beetle population. Safranyik and Carroll (2006) identify four stages of the mountain pine beetle population cycle: endemic, incipient-epidemic, epidemic, and postepidemic. While both 2003 and 2004 can be considered in an epidemic state, the shift in 2004 represents an escalation along this epidemiological continuum. The strengthening of the mortality-diameter relationship is thought to occur until the supply of large diameter trees is exhausted and the epidemic collapses.

Geographical variation of dispersal appears to have been occurring in the study area. Proportionally, spot proliferation occurred more often in the subboreal spruce dry cool subzone than other areas. Mountain pine beetles prefer large trees, but the temporal attack pattern in dbh was not different in the two subzones investigated here (Table 6). This suggests that the distance traversed by dispersing beetles is not exclusively related to the population of susceptible hosts, and may be more related to beetle-specific biological characteristics. Models of mountain pine beetle dispersal based solely on the spatial distribution of hosts may be failing to capture the complexity of the process.

Spot proliferation may be more common in these areas for a number of reasons. First, the current infestation has been active in the Morice area since the early 1990s. The previous spatial patterns of infestation may be influencing the patterns observed in 2003 and 2004 (Mitchell and Preisler 1991). To further explore the increased occurrence of spot proliferation within the dry cool subzone, it would be informative to see if previously infested trees or other forest disturbances such as cut blocks influence the patterns of movement observed here. The conditions in this subzone

are also more suitable for successful beetle emergence (drier and warmer), and therefore infestations may be more successful in these areas. In the dry cool subzone, where temperatures are warmer and climate is drier than the moist cold subzone, the mountain pine beetle will likely disperse over greater extents. The question remains as to whether the observed variability in dispersal patterns is related to population processes, biological processes or, perhaps more likely, a combination of the two.

The dominance of spot proliferation in the dry cool subzone is an important finding. From an operational perspective, management activities may be better allocated to areas where the risk of spatially extensive spread is greatest. If beetles disperse further and more often in a particular type of habitat, new spot infestations identified in these areas should be the focus of management efforts. BEC subzones offer an appropriately scaled classification for characterizing biogeoclimatic influences on dispersal and the associated risk in infestation spread. These could be used in planning management at the landscape scale. However, a more thorough understanding of the ecological mechanisms causing variation in dispersal of mountain pine beetles is needed. As hypothesized by Borden et al. (1986), variations in physiological fitness and pheromone responsiveness is one possible explanation.

The results of this analysis indicate that, at the very least, dispersal is not solely dictated by the distribution of susceptible host trees, large or small. The pattern of preferential selection of large trees (Table 6) has been frequently observed (i.e., Cole and Amman 1980, Mitchell and Preisler 1991, Preisler and Mitchell 1993). Large-diameter trees spur infestation spread simply by producing large quantities of beetles. How this influences beetle dispersal is unknown. In our analysis, tree diameter does not appear related to variations in spot growth and spot proliferation.

Variations in pheromone communication could also have an effect on dispersal behavior, given the large role pheromones play in coordinating mass attacks. Logan et al. (1998) demonstrate that as an infestation switches from endemic to epidemic, the spatial spread changes from one determined by the spatial distribution of susceptible host trees, to one determined by the semiochemical landscape. Thistle et al. (2004) showed how dispersion of surrogate pheromone plumes were dependent on the ambient mixing environment, influenced mainly by atmospheric stability, wind speed, and stand characteristics such as stem density. In the coniferous stands examined, as local microclimates became more unstable in the late morning to late afternoon, pheromone plumes were less concentrated and showed less directional consistency.

In our analysis, epidemic conditions and the observed trends in infestation growth and proliferation in relation to the distribution of host trees indicates that other factors are also influencing spread. Variations in the movement patterns of dispersing beetles appear to be related to biogeoclimatic classification of habitat and infestation intensity. It is possible that the biogeoclimatic classifications in this analysis provide some level of differentiation of atmospheric stability, and therefore variations in

pheromone plume concentration during mountain pine beetle dispersal. It is interesting to note that the variable surrogate pheromone plume concentrations observed in Thistle et al. (2004) were at a similarly local scale (5 to 30 m) to our analysis of infested tree patterns. Further research into the relationship among mountain pine beetle dispersal, pheromone concentrations, and the spatial pattern of infested trees should be conducted. Whether the variations in movement patterns detected here are the results of pheromone connectivity, beetle specific biological variations induced by different environments, or other mechanisms is unclear.

This research identifies some of the characteristics of locations where spot growth and spot proliferation occur. An enhanced understanding of mountain pine beetle dispersal will greatly benefit forest managers and modeling of infestation spread. More research is needed to incorporate dispersal variability into spatial models of infestation spread. However, the trends identified in this analysis offer an important source of information for future research into mountain pine beetle dispersal and infestation spread.

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