Random acts of weevil: A spatial analysis of *Hylobius warreni* attack on *Pinus contorta* var. *latifolia* in the sub-boreal spruce zone of Northern British Columbia

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Abstract

The Warren root collar weevil (*Hylobius warreni*) is a native pest of lodgepole pine (*Pinus contorta* var. *latifolia*) in western North America. Damage caused by larval feeding at the root collar and roots often results in low to moderate levels of mortality in many regenerating lodgepole pine stands. We investigated the spatial distribution of lodgepole pine trees, weevil-attacked trees, and mortality due to attack. Stem maps of all lodgepole pine trees were generated in nine, 50-m × 50-m plots in six pine plantations infested by *H. warreni*. All trees in each plot were assessed for attack and mortality. In all plots, live-attacked trees were significantly larger than live-nonattacked trees. In each of three plantations, two contiguous plots were established to allow assessment of within-site variation and spatial structure variation at different scales. We used Ripley's univariate $L(t)$ function to analyze the spatial distributions of all host trees, attacked host trees, and dead attacked host trees, respectively. The distribution of attacked trees generally coincided with the distribution of host trees. The distribution of attack did not change with increasing attack intensity among plots, but did so within plots. Trees killed by *H. warreni* were randomly distributed in all plots except one, and spatial distribution was not affected by attack intensity. Mortality increased as a function of attack. Our findings support that this insect does not aggregate, and that virtually all lodgepole pine are potentially susceptible to attack, i.e., host distribution alone largely explains distribution of both attack and mortality.

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Lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex. Loud.) is the most important conifer species to the forest industry in British Columbia (BC). Large areas of harvested land are replanted with this species each year. The Warren root collar weevil (*Hylobius warreni* Wood) (Coleoptera: Curculionidae) occurs throughout the boreal forests of North America, and is a significant pest of lodgepole pine (Cerezke, 1994). Lodgepole pine is susceptible to attack by *H. warreni* at all life stages, and in younger stands growth loss and mortality may result (Cerezke, 1994). Mortality usually does not exceed 5%, but can be much higher (Cerezke, 1994; Cerezke and Pendrel, 1995). Increasing use of lodgepole pine for regeneration of harvested areas in BC has resulted in large areas of host trees potentially susceptible to mortality or severe growth loss.

Cerezke (1994) summarized what is known about the biology and management of the Warren root collar weevil. In BC, the primary host is lodgepole pine, but other *Pinus* spp., as well as *Picea* spp. (spruce), *Abies* spp. (true firs), and *Larix* spp. (larch) are attacked. The flightless adults feed on twigs, bark, and needles of host trees, but do not cause appreciable damage. Adults mate, and females oviposit between May and September. Eggs are deposited in the litter adjacent to host-tree surface roots or root collars, or the female chews a small hole in the bark at the root collar, oviposits and then covers the egg with chewed bark and/or excreta. *H. warreni* larvae normally require 2 years for full development from egg to adult. They feed on host phloem, with damage increasing as larvae mature. Due to the defensive reaction to damage by the host, a characteristic protective cover of hardened resin and soil is created by the larva (Cerezke, 1994).

H. warreni is present in at least 19% of lodgepole pine stands (all age classes) in BC (Hodge et al., 1994), but in the central

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interior this number is probably much higher (B.S. Lindgren, personal observation). Following harvesting of an infested stand, larvae are able to complete their development in stumps. Planting of lodgepole pine soon after harvesting provides an abundant host resource for surviving and emerging adults (Cerezke, 1994), negating the need for long-range dispersal.

Dispersal of the Warren root collar weevil has been shown to be non-directional (Cerezke, 1994), or random (Cerezke and Pendrel, 1995). Dispersal distances of adult *H. warreni* have been documented to average approximately 2.3 m, to a maximum of 11.3 m in one night (Cerezke, 1994). Thus, this weevil is capable of large dispersal distances over the course of a season, but it is generally thought that the adults only move an average of 13 m per annum (Henigman et al., 2001).

Oviposition sites may also be randomly chosen, as host trees are encountered by *H. warreni* adult females. There is no evidence to suggest that *H. warreni* is attracted to "susceptible" host trees by chemical cues (Cerezke, 1994; B.S. Lindgren, unpublished data). Visual cues may influence host selection, because larger trees tend to sustain higher levels of attack (Cerezke, 1994). Weevils do orient preferentially to relatively larger vertical silhouettes in a laboratory arena (B.S. Lindgren, unpublished data).

Cerezke (1994) considers the mortality of lodgepole pine resulting from weevil attack to be randomly distributed, but Herring and Coates (1981) documented weevil attack and mortality as being clumped. Neither of these studies included an in-depth analysis of the spatial structure of the attack. Quantifying spatial characteristics by ocular assessment is not always a reliable means of classifying distribution. "The human eye (plus brain) is quite adept at classifying point patterns, but is easily fooled," (Ripley, 1981, p. 148).

Although there has been a proliferation of statistical techniques developed to quantify and test the significance of the spatial distribution of points (e.g., Ripley, 1981; Dale, 1999), little is known about the spatial distribution of weevil attack and mortality of young lodgepole pine. In this study we examined the spatial distributions of attack and mortality in *H. warreni*-infested young lodgepole pine stands. Our objectives were to: (1) determine how attack and mortality were distributed by tree size; (2) identify spatial distributions of attack and mortality of lodgepole pine by *H. warreni*; and (3) determine if the intensity of *H. warreni* attack on lodgepole pine will influence the spatial distributions of attack and mortality. An understanding of the spatial distribution of attack and mortality will contribute to an increased understanding of potential factors of host susceptibility and mechanisms of host selection. Such knowledge would be of importance for management of this insect.

1. Materials and methods

We selected six sites (regenerated cut blocks) for the study. Criteria for site selection were even-aged, 5–9-year-old stands with a homogeneous lodgepole pine component containing <3000 stems/ha on relatively flat ground. Furthermore, the stand had to have >2.5% observable estimated mortality and
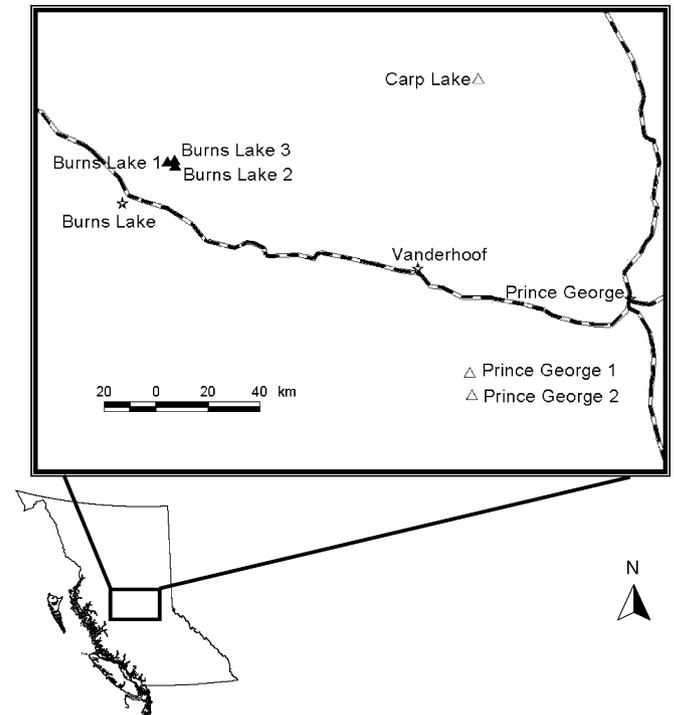

Fig. 1. Map of British Columbia with inset showing locations of study plots. ☆, Nearest large communities; ▲, contiguous plots consisting of two adjacent 50-m × 50-m subplots; △, single 50-m × 50-m plots.

the site had not been subjected to mechanical site preparation. All sites were in the sub-boreal spruce (SBS) biogeoclimatic zone (Meidinger and Pojar, 1991). Six 50-m × 50-m plots were established on three of the sites (Burns Lake 1, 2, and 3; Fig. 1), located near Burns Lake, BC (54°21–22′N, 125°28–30′W), about 230 km west of Prince George, BC. These plots were arranged as paired, contiguous subplots to allow analysis of spatial data at a slightly larger (50-m × 100-m) scale. Thus, each Burns Lake plot consisted of two subplots, which we will refer to as Burns Lake 1-1 and 1-2, 2-1 and 2-2, and 3-1 and 3-2. The Burns Lake sites were all in the dry-cool subzone of the SBS (Meidinger and Pojar, 1991), and were logged between 1995 and 1996. The sites were planted in 1996 with lodgepole pine, i.e., planted pine were 8 years old at the time of data collection. A seventh plot was located near Carp Lake, BC (Carp Lake; Fig. 1) (54°40′N, 123°40′W), about 150 km north of Prince George, and was classified in the moist cool subzone of the SBS, and planted pine were 7 years old. The final two plots, Prince George 1 (53°39′N, 12°42′W) and Prince George 2 (53°35′N, 123°41′W), were located ca. 80 km southwest of Prince George (Fig. 1), and were classified in the moist cold and dry warm subzones of the SBS, respectively. The planted trees on these sites were 5 and 6 years old, respectively.

1.1. Data collection and analysis

Data were collected between May and July 2003. Cut blocks were stratified and areas estimated to contain >2.5% observable mortality were delineated. A grid of possible sampling points was superimposed over the stratified areas and

the location for a 50-m × 50-m (0.25-ha) plot was randomly selected using a random number table. Starting at a reference point, for which coordinates were recorded with a handheld GPS unit (eTrex, Garmin International Inc., Olathe, KS), coordinates of all lodgepole pine trees >1 cm diameter at the root collar were determined using a Criterion 400 Laser (Laser Technology Inc., Engelwood, CO). On each of the three Burns Lake cut blocks, two contiguous plots were established to enable analysis at a larger scale (see Fig. 1). For these sites, the second plot was chosen to begin from a randomly selected side of the first plot. Data were collected as an independent plot, exactly as the first.

Data recorded for each mapped tree included: height, location, attack status, whether it was live or dead (or moribound), and tree origin (planted/natural/unidentified). Other forest health problems (e.g., stem rusts) were noted when encountered, but are not reported on here, because their incidence was insignificant. Trees were identified as being attacked as per Cerezke (1994) and Henigman et al. (2001). Our criteria for dead or moribound trees included >75% girdling of the root collar, discoloration of needles to yellow or red, and lack of bud growth. We also recorded plot descriptors (vegetation, slope, aspect, and stems/ha) for each site.

We examined the relationship between mortality and attack intensity using correlation analysis. We tested whether the height of attacked trees differed from those of unattacked trees by a nested analysis of variance (Statistica Version 6.1, Statsoft Inc., Tulsa, OK), with attack nested in plot (fixed effects). Heights of dead attacked trees were excluded because mortality would have occurred over a number of years. We used Bonferroni post-hoc comparisons (Zar, 1999) to examine plot and attack effects for those ANOVAs having significant main effects. Homogeneity of variances was examined with Levene's test (Zar, 1999).

Spatial analyses were conducted using the ADS in ADE-4 software package (available at: http://pbil/univ-lyon.fr/ADE-4/, Thioulouse et al., 1997). We used the linearized form $L(t)$ of Ripley's K-function, which has been widely used to test the spatial distribution of point data (Ripley, 1981; Getis and Franklin, 1987; Dale, 1999; Goreaud and Pélissier, 1999; Pélissier and Goreaud, 2001; Dale et al., 2002). The second-order analysis of Ripley's $K(t)$ and $L(t)$ functions examines the cumulative frequency distribution of the distances between all events/objects within a site, based on an examination of known distances between pairs of events/objects (Dale, 1999). The $L(t)$ function is determined by tallying the number of same events (points) within a designated radius from a randomly-selected single point within the study area (Wang et al., 2002). Ripley's K-function allows the analysis of spatial distributions without explicit knowledge of what is driving them. The expected density of nearest neighbors in proximity to a random point is found by estimating its mean over the entire distribution. The prediction of a random distribution can be tested by simulating a random process with the Monte Carlo method (Dale, 1999). These simulations are based on maintaining the same levels of intensity as the distribution detected in the data. The confidence interval that is constructed to test the prediction of randomness will

display a characterization of the distribution. Scales at which the function are above the upper confidence limit is considered clumped ($L(t) > 0$), within the confidence interval is considered random ($L(t) = 0$), and below the confidence limit the distribution are interpreted as dispersed ($L(t) < 0$). $L(t)$ functions that show increasing clumping at large scales are indicative of some heterogeneity in the point distribution, and in these cases finer-scale spatial structures depicted by the $L(t)$ function are averages of the varying structures present (Pélissier and Goreaud, 2001). To increase the precision of the confidence interval constructed, 1000 or more Monte Carlo simulations are utilized (Ward et al., 1996).

We assumed that any driving factor influencing the distribution was unknown. Therefore, the expected density of nearest neighbors in proximity to a random point was found as per Pélissier and Goreaud (2001). Plot edge effects (the variation of distribution at edges of a bounded plot; MacLennan, 1991) were accounted for using Ripley's local correction method ($L(t)$) (Goreaud and Pélissier, 1999). To compare the effects of scale at the 50-m × 50-m and 50-m × 100-m levels, we compared program outputs at both scales for Burns Lake 1, 2, and 3 plots. Small scales (2.0 and 3.0 m) were of interest to us because they approximate the initial target and minimum inter-tree spacing of trees at the time of planting (2.0-m minimums and 2.9-m target). The maximum possible scale is half the width of the plot, i.e., 25 m for the individual plots and 50 m for the contiguous plots.

For spatial analyses of 50-m × 50-m plots, the Burns Lake subplots were considered as independent plots ($N = 9$) since the plots in these cases are not used as replicates in a statistical sense. Otherwise they were treated together as plots ($N = 3$ for 50-m × 100-m spatial analyses; $N = 6$ for all other analyses).

2. Results

The six regenerated sites used in this study were relatively similar, apart from some differences in biogeoclimatic zone classification. Although plots appeared environmentally homogeneous at the scale of study, there were some differences at the stand level in terms of age of planted trees (5–8 years) and stem density (∼1500 to 4000 ha^{-1}). Stem density was affected in part by varying amounts of natural regeneration ingress. Between 362 and 924 potential host trees (at least 1 cm diameter at the root collar) were stem-mapped in the nine 50-m × 50-m plots (Table 1). The percentage of attacked trees ranged from 10.5 to 45.9%, dead attacked trees from 1.2 to 16.6%, with eight of the nine plots below 5.2% mortality (Table 1). There was a strong correlation ($r = 0.87$, $P = 0.024$, $N = 6$) of attack and mortality. In the Carp Lake plot, 36.1% of all attacked trees had died, whereas 9.6–17.1% of attacked trees had been killed in the other plots. Total attack in the Carp Lake plot was very high, but a similar high attack rate found in Burns Lake 2-2 (Table 1) resulted in only 11.7% of the attacked trees dying.

Attack on lodgepole pine by *H. warreni* in these plots occurred on both planted and natural trees, with attacks on trees as small as 44 cm. Tree height varied significantly among plots ($F_{5,4771} = 151.30$, $P < 0.001$). Mean height of live attacked

Table 1
Summary data of lodgepole pine trees attacked by *H. warreni* in descending order of total percent attack, and the total number of trees assessed and stem-mapped in 50-m × 50-m plots

Plot	Dead attacked (%)	Live attacked (%)	Total attacked (%)	Total # trees (N)
Carp Lake	16.6	29.3	45.9	362
Burns Lake 2-2	5.0	37.7	42.6	563
Burns Lake 3-1	5.2	26.1	31.3	537
Burns Lake 2-1	4.2	26.9	31.1	569
Prince George 1	3.5	20.4	23.9	461
Burns Lake 3-2	2.5	13.5	16.0	564
Burns Lake 1-1	1.2	11.2	12.5	570
Prince George 2	1.3	10.5	11.8	924
Burns Lake 1-2	1.8	8.8	10.5	457
Mean (±S.D.)	4.59 (4.75)	20.49 (10.11)	25.07 (13.45)	556.33 (155.21)

trees was significantly greater than that of live not attacked trees within plots ($F_{6,4771}$ = 142.62, $P < 0.001$). In all height classes above 150 cm, more than 40% of available trees had been attacked (Fig. 2). The number of dead trees increased from the lowest height classes and then decreased again (Fig. 2).

Fig. 3 shows an example of the stem mapped live unattacked, live attacked, and dead attacked trees in Burns Lake subplot 2-2 and Fig. 4 shows the corresponding output of Ripley's univariate $L(t)$ function. Ripley's $L(t)$ function revealed that spatial distributions of lodgepole pine trees above 1 cm diameter at the root collar varied considerably among 50-m × 50-m plots (Fig. 5, upper bars). In the Carp Lake and Prince George 1 plots, and the Burns Lake 1-1 subplot, trees were mostly clumped at all scales (Fig. 5). In the Burns Lake 2-2 (Fig. 4), Burns Lake 3-1, and Burns Lake 3-2 subplots trees were dispersed at 0.5–2.5 m, and random at all other scales (Fig. 5). In the remaining plots, spatial distributions of potential host trees were variable at different scales (Fig. 5).

The spatial distribution of attacks (lower bars) can be visually compared with tree distributions (upper bars) in Fig. 5. Attack distributions largely corresponded with the host distribution in the Carp Lake plot, and the Burns Lake 1-1,

Burns Lake 3-1, and Burns Lake 3-2 subplots (Fig. 5). In addition, the distribution of attacks corresponded with the tree distribution at scales above 16 m in the Prince George 2 plot and the Burns Lake 1-2 subplot. Attacks were dispersed at small scales in all 50-m × 50-m plots except in Carp Lake, Prince George 2, and Burns Lake 1-1 (Fig. 5). Except for the Prince George 1 plot, where the tree distribution at small scales was clumped, this corresponded with the distribution of the host trees. In the Carp Lake plot, the distribution of attacks was clumped at all scales (except at 1.5 m) (Fig. 5), whereas in Prince George 2 the distribution of attacks was random at all scales except between 1.5 and 6.5 m, where it was clumped. In the Burns Lake 1-1, Burns Lake 2-1, and Burns Lake 2-2 subplots, attack distribution was mostly clumped at larger
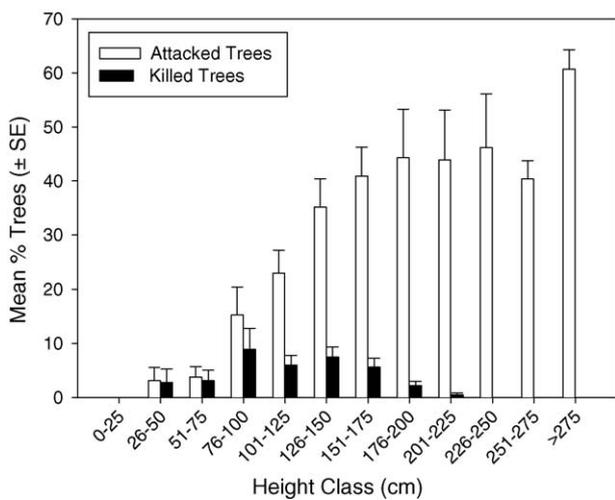

Fig. 2. Percentage (±S.E.) of available trees attacked (open bars), and killed (closed bars) by the Warren root collar weevil by height class in six 5–8-year-old stands of planted lodgepole pine.
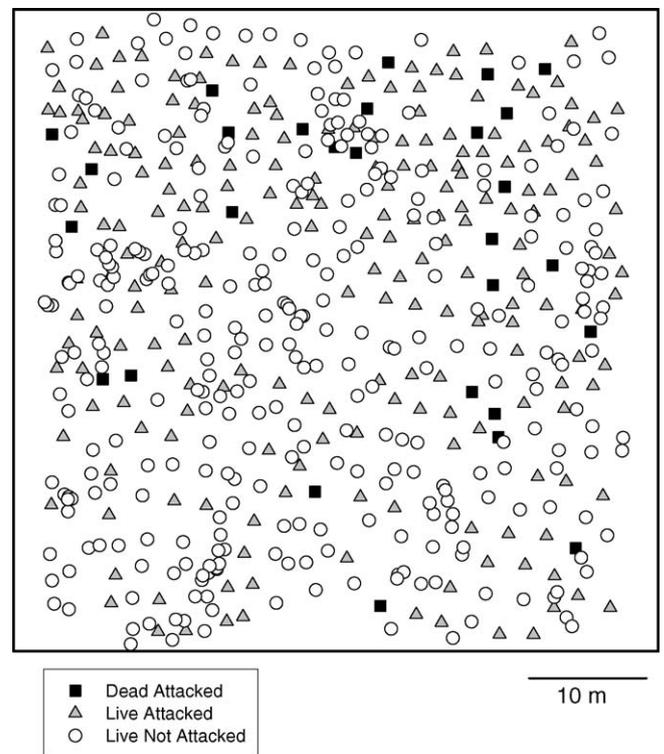

Fig. 3. The distribution of lodgepole pine trees (>1 cm diameter at root collar) in the Burns Lake 2-2 50-m × 50-m subplot, categorized as live or dead and attacked or not attacked by *H. warreni*.
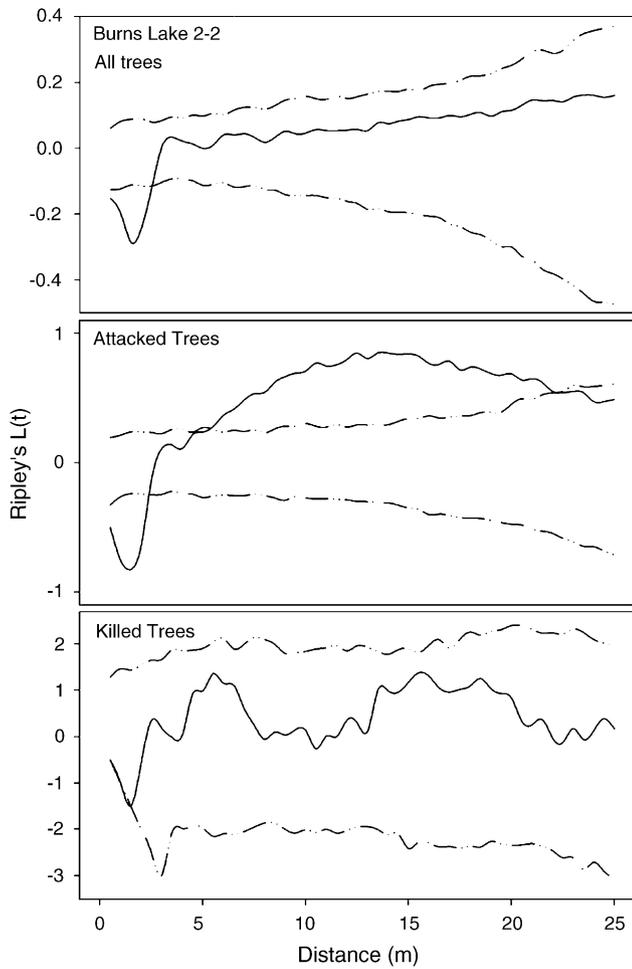
Fig. 4. Examples of Ripley's *L*(*t*) function (solid lines) showing the spatial distribution of all lodgepole pine trees potentially susceptible to attack (>1 cm diameter at the root collar), trees attacked, and trees killed by the Warren root collar weevil, *Hylobius warreni*, in the Burns Lake 2-2 50-m × 50-m subplot shown in this figure. Dashed lines represent the upper and lower 99% confidence intervals (CI) based on Monte Carlo simulation. Ripley's *L*(*t*) values above the upper CI are considered clumped, values between the upper and lower CI are random, and values below the lower CI are dispersed.
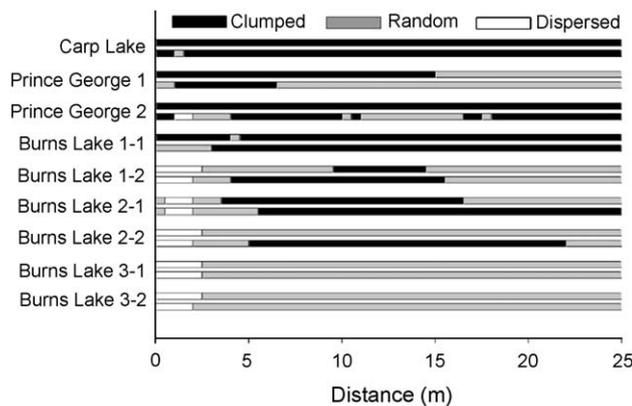

Fig. 5. Summary graphical representation of spatial distributions of all lodgepole pine trees (upper bar in each pair) and attacked trees (lower bar in each pair) at distances up to 25 m in nine 50-m × 50-m plots. Spatial distributions were generated from Ripley's *L*(*t*) function (see text).
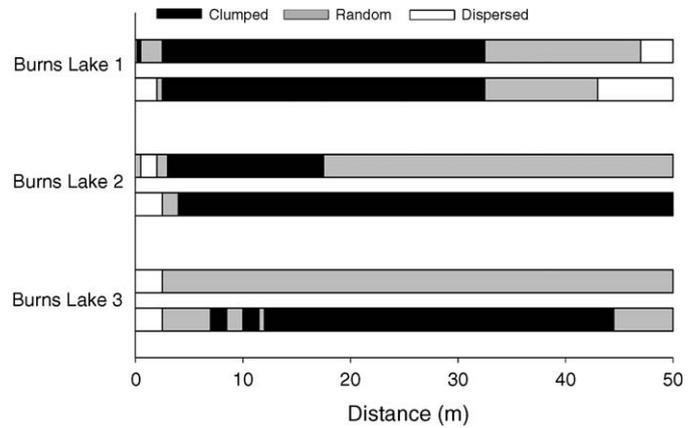

Fig. 6. Summary graphical representation of spatial distributions of all lodgepole pine trees (upper bar in each pair) and attacked trees (lower bar in each pair) at distances up to 50 m in three 50-m × 100-m plots. Spatial distributions were generated from Ripley's *L*(*t*) function (see text).

scales, whereas it was mostly random in the Burns Lake 3-1 and Burns Lake 3-2 subplots. In the remaining plots (Burns Lake 1-2 and Prince George 1) spatial distributions of attacked trees were variable at different scales (Fig. 5).

The spatial distribution of mortality could not be reliably determined at scales less than 5 m due to too few observations. At larger scales mortality due to weevil attack was random in eight of the nine plots (Fig. 5). In the remaining plot (Carp Lake) it was strongly clumped.

In all three contiguous 50-m × 100-m plots at the Burns Lake sites, potential host trees were dispersed or random at scales up to 2.5 or 3 m (Fig. 6). At larger scales tree distribution was clumped and then random with increasing scale in Burns Lake 1 and Burns Lake 2, and even became dispersed at 47.5–50 m scales in Burns Lake 1 (Fig. 6). In the Burns Lake 3 plot tree distribution was random at all scales 3 m and above (Fig. 6).

The distribution of attacks in all three contiguous plots was dispersed or random at scales up to 3 m, and generally clumped at larger scales (Fig. 6). In Burns Lake 3, the distribution became random at 45–50 m scale. In Burns Lake 1, attacks were random at 33 and 43 m scales, and became dispersed above 43 m (Fig. 6).

Mortality due to weevil attack was randomly distributed at moderate to large scales in all three 50-m × 100-m plots (Fig. 6). As with the 50-m × 50-m plots, sample sizes were too low to reliably interpret spatial distributions at scales below 2 m.

3. Discussion

The levels of attack and mortality we observed are generally consistent with other studies (Cerezke, 1994; Cerezke and Pendrel, 1995). Differences in site and stand attributes may account for some of the variation in attack intensities among the plots, but we found no specific site or stand attribute that would explain this variation. It is possible that any relationship between stand or site parameters and weevil attack interacts

with weevil population size. Because we could not measure the weevil population directly, variation in this parameter would obscure any relationships.

The level of mortality at five of the six sites (1.2–5.2%) is typical for most lodgepole pine plantations affected by *H. warreni* (Cerezke, 1994). The sixth site had unusually high mortality (16.6% of all trees or 36.1% of attacked trees), which may be a function of a relatively high insect population combined with a low density of host trees. Cerezke and Pendrel (1995) reported that there is an association between decreasing tree density and increasing attack percentage.

The relationship between the percentages of attacked and killed trees supports Cerezke (1994), who assumed that higher concentrations of attack would lead to increased mortality. Our data indicate that this is only true for relatively young trees, however, and this is consistent with the observation that host mortality resulting from attack is usually confined to younger stands (Cerezke, 1994). Attacks will continue to occur throughout the life of the stand (Hodge et al., 1994). In theory, attack should increase in direct proportion to the weevil population, but mortality should first increase, and then decrease as trees reach some critical diameter above which complete girdling is less probable. As diameter increases, complete girdling of the root collar by *H. warreni* larval feeding becomes less frequent, because attack is shifted from the root collar to major roots (Cerezke, 1994). Mean attack rates for all sites exceeded 40% of available trees in all height classes above 150 cm (Fig. 2), but mean percent mortality declined with increasing height in the same height classes. This indicates that the critical size at which a tree may survive attack is reached at a fairly young age in vigorous stands. Nevertheless, it is likely that attacked trees may sustain significant growth losses due to weevil damage (Cerezke, 1994), and these high levels of attack should be viewed with some concern.

Five of the six sites were artificially regenerated and we expected that the distribution of hosts would be dispersed in these plots. The distribution of potential host trees for four of the nine 50-m × 50-m plots was dispersed only at scales between 0.5 and 2.5 m, and for a fifth plot between 1 and 2 m (Fig. 6, upper bars). Two meters is the minimum inter-tree spacing in most planting contracts in the interior of BC. The clumped or random spatial distribution of hosts at larger distances is probably due to varying levels of ingress of naturally regenerated lodgepole pine, as well as varying levels of early mortality due to frost, flooding, or drought after planting (Lavender et al., 1990). Furthermore, slash and other obstacles may have led to inconsistent inter-tree spacing. Groups of naturally regenerated trees were observed in several of the plantations, likely occurring where branches (with cones) had been broken from lodgepole pine trees as they were felled or skidded to the road or landing.

The spatial distribution of attacked lodgepole pine generally correlates with the host distribution in most plots, although there is considerable variation (Figs. 5 and 6). This supports the observations that dispersal of *H. warreni* is random (Cerezke and Pendrel, 1995) and non-directional (Cerezke, 1994), and also suggests that lodgepole pine is generally susceptible to

attack if they are large enough to support the developing larva. This supports the notion that any lodgepole pine of sufficient size would be a potentially suitable host to *H. warreni*. Although attacks on naturally regenerated lodgepole pine trees were observed, most of the attack was found on the larger, planted trees. Planted trees comprised the majority of susceptible stems (>1 cm diameter at the root collar) present on most of the sites, and hence appeared to largely determine the potential spatial distribution of attack. Cerezke (1994) found that average nightly dispersal of adult weevils coincided with the average inter-tree spacing of the mature stand he studied. This is also reflected in the results of our study in that the attack distribution matches the total tree distribution at small scales for all but two of the nine 50-m × 50-m plots (Fig. 5). These distances approximate the minimum inter-tree distance and the average target distance, respectively, for lodgepole pine plantations in northern BC. At small scales, therefore, weevil attack distribution may be determined by the mean inter-tree distances of susceptible host trees regardless of the insect population. At larger scales the distribution of attack may depend in part on the size of the weevil population, although we found no consistent trends associated with the level of attack.

Individual plot attributes appear to influence host and attack distribution. In the Prince George 2 plot, the distribution of attacks and host trees did not match between 7 and 15 m. This plot has the highest density with 3696 stems/ha, although the attack level is the second lowest at 11.80%. The high density in this stand is due to a high ingress of small naturally regenerated trees, which causes the distribution of potential host trees to be clumped. These naturally regenerated trees are not as susceptible to attack as the larger planted trees, and therefore the spatial distribution of attacks is mostly driven by the planted trees, which would tend to be randomly distributed. Similarly, the Prince George 1 plot, which was the youngest stand sampled (5 years), had a clumped distribution of potential host trees, probably as a result of significant ingress of naturally regenerated trees. The attack distribution in this plot oscillated between random and clumped at scales above 5 m, but corresponded with the tree distribution between 5–9 m, and above 19 m in spite of a relatively high level of attack (23.9%). Nevertheless, the overall trend of the Ripley's $L(t)$ function for attacks in both of these stands followed that of the host trees, but was less strongly clumped than the host tree distribution.

We established the contiguous plots (50 m × 100 m) because it is conceivable that *H. warreni* moves very little when in a suitable habitat (Cerezke, 1994). Thus, even moderate increases in scale could affect spatial distributions. The spatial distributions of attack in the contiguous plots did not differ from the smaller plots, except that the distribution of attacks in Burns Lake 3 was random when analyzed in the 50-m × 50-m subplots individually (Fig. 5), but clumped when analyzed as a contiguous plot (Fig. 6). Also, when analyzed individually, each of the six 50-m × 50-m plots had an attack distribution that paralleled the distribution of the hosts. When analyzed as 50-m × 100-m plots, this was only the case on one of the three sites (Burns Lake 1, Fig. 6). The disparity in distributions in

these larger plots can be explained by different intensities of attack between the two smaller plots that were combined. The two plots in Burns Lake 1 were very similar in their levels of attack (12.46 and 10.50%) (Table 1), and maintained the correlation between spatial distributions of attack and host distribution. The Burns Lake 3-1 and 3-2 subplots had very different levels of attack (15.96 and 31.28%) (Table 1), which resulted in an uneven distribution of attack across the combined plot. This probably also explains the tendency toward clumping of mortality at scales between about 5 and 20 m when the plots were analyzed as a contiguous 50-m × 100-m plot (Fig. 6). The reasons for the higher level of attack in one plot may be attributed to a difference in microclimate (MacLennan, 1991; Johnson and Milne, 1992; Dale, 1999; McIntyre and Wiends, 1999). The Burns Lake 3-2 subplot is at a higher slope position and consequently drier, which may explain the lower levels of attack there (Herring and Coates, 1981; Cerezke, 1994). Microclimatic differences have been shown to influence the dispersal of other *Hylobius* species, e.g., *Hylobius abietis* (Nordlander et al., 2003).

The spatial distribution of dead *H. warreni*-attacked lodgepole pine trees could not be determined at the lowest scales due to low sample size. Nevertheless, our results generally support Cerezke's (1994) conclusion that mortality from attack is random. Only in one plot (Carp Lake) was mortality strongly clumped, as were the distributions of both host trees and attacks. A possible reason for the strongly clumped distribution of host trees, attacks, and mortality in this plot is its low stem density (the lowest at <1500 stems/ha). Cerezke and Pendrel (1995) found increased attack and mortality levels in thinned lodgepole pine stands because of more intense pressure on the remaining stems. The Carp Lake plot was also unusual among the plots because of its high level of mortality (16.57%). Such high mortality rates are not necessarily unusual for plantations in the central interior of BC, however (Cerezke, 1994; Cerezke and Pendrel, 1995), and may become increasingly common. In north central BC, mortality caused by *H. warreni* appears to be increasing, and mortality up to 40% has been reported in some areas (K. White, Regional Entomologist, BC Ministry of Forests, Smithers, BC, personal communication).

Our analyses were dependent on assumptions of homogeneity and isotropy in larval and host distributions, which were necessary to isolate variability in the distributions present (Ripley, 1981; Fortin et al., 2002). Sites were chosen to be homogeneous at the scale of the plots. Our results show that host distribution is often, but not always, an overriding factor in determining the distribution of attacks by *H. warreni*, but that mortality tends to be randomly distributed. Due to site and stand variability (heterogeneity) normally present in biological systems, however, an examination at a larger scale (e.g., stand level) may yield different results (Ripley, 1981; Getis and Franklin, 1987; Dale et al., 2002; Fortin et al., 2002). The scale of our study was considered to be reasonable given the range in dispersal distances reported in the literature on this weevil (Cerezke, 1994).

The levels of attack by *H. warreni* in lodgepole pine plantations are not generally perceived by forest managers to threaten the potential of a plantation to reach a free-to-grow state, which is the point at which responsibility reverts back from the licensee to the BC Ministry of Forests (Province of British Columbia, 2003). In part, this is due to the fact that excavation of the root collar of every possible host is necessary to determine attack status. This study shows that some plantations have a high level of attack (up to 45.86%), which may be more of a cause for a concern when considering that attack can greatly impede productivity of the host (Cerezke and Pendrel, 1995; Hunter, 2001). Attacks also generally continue to occur on the same site (and many times the same trees) as the stand ages (Cerezke, 1970), potentially leading to significant growth losses over time.

Because all host trees appear to be equally susceptible to attack, it is probably unrealistic to prevent weevil attack. If planted at sufficiently high densities, mortality will not normally be high enough to threaten a stand. Planted trees with severe root fault (e.g., so called J-root caused by improper planting), however, appear to be more likely to suffer mortality than naturally regenerated trees, even though there is no difference in susceptibility to attack (Robert, 2004). Therefore, natural regeneration may be preferable to planting in areas with high weevil populations.

Our results indicate that at the small scales we studied the insect, host tree distribution appears to be the most important, but not the only factor determining the distribution of attack by *H. warreni*. Future studies should be conducted at a larger scale (stand level), and should include host-microsite measurements (e.g., duff depth, elevation, moisture) to elucidate potential mechanisms responsible for the distributions of both weevil attack and mortality. Furthermore, behavioral studies that we have initiated may be helpful in gaining an increased understanding of host selection mechanisms by the Warren root collar weevil.

Acknowledgements

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