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Probability of Attack by Southern Pine Beetle in Relation to Distance from an Attractive Host Tree

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ABSTRACT. The pattern of southern pine beetle (SPB) attack was examined in two infestations in East Texas to determine the probability of host tree attack (PA) as a function of distance (X) from a recently attacked tree (pheromone source). In an infestation having a low rate of newly attacked trees per day and only a few pheromone sources occurring simultaneously, distance was a critical factor in determining PA . The probability decreased as $\ln X$, and was described by the regression model, $\hat{PA} = 0.06757 - 0.2583 \ln X$. Distance, however, was less critical in a larger infestation which had multiple pheromone sources occurring simultaneously and a high rate of new trees attacked each day. Implications for pheromone control strategies utilizing SPB attractants are discussed. FOREST SCI. 24:574-580.

ADDITIONAL KEY WORDS. *Dendroctonus frontalis*, bark beetles, pheromones, insect control.

ATTACK OF SOUTHERN PINES by the southern pine beetle (SPB), *Dendroctonus frontalis* Zimm., is mediated by a pheromone system consisting of host tree volatiles and behavioral chemicals produced by the attacking beetles (Renwick and Vité 1970). Flight, landing, and boring activity of the beetles is concentrated in the area of the most recent source of attractant (Coster and Gara 1968). As the level of attraction increases, the focus of flight, landing, and boring activity is centered on an adjacent tree (Gara and Coster 1968), causing an infestation to enlarge. An increase in concentrations of inhibitory chemicals at an attacked tree may also contribute to the "switching" of activity to adjacent trees (Renwick and Vité 1970). Only those trees within a critical distance of a pheromone source, estimated to be 20 to 25 feet, are likely to be attacked (Gara and Coster 1968).

The following study was conducted to quantify the relationship between distance

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from an attractive source and the probability of a tree being attacked by SPB. This information is necessary in developing control strategies using aggregating pheromones and in evaluating the effects of stand spacing on growth of SPB infestations.

MATERIALS AND METHODS

Study Areas.—Two SPB infestations, termed Bald Hill and Cypress Lake, were investigated during 1975 and 1976. They were 8–10 miles east of Diboll, Texas, on flat terrain in pine-hardwood stands. Stand characteristics of the 2 locations were as follows:

		<i>Bald Hill</i>	<i>Cypress Lake</i>
Basal area pines	m ² /ha	30.0	22.9
Average dbh	cm	20.4	26.0
<i>Pine composition:</i>			
Loblolly	percent	83.5	98.8
Shortleaf	percent	16.5	1.2
Total trees attacked during study ...	number	161	28
Duration of study	days	24	83

The Bald Hill study was conducted from October 9 through November 2, 1975, during the course of a test of synthetic *endo*- and *exo*-brevicomin as inhibitors of SPB activity (Payne and others 1977). The Cypress Lake study was conducted from July 18 through October 29, 1976 (excluding the 20-day period, August 4–24) and also included a period (August 28–October 3) of *endo*- and *exo*-brevicomin tests.

Trapping Grid.—Flight activity was monitored with a gridwork of sticky traps. Each trap consisted of four vanes (7 mesh/cm fiberglass screen) coated with Stikem Special¹. Vanes in the Bald Hill study were 0.90 × 2.10 m, whereas in the Cypress Lake study they were 0.60 × .90 m. The vanes were supported on pipe standards and centered at ca 3 m above ground level, the area of maximum beetle landing on host trees (Coster and others 1977). Beetles were removed from the flight traps daily prior to 10:00 am CDT for counting and sexing.

A centric systematic sampling approach was utilized, with flight traps centered in 15 m square cells within the overall grid. Grid size varied from 3 × 3 (9 cells) during the inhibitor tests, to 5 × 5 (25 cells) in the remainder of the Cypress Lake study. Grids were periodically repositioned, as necessitated by the growth of the infestation, so that they remained centered on the pheromone sources (most recently attacked trees).

Stands within the grids were mapped to include the location, species, and dbh of all host trees. Trees previously attacked by SPB were classified as to predominant beetle life stage present at dbh (visual inspection in the field), and the area was checked daily for new attacks.

Peak attractiveness of attacked trees to flying SPB is on the 3rd day after attack, and by the end of the 7th day of attack about 99 percent of the total responding population has arrived (Coster and others 1977). Therefore, each tree which came under attack during the course of the study was considered an active pheromone source for 7 days after initial attack. Trees surrounding an active pheromone source that were subsequently attacked (*SA*) were tabulated by 1 m

¹ Manufactured by Michel and Pelton Company, 5743 Landregan Street, Emeryville, CA 94608.

distance classes. Fifteen distance categories were recognized (1–15 m). The probability of attack (PA) for trees within each category (X) was estimated by

$$PA_X = SA_X/TA_X,$$

where TA_X is the number of host trees available for attack in X .

For the sake of clarity, the term distance (X) will be used to refer to these distance classes, with the specific value referring to the upper limit of each distance class in meters (i.e., $X = 1$, refers to the distance class from 0–1 m).

Analyses.—Prior to analysis, it was necessary to determine whether data from the infestations could be combined, and also whether the synthetic brevicomins had modified SPB density, distribution, or the rate of attacks on new trees. Three parameters were selected for comparison between sites and between brevicomin release periods and control periods within sites: (1) mean catch/trap/day (FTC), adjusted as necessary for differences in trap size, (2) number of trees attacked/day (NTA), and (3) Lloyd's index of patchiness (IP) (Lloyd 1967).

IP may be calculated from daily trap catch (quadrat count) as follows (Lloyd 1967):

$$IP = \frac{\hat{m}}{m} = \left(\frac{\sum x(x-1)}{\sum x} \right) / \left(\frac{\sum x}{n} \right),$$

where x = individual trap catch, n = the number of traps, \hat{m} = Lloyd's mean crowding index, and m = mean flight trap catch.

IP bears the following relationship to unity (Lloyd 1967):

$IP > 1$	Aggregated distribution
$IP = 1$	Random distribution
$IP < 1$	Uniform distribution

IP is related to other commonly used indices of dispersion as follows:

$$IP = 1 + \frac{CD - 1}{n} = 1 + \frac{1}{k} \approx E(I_\delta),$$

where $CD = s^2/m$ = the Coefficient of Dispersion (Southwood 1966), k = the exponent of the negative binomial distribution, I_δ = Morisita's Index of Dispersion (Morisita 1959), and the other parameters are as previously defined. Also,

$$IP \approx \beta, \quad \text{if } \alpha = 0,$$

where β = the slope coefficient and α = the y -intercept of the regression of \hat{m} on m (Iwao and Kuno 1971).

Although no assumptions concerning the underlying trap catch distribution are required for use of IP , sampling must be carried out *within* the smallest aggregation unit (i.e., the distribution in the quadrat or immediate vicinity of the trap must be random or uniform). In terms of the $\hat{m} - m$ regression, $\alpha = 0$ implies that the basic population unit is the individual rather than a clump of individuals. Therefore, if $\alpha = 0$, the sampling requirement for use of IP is met and $\beta \approx IP$.

Coster and Johnson (1978) have shown that the $\hat{m} - m$ regression may be used to characterize SPB distribution based on trapping grids similar to that described here, and that α does not deviate significantly from zero. Therefore, IP may be used to characterize daily aggregation patterns of SPB.

Due to nonnormal distribution of the FTC and NTA data, nonparametric Kruskal-Wallis tests were used for these comparisons. For the sake of consistency, Kruskal-Wallis tests were also used for the IP comparisons.

Simple linear regressions were run on PA using two transformations of X as suggested by the distribution of the PA data over distance. Transformations in-

TABLE 1. SPB flight trap catch (FTC), number of trees attacked/day (NTA) and Lloyd's index of patchiness (IP) for two infestation areas.

Infestation	FTC ± SE ^a	NTA ± SE	IP ± SE
Bald Hill	229.70 ± 52.70	6.71 ± 0.92	2.53 ± 0.20
Cypress Lake	36.41 ± 4.42	0.34 ± 0.09	3.17 ± 0.18

^a FTC adjusted for smaller trap size in Cypress Lake study as follows:

$$FTC' = FTC \times 3.5.$$

cluded the natural log of distance (ln X) and the inverse square of distance (1/X²).

Statistical tests were judged significant at the 0.05 probability level.

RESULTS

Comparisons of FTC, NTA, and IP between Bald Hill and Cypress Lake indicate significant differences in all 3 parameters (Table 1). Flying SPB populations were greater, more trees were attacked/day, and the flying SPB population was more dispersed in the Bald Hill site than in the Cypress Lake site. Since differences in SPB density and distribution between the two study sites might be expected to result in differences in attack patterns, separate regressions were run for each infestation.

With regard to within-infestation differences between periods of brevicomin release and periods when the chemicals were absent, no significant differences between means for the 3 parameters were found. Therefore, data from brevicomin release periods were combined with those from nonrelease periods to produce the total data set for each infestation.

Simple linear regressions on PA with the best predictor selected from the 2 distance transformations resulted in low r² values and suggested lack-of-fit of the regression models (Table 2). ANOVA tests for lack-of-fit, however, indicated that lack-of-fit was not significant in either regression model, suggesting that the low r² values were due to a high between-pheromone-source variance. This variance was reduced by pooling TA and SA values for each X and calculating:

$$PA_{X'} = \frac{\sum_{i=1}^n SA_{X,i}}{\sum_{i=1}^n TA_{X,i}},$$

where i = 1, . . . , n and n = total number of pheromone sources. The results,

TABLE 2. Regression parameters for the best fitting simple linear regressions of PA and PA' on transformed distance.

Study site	Y	X	α	β	SE _β	SE _{y,x}	r ²	N
Cypress Lake	PA	1/X ²	0.0431	2.6904	0.3436	0.2512	0.1951	255
	PA'	1/X ²	0.0607	2.4219	0.2325	0.0507	0.9005	14
	PA'	ln X	0.6757	-0.2583	0.0308	0.0678	0.8544	14
Bald Hill	PA	ln X	0.4155	-0.0454	0.0206	0.3846	0.0039	1233
	PA'	ln X	0.4044	-0.0525	0.0083	0.0243	0.7540	15

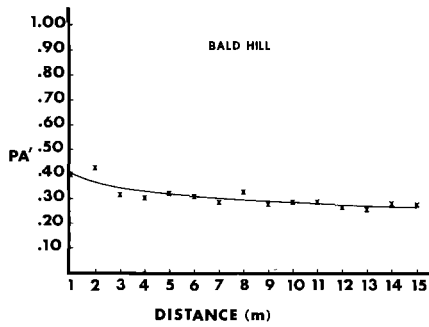


FIGURE 1. Pooled probability of attack (PA') and the $\ln X$ transformation simple linear regression for the Bald Hill infestation.

shown in Table 2, further support the lack-of-fit tests, since virtually the same regression coefficients resulted in acceptable r^2 values.

Moreover, although the $1/X^2$ transformation produced the best fitting regression model in the Cypress Lake study (as indicated by the r^2 value), the $\ln X$ transformation also produced an acceptable r^2 value (Table 2). Since it is desirable to view the PA /distance relationship in large spots (e.g., Bald Hill) and intermediate-sized spots (e.g., Cypress Lake) as part of a continuum, a strong argument can be made for utilizing the $\ln X$ transformation for the Cypress Lake data as well as the Bald Hill data.

Probability of attack (PA') values are presented in Figures 1 and 2, with the $\ln X$ transformation simple linear regressions overlaid (transformed distances have been returned to their original form).

DISCUSSION

Considerable difference between the Bald Hill and Cypress Lake pattern of the PA /distance relationship existed. The Bald Hill study showed little dependence of PA on distance from an active pheromone source, whereas the Cypress Lake study showed a marked decrease in PA with increasing distance from the pheromone source.

The infestations were very different in beetle population density, number of infested trees, and rate of new attacks. At Bald Hill, several active pheromone

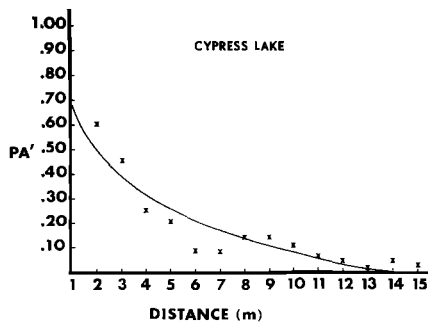


FIGURE 2. Pooled probability of attack (PA') and the $\ln X$ transformation simple linear regression for the Cypress Lake infestation.

sources occurred simultaneously while this phenomenon was rare at Cypress Lake. Multiple pheromone sources would lead to "distance-averaging," i.e., simultaneous classification of a tree into more than one distance about the different pheromone sources. The result is a PA which is a function of the various distances.

Another factor influencing the PA /distance relationship is the more dispersed population in the Bald Hill study (as indicated by IP in Table 1). This signifies reduced aggregation around any single pheromone source and a resultant reduced importance for distance as a determinant of PA . At Cypress Lake, however, beetles were more aggregated about pheromone sources (IP in Table 2) and the presence of multiple pheromone sources was considerably reduced. The PA /distance relationship is still confused by some distance-averaging, but to a lesser extent than in the Bald Hill study.

Regardless of these drawbacks, and recognizing that PA , while dependent to a large extent on distance, must also be influenced by other parameters (e.g., meteorological, brood source availability and location, etc.), we feel that the relationship described by the $\ln X$ regression models represent good estimates of PA with distance for small to intermediate-sized infestations (such as the Cypress Lake infestation), and large infestations (such as the Bald Hill infestation).

For small to intermediate-sized infestations, the results tend to support the conclusions of Gara and Coster (1968) that intertree distance is an important factor influencing spread of infestations and that a pheromone source is unlikely to induce attack on trees farther away than 6–7.5 m. Figure 2 indicates a PA of < 0.20 for this distance. This probability includes an artifact due to distance-averaging that, if removed, would further reduce the actual probability level.

The implications of the attack-distance relationship for spread of small to intermediate-sized SPB infestations are clear. Provided that flying beetle populations are present in an infestation, the infestation will continue to enlarge as long as suitable tree-spacing conditions prevail in the stand. Closer spaced stands ($< 3\text{--}4$ m) have a high probability that "attack-switching" (Gara and Coster 1968) will take place and adjacent trees will be colonized. When spacing is $> 3\text{--}4$ m, attack-switching is less likely to occur, emerging beetles will disperse from the infestation, and the infestation will cease to enlarge.

For large infestations with high SPB density, attack-switching may occur at wider tree spacing due to the reduced importance of the PA /distance relationship. This implies that an infestation, once it has become established in an area with close tree spacing, may expand into adjacent areas with wide tree spacing provided that population density is sufficiently high.

Comparison of Cypress Lake and Bald Hill results also suggests that pheromonal control strategies that attempt to "disrupt" or "confuse" normal SPB aggregation in large infestations using attractants may encounter difficulties. These strategies attempt to bring about disruption by saturation of an environment with multiple sources of synthetic pheromone. At Bald Hill, multiple sources of natural pheromone were present concurrent with a high attack rate of trees (Table 1) and a high PA at greater distances from the pheromone sources (Fig. 1). Increased dispersion of the population under such conditions probably results from (1) aggregation in the immediate vicinity of the several sources within the infestation and (2) from a less focused orientation because of the generally high level of pheromone throughout the area. Thus, although population dispersion was increased, the high levels of pheromone from multiple sources caused the attack probability to be high ($\overline{PA} = 0.31$) throughout the area. A field test of the

disruption strategy against SPB by Vité and others (1976) produced results essentially in agreement with our observations.

The use of point source release of attractant in intermediate-sized infestations, however, may have potential. If the dispersion of the beetle population can be forced into a multiple-pheromone-source pattern (i.e., reduced importance of distance from pheromone source due to distance-averaging), through proper placement of point source release units, the probability of successful attack may be reduced due to lack of sufficient population density aggregated about any one source. That is, the SPB may not be "confused," but it might be "tricked."

We believe the regression models developed herein will serve as a useful starting point for inclusion of stand spacing as a variable in modeling infestation growth and stand susceptibility as well as being of use in the evaluation of pheromone control strategies.

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