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Dispersion patterns of *Dendroctonus frontalis* and its predator *Thanasimus dubius*: Influence of behavioral chemicals¹

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Spatial aggregation patterns of flying southern pine beetles, *Dendroctonus frontalis* ZIMM., and the predator *Thanasimus dubius* F. (Cleridae) were determined within five natural infestations of southern pine beetle in eastern Texas. Aggregation patterns were quantified using the Index of Patchiness and Iwao's technique of regressing mean crowding on mean density.

Both species had clumped dispersion patterns. Southern pine beetle dispersion was inversely associated with the number of new host trees colonized each day; aggregation was greatest where pheromone sources were few. Aggregation of the *T. dubius* populations was directly related to the degree of pine beetle aggregation but not to actual pine beetle density.

Distance of unattacked trees from recently attacked trees serving as pheromone sources affected dispersion of flying southern pine beetles. The probability of attack for unattacked trees in small infestations decreased with distance from recently attacked trees and was described by the model $PA = 0.6757 - 0.2583 \ln X$ (PA = probability of attack, X = distance from recently attacked tree). In large southern pine beetle infestations distance from previously attacked trees was less critical. In these cases, however, a higher PA occurred throughout the infestation.

Implications for pheromone control strategies utilizing southern pine beetle attractants are discussed.

Many bark beetles in the family Scolytidae produce aggregation pheromones which are released when the beetles locate a suitable breeding habitat. In combination with host-produced volatiles, the pheromones cause a marked degree of aggregation of flying beetles which in turn, results in mass attack of the host tree. Pheromone systems are known for 16 bark beetle species (VITÉ & FRANCKE, 1976).

The southern pine beetle, *Dendroctonus frontalis* ZIMM., occurs in pine forests throughout the southern and southeastern U.S., Mexico, Guatemala, and Honduras. Aggregation for attack and breeding is in response to a system of volatiles composed of the insect-produced compound frontalin and the host tree-produced compound alpha-pinene (KINZER *et al.*, 1969). Females initiate attack but both sexes subsequently respond to the pheromone system (RENWICK & VITÉ, 1969). The density of flying beetles increases with proximity to freshly attacked trees (pheromone sources) (COSTER & GARA, 1968) and, when population levels are high and the rate of attack is rapid, mass attack by the responding beetles subsequently is concentrated on an adjacent tree (GARA & COSTER, 1968). The pattern of arrival of beetles at trees under mass attack and the vertical distribution of beetles as they arrive at such trees have been described (COSTER *et al.*, 1977). As the level of attraction increases, the focus of flight, landing, and boring activity is centered on an adjacent tree (GARA & COSTER, 1968), causing an infestation to

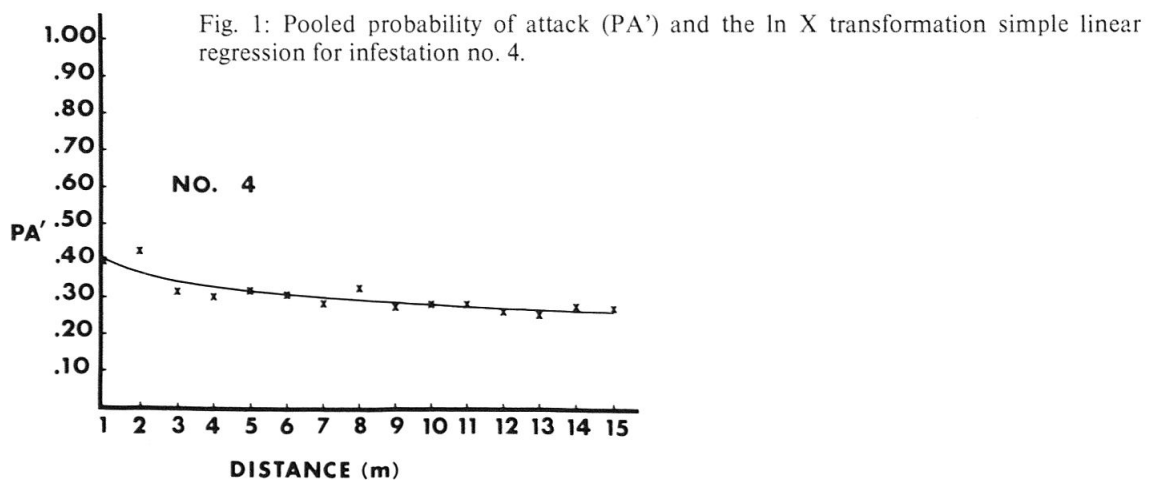
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enlarge. An increase in concentrations of inhibitory chemicals at an attack tree may also contribute to the «switching» of activity to adjacent trees (RENWICK & VITÉ, 1970). Only those trees within a critical distance of a pheromone source, estimated to be 6–8 meters, are likely to be attacked (GARA & COSTER, 1968).

Thanasimus dubius (F.) is a common clerid beetle predator of southern pine beetle (FRANKLIN & GREEN, 1965; THATCHER & PICKARD, 1966; MOORE, 1972). Adults of the clerid feed mostly upon adult bark beetles while the larvae feed beneath the bark on immature southern pine beetle. Adult *T. dubius* have been observed in large numbers on trees undergoing attack by southern pine beetle (VITÉ *et al.*, 1964) and have been demonstrated to aggregate at these trees in response to frontalin (VITÉ & WILLIAMSON, 1970), a component of the southern pine beetle aggregation pheromone (KINZER *et al.*, 1969). The diurnal pattern of response by adult *T. dubius* to attractant sources follows closely that of the bark beetle (VITÉ & WILLIAMSON, 1970; DIX & FRANKLIN, 1977; DIXON, 1977) and peak numbers of the adult clerids arrive soon after the trees are attacked by southern pine beetle (CAMORS & PAYNE, 1973; DIXON, 1977).

The effects of pheromones on dispersion of the southern pine beetle are vital considerations in its population dynamics. During periods of low population levels the primary resource exploited by the beetle is an ephemeral one consisting of weakened and damaged pines. These may quickly pass to a physiological condition unsuitable for colonization and/or brood development. Pheromones emitted by attacking beetles ensure utilization of such temporary habitats. Healthy vigorous trees are attacked when beetle populations are high. Pheromones facilitate such attacks by inducing «en masse» aggregation with the result that vigorous host trees are overcome and rendered suitable for colonization and brood development. Since both sexes arrive at host trees, aggregation also facilitates mating through the increased number of sexual encounters in the aggregation.

Aggregation incorporates a number of behavioral responses to environmental stimuli which, when considered collectively, are indicative of behavior that is characteristic of a species (TAYLOR, 1971). Indices to quantify aggregation were suggested by TAYLOR to be of value in studying the responses of populations to environmental stresses. Such indices would also appear to be useful in quantifying changes in population dispersion in response to pheromone, including both attractant and inhibitory pheromone systems. This information, in turn, would lend



understanding to population dynamics studies and to evaluation of pheromone systems for pest management applications.

HEDDEN & GARA (1976) applied MORISITA's index of dispersion (MORISITA, 1959) to within-tree distribution of the Douglas-fir beetle, *Dendroctonus pseudo-tugae* HOPK. Flight aggregation of bark beetles has been quantified for two species of *Ips* in a study by MASON (1970). The beetles exhibited a high degree of flight aggregation and MASON used aggregation indices (The slope of TAYLOR's power function and MORISITA's index) to make inferences about the relative «aggressiveness» of the two beetles in colonizing host trees.

This paper reports on studies to compare dispersion patterns of flying southern pine beetles and adult *T. dubius* within infestations, to quantify daily flight aggregation, and to develop a technique for estimating effects of pheromones on dispersion patterns of the bark beetles.

MATERIALS AND METHODS

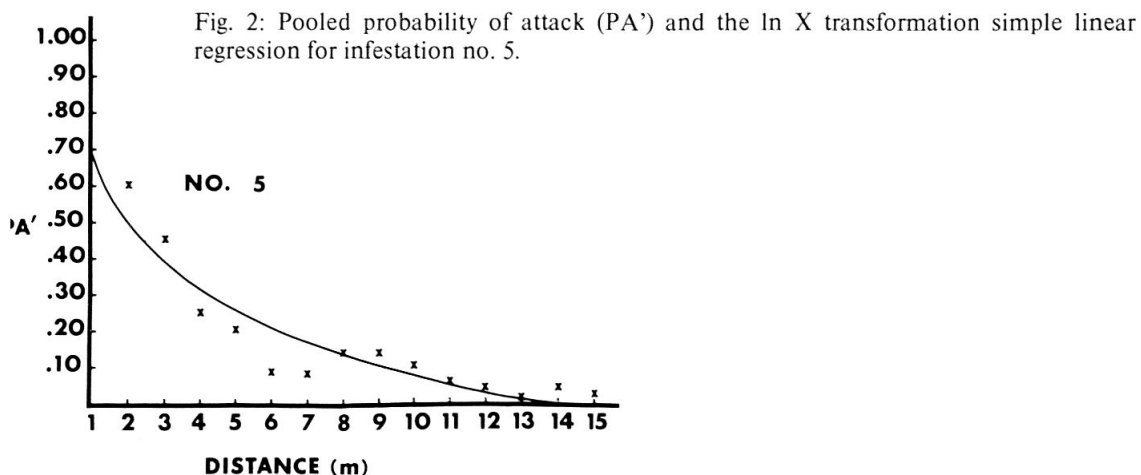
The study areas

Southern pine beetle flight activity was monitored in five infestations from 1974–1976. The infested stands were all on flat terrain in eastern Texas and consisted primarily of loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*). The number of trees attacked by southern pine beetles at the beginning of each study ranged from 20–500. Mean diameter at breast height for the stands ranged from 16–27 cm and stand density, as measured by basal area, ranged from 17–30 m²/ha.

In three areas studied during 1974 flight activity of southern pine beetle and *T. dubius* were monitored concurrently. These observations form the basis for analysis of dispersion patterns. The remaining two infestation study areas (nos. 4 and 5, fig. 1 and 2) were used to collect data on the relationship of distance between pheromone sources (attacked trees) to attack rate by beetles on trees and to study changes in dispersion pattern of the beetle in relation to pheromone sources.

Flight sampling grid

Spatial distribution of aerial populations of southern pine beetle occurs on two different scales. The first is infestations, that include one or more adjacent



trees colonized by the beetle. Density of flying beetles is very high within 30–50 m of these infestations but becomes very low beyond this distance (T.L. PAYNE & J.E. COSTER, unpublished). The infestation is, therefore, a recognizable natural unit within which to sample airborne beetles. It is also the focus for insect control efforts. The second scale is the distribution of these infestations throughout the forest. This study is concerned only with the former aspect of southern pine beetle distribution.

A centric systematic sample scheme was used in which sticky flight traps were positioned at the center of each quadrat to produce a systematic grid of the traps. Systematic grid samples have been shown to more accurately estimate insect aggregation patterns than do random samples (HAIRSTON *et al.*, 1971) and WATT (1968) suggested that the use of grid systems is the only reasonable approach to the development of dispersal models to describe insect distribution through time and space. An intertrap distance of 15 m was used representing a compromise between fine-scale trapping and labor expenditure.

Flight traps

Each trap consisted of four wings or vanes supported so that vane centers were ca. 1.4 m above the ground. The vanes were constructed of fiber glass insect screen (7 mesh/cm) and coated with Stickem Special[®]. Traps were centrally located in each of the 15 x 15 m quadrats. In 1974, they were arranged in a 5 x 6 grid system; 1975–76 3 x 3 and 5 x 5 grids were used. Each grid was oriented so that its long axis was more or less parallel with the anticipated direction of spread of the infestation and so its center was near the most recently mass attacked pine.

In 1974, traps were equipped with devices containing an attractant mixture of frontalin and alpha-pinene (KINZER *et al.*, 1969; RENWICK & VITÉ, 1969) that evaporated ca. 2 mg of frontalin and 5 mg of alpha-pinene/trap/day. Previous field tests had indicated that release of the chemicals at these rates would provide short-range attraction to flying southern pine beetles but was not attractive enough to induce attack on trees 2.5–3.0 m from the release point. Attractants were not used in the 1975–76 studies.

Monitoring procedures

Beetles were removed from the traps and counted daily. The infestations were also inspected daily for newly attacked trees and, when such trees were found, their location and date of attack were recorded. The observation period in 1974 was for 20 consecutive days in each of the three infestations. In 1975 the infestation was monitored for 24 days while in 1976 the study area was monitored for 83 days.

Aggregation indices

A number of ways of measuring the degree of aggregation of populations have been proposed. COSTER & JOHNSON (1979) investigated five methods for measuring southern pine beetle dispersion: MORISITA'S index of dispersion

(MORISITA, 1959, 1962), Lloyd's index of patchiness (LLOYD, 1967), the coefficient of dispersion (STITELER & PATIL 1971), Taylor's power function (TAYLOR, 1961, 1971), and the mean crowding-mean density regression (IWAO, 1970; IWAO & KUNO, 1971). After comparison with field data COSTER & JOHNSON (1979) proposed an approach utilizing Iwao's regression of mean crowding (\bar{m}^*) on mean density (m) coupled with the index of patchiness (IP). The index of patchiness (IP) is given by the ratio \bar{m}^*/m where

$$\bar{m}^* \text{ (mean crowding)} = \frac{\sum_{i=1}^N X_i (X_i - 1)}{N \sum_{i=1}^N X_i} \quad \text{and} \quad m \text{ (mean density)} = \frac{\sum_{i=1}^N X_i}{N}$$

where total number of quadrats is N and X_i is the number of individuals in the i th quadrat. The value of IP is greater than unity in an aggregated pattern, equal to unity in a random pattern, or less than unity in a uniform (regular) pattern.

IP is essentially defined by \bar{m}^* which is the mean number, per individual, of other individuals in the quadrat and is adjusted for change with population density by m . When \bar{m}^* is high and m low, pronounced density contrasts are indicated and, likewise, when $\bar{m}^* \approx m$ the relationship implies negligible density contrasts. Although LLOYD (1967) restricted his treatment of IP to cases in which the underlying distribution was a negative binomial, it is not dependent on this assumption.

IWAO (1970) has suggested the regression of \bar{m}^* on m for quantifying aggregation. The relationship is

$$\bar{m}^* = \alpha + \beta m,$$

where α is the intercept on the \bar{m}^* axis and β the regression coefficient. Parameter α is termed the index of basic contagion (i.e. the basic population unit, individuals, groups of individuals, etc.) and takes a positive value for colonial populations and a zero value where there is no tendency for individuals to group at low population density or where repulsion between individuals occurs. Dispersion of individuals in relation to density is indicated by β , the density-contagiousness coefficient. It will be less than, equal to, or greater than unity in uniform, random, or aggregated patterns. In other words, α is a measure of «swarm» size and β is a measure of the spatial pattern of the «swarms».

Analysis of a series of quadrat data, obtained from centric systematic samples, proceeds as follows using the method of COSTER & JOHNSON (1979). Mean crowding and mean density are computed for each sample period. Using either linear regression or analysis of covariance techniques, a regression of \bar{m}^* on m is obtained and the α is tested for significant deviation from 0.

Using the information obtained about α and β , the underlying statistical distribution of the dispersion pattern may be characterized (IWAO & KUNO, 1971). The value of α indicates certain characteristics of the species aggregation behavior since it implies that an individual of the species will share the quadrat with α other individuals under low population density.

If $\alpha = 0$, the IP value may be used to compare within-species population dispersion for specified conditions. Techniques for comparing data distributed as a

negative binomial are provided in LLOYD (1967), however nonparametric statistics (or parametric statistics, if assumptions are met) may be applied for comparison of multiple observations, regardless of underlying distribution.

Analysis of pheromone source-distance data

Peak attractiveness of attacked trees to flying southern pine beetle is on the 3rd day after attack, and by the end of the 7th day of attack about 99% of the total responding population has arrived (COSTER *et al.*, 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 distance classes (DCLASS) using computer mapping routines. Fifteen DCLASS categories were recognized (1-15 m). The probability of attack (PA) for trees within each DCLASS was estimated by

$$PA = \frac{SA}{TA},$$

Where TA is the number of host trees available for attack within the DCLASS. Simple linear regressions were run on PA using two transformations of DCLASS as suggested by the distribution of the PA data over DCLASS. Transformations included the natural log of DCLASS (LNDCASS = ln DCLASS) and the inverse square of DCLASS

$$(INVQSR = \frac{1}{(DCLASS)^2}).$$

These preliminary regressions produced poor results, however, due to high statistical variance between pheromone source. This variance was reduced by pooling the TA and SA values for each class and calculating PA on that basis. Statistical tests indicate significance in fit of the model. Subsequent analysis used the pooled computation of PA.

RESULTS

Infestation development and insect numbers

The progression of attack in each infestation was generally to the nearest uninfested tree. In no case did the synthetic frontalin and alpha-pinene alter the natural tree-by-tree progression nor did the chemicals induce attack of trees adjacent to the traps. Three statistical outliers (mean trap catch ≥ 41) were eliminated from Infestation 3 prior to analysis using DIXON's test for outliers (DUNN & CLARK, 1974).

The number of southern pine beetle and *T. dubius* caught are shown in table 1. MANN-WHITNEY tests were used to contrast all pairs of means since the distributions of both southern pine beetle trap catch and trees attacked per day were non-normal. Southern pine beetle trap catches were all significantly different

from one another and flying beetle density in the infestations was ranked as infestation no. 3 > infestation no. 2 > infestation no. 1. *T. dubius* numbers did not differ between infestation 1 and 2. Both infestations, however, had significantly greater *T. dubius* density than no. 3. The rate of attack of new trees was less in no. 2 than in the other two.

The ratio *T. dubius*: southern pine beetle varied widely between the three infestations; it was 1:3.4 at no. 1, 1:0.98 at no. 2, and 1:46.6 at no. 3. The ratios between the two species varied significantly among infestations (χ^2 test). It was lowest in the smallest infestations (no. 1, no. 2) and highest in the large infestation (no. 3). Variations in the ratio may be due to the general lack of synchrony between life cycles of the two species (THATCHER & PICKARD, 1966) and differences in age of the infestations (DIXON, 1977).

The degree of association between trap catches of southern pine beetle and *T. dubius* was measured using a 2 x 2 contingency table arrayed for the presence or absence of each species on each trap for all infestations. The observed values were compared to expected values by a chi-square test (POOLE, 1974). The test was highly significant ($P \geq .001$), indicating that distributions of the species are dependent. Examination of the contingency table indicated that the chi-square value was due to greater than expected numbers of insects in the cells where both species were either absent or both were present. The positive association between southern pine beetle and *T. dubius* was further verified by a highly significant ($P \leq .001$) PEARSON'S correlation coefficient.

Aggregation indices

LLOYD'S Index of Patchiness, IP, was calculated for both species in each infestation. Prior to application of statistical analyses the frequency distributions of IP values were tested using Kolmogorov-Smirnov tests for goodness-of-fit to a normal distribution. The distribution of IP values for southern pine beetle was normally distributed whereas the distribution of *T. dubius* values differed significantly from normality.

IP values are shown in table 2. Highly aggregated patterns are indicated for both species in all infestations. IP values were contrasted using MANN-WHITNEY tests.

Within each infestation, *T. dubius* was less aggregated than southern pine beetle. Average IP for southern pine beetle was 1.8 times that for *T. dubius*. The mean contrasts show that both southern pine beetle and the clerid were most highly aggregated in infestation no. 2. Interestingly, this area had the lowest southern pine beetle flight density and the highest flight density of *T. dubius* (table 1). The greater degree of southern pine beetle aggregation in infestation no. 2 supports the prediction of KNIPLING & MCGUIRE (1966) that pheromones will be relatively more effective in aggregating low-level populations than high-level populations. The result also suggests that a predator such as *T. dubius* utilizing a kairomone response to locate prey also may become more aggregated when the prey's pheromone level is low.

Aggregation in infestations 1 and 3 did not differ significantly for either species (table 2), even though mean densities of both beetles differed between the areas (table 1). The increased dispersion in these two areas is thought to result from the higher rate of attack on trees (table 1) which in turn, produced more

Table 1: Numbers of SPB and *T. dubius* caught on sticky traps and the average number of trees attacked per day (NTA) in 3 infestations.

Infestation	Trapping days	NTA	SPB		T. dubius	
			Total no.	Mean no./trap/day	Total no.	Mean no./trap/day
1	20	1.35a	1,570	2.62 a	465	0.77 a
2	17	0.35b	532	1.04 b	395	0.77 a
3	17	2.00a	4,058	7.96 c	149	0.24 b

Table 3: Parameters for regression of mean crowding on mean density for SPB and *T. dubius* in three infestations.

Infestation	n	α		β +SE		r^2		SE \hat{y}	
		SPB	T. dubius	SPB	T. dubius	SPB	T. dubius	SPB	T. dubius
Combined	54	2.69	.57	5.10 ± .44	2.53 ± .48	.73	.35	13.76	1.62
1	20	3.04	.47	4.17 ± .29	2.12 ± .56	.92	.44	3.14	1.34
2	17	1.92	2.25	5.57 ± .85	1.57 ± 1.53	.74	.25	1.66	2.18
3	17	8.43	-.08	4.72 ± 1.25	3.30 ± .76	.49	.56	24.84	.78

Means in column followed by the same letter are not significantly different ($P \leq .05$).

pheromone sources. Extension of the pheromone odor plume would stimulate both beetle landing and general flight activity to occur over a larger area (COSTER & GARA, 1968).

The \bar{m} - m regression was done for each infestation and for the three infestations combined. Parameters are shown in table 3. The ANCOVA showed no significant interactions for either species (i.e., slopes of the separate regressions were homogenous); effects of m on \bar{m} did not differ from infestation to infestation and further examinations of the relationship were, therefore, permissible. In addition the combination of individual infestations (as dummy variables) with m significantly increased the ability to predict \bar{m} as compared to using m as the only dependent variable. This was true for both species.

Analysis of the individual effects of infestation and m on \bar{m} for southern pine beetle revealed that m alone was a highly significant predictor ($P \geq .005$) of \bar{m} . On the other hand, individual infestations were not significantly correlated with \bar{m} , allowing the use of a combined regression of \bar{m} on m to characterize southern pine beetle aggregation. The combined regression is (table 3):

$$\text{Southern pine beetle } \bar{m} = 2.69 + 5.10 m$$

Mean density alone was also a highly significant predictor ($P \leq .005$) of \bar{m} for the clerid. However, \bar{m} was also highly correlated ($P \leq .005$) with infestations indicating caution in the use of combined regression to characterize aggregation of *T. dubius*. Apparently its degree of aggregation is determined not only by population density but also by intrinsic site factors.

Standard error of the estimates, $SE_{\hat{y}}$, were used to construct 95% confidence intervals about α and we found no significant difference from 0 for either *T. dubius* or southern pine beetle. An $\alpha = 0$ implies that the basic aggregation unit of southern pine beetle and *T. dubius* is the individual insect (IWAO & KUNO, 1971) and that, in the absence of pheromones, both species were randomly distributed. An α value > 0 on the other hand, would be evidence of «swarming» and the insects would occur in discrete clumps, even though the clumps or swarms, themselves may be randomly distributed.

Table 2: Index of patchiness ($IP \pm SE$) for SPB and *T. dubius* in three infestations.

Infestation	IP	
	SPB	<i>T. dubius</i>
1	5.97 \pm .61 a	3.15 \pm .82 a
2	7.84 \pm .60 b	5.22 \pm 1.10 b
3	6.78 \pm .80 ab	2.33 \pm .55 a

Means in a column followed by the same letter are not significantly different ($P \leq .05$).

Table 4: Southern pine beetle flight trap catch (FTC), number of trees attacked/day (NTA) and index of patchiness (IP) for two infestation areas.

Infestation	FTC \pm SE	NTA \pm SE	IP \pm SE
4	229.70 \pm 52.70	6.71 \pm 0.92	2.53 \pm 0.20
5	36.41 \pm 4.42	0.34 \pm 0.09	3.17 \pm 0.18

As with IP, the β values (table 3) indicate a higher degree of aggregation for southern pine beetle than for *T. dubius* and a highly aggregated pattern for both species. The mean β for southern pine beetle was 2.1 times that for *T. dubius*.

Pheromone source-distance

Comparison of mean southern pine beetle catch/trap/day (FTC), number of trees attacked/day (NTA) and index of patchiness (IP) for infestations 4 and 5 are shown in table 4. Flying southern pine beetle populations were greater, more trees were attacked/day and the flying population was more dispersed in infestation no. 4 than in infestation 5.

Both transformations produced acceptable fitting models for the estimate of PA in relation to distance from pheromone sources. Since it is desirable to view this relationship as part of a continuum from small infestations (no. 5) to large infestations (no. 4), we feel the LNDCLASS transformation is more suitable. Probability of attack values are presented in figures 1 and 2 with the fitted model overlaid (transformed distances are returned to original form).

Considerable difference between the patterns of the PA/DCLASS relationship exist for the two sites. Infestation no. 4 showed little dependence of PA on distance from an active pheromone source, whereas the other infestation 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 no. 4, several active pheromone sources occurred simultaneously while this phenomenon was rare at no. 5. Multiple pheromone sources would lead to «distance-averaging», i.e., simultaneous classification of a tree into more than one DCLASS about the different pheromone sources. The result is a PA which is a function of the various distance classes.

Another factor influencing the PA/DCLASS relationship is the more dispersed population in no. 4 (as indicated by IP in table 4). This signifies reduced aggregation around any single pheromone source and a resultant reduced importance for distance as a determinant of PA. At no. 5, however, beetles were more aggregated about pheromone sources (IP in table 4) and the presence of multiple pheromone sources was considerably reduced. The PA/DCLASS relationship is still confused by some distance-averaging, but to a lesser extent.

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 LNDCLASS regression models represent good estimates of PA with distance for small to intermediate-sized infestations (such as no. 5), and large infestations (such as no. 4).

For small to intermediate-sized infestations, the results tend to support the conclusions of GARA & COSTER (1968) that inter-tree distance is an important factor influencing spread of infestations and that a pheromone source is unlikely to induce attack on trees further away than 6–7.5 m. Fig. 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.

DISCUSSION

The results of these studies suggest interesting relationships between population densities, aggregation tendencies, and attack of host trees for the two beetle species. Not unexpectedly, there was a general positive association between mean southern pine beetle density and number of trees attacked per day (NTA). Mean values for the two variables rank in the same sequence for the three infestations. The degree of southern pine beetle aggregation as measured by IP and β , was inversely associated with NTA; aggregation was greatest in the infestation where the fewest pheromone sources (newly attacked trees) occurred. Ranking of population densities of *T. dubius* in the three locations was totally different than for southern pine beetle; where southern pine beetle density was highest (infestation no. 3) *T. dubius* was lowest, and vice versa. Degree of aggregation of southern pine beetle and *T. dubius*, however, followed the same relative trends from one infestation to another. Relative density of *T. dubius* also follows trends in southern pine beetle aggregation. The mechanism of co-aggregation between the species is represented as follows.

High density of flying southern pine beetle results in more rapid rate of attack of trees within an infestation. Consequently, on any given day there are more active pheromone sources within the infestation than in one where attack rate, and southern pine beetle density, are low. Simultaneous occurrence of multiple pheromone sources within an infestation causes adult southern pine beetle distribution to be more dispersed than in an infestation where only one or two attractive trees occur. Aggregation pattern of the predator then tracks the pattern of southern pine beetle. Thus, the causal pathway for co-distribution of the two beetles within an infestation is: southern pine beetle density \rightarrow NTA \rightarrow southern pine beetle distribution \rightarrow *T. dubius* distribution \rightarrow *T. dubius* density.

This relationship is further supported by the \bar{m} - m regressions. For southern pine beetle, a reasonably good model ($r^2 = 0.73$) was characteristic for the species over all three locations. For the clerid, the combined model accounts for much less of the variation in aggregation ($r^2 = 0.35$), indicating that aggregation was not strongly a species characteristic and must be considered on an infestation-by-infestation basis. Its aggregation is also conditioned, in large part, by environmental attributes such as degree of aggregation of the prey.

Kairomone response of certain insect enemies of scolytids is well documented (BORDEN, 1974) and occurs for *T. dubius* in response to southern pine

beetle aggregation pheromones (VITÉ & WILLIAMSON, 1970). This study further demonstrates parameters such as IP and the intercept and slope co-efficients of the $\bar{m}-m$ regression are useful in quantifying aggregation (COSTER & JOHNSON, 1979) and that they also are valuable in comparing aggregation of two species that respond to a common stimulus. Simultaneous monitoring of changes in aggregation of a pest and its important insect enemies in response to behavioral chemicals would be useful in assessing survey and control strategies utilizing such behavioral chemicals.

The implications of the attack-distance relationship for spread of small to intermediate-sized 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 (< 3–4 m) have a high probability that «attack-switching» (GARA & COSTER, 1968) will take place and adjacent trees will be colonized. When spacing is > 3–4 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 southern pine beetle density, attack-switching may occur at wider tree spacing due to the reduced importance of the PA/DCLASS 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 infestations 4 and 5 suggests that pheromonal control strategies that attempt to «disrupt» or «confuse» normal southern pine beetle 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 infestation 4, multiple sources of natural pheromone were present resulting in a high attack rate of trees (table 4) 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 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 (PA = 0.31) throughout the area. A field test of the disruption method against southern pine beetle by VITÉ *et al.* (1976) produced results essentially in agreement with our observations.

The use of point source of release 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 southern pine beetle may not be «confused», but it might be «tricked».

The existence of synthetic behavioral chemicals for many insects has led to proposals for their incorporation into pest management schemes. Assessment of the efficacy of such chemicals is difficult, however, and is usually done using various estimates of changes in population density. However, since many insect pheromones, especially the aggregation pheromones of Scolytidae, appear to exert major influences on dispersion patterns of the insect, it is suggested that use of

experimental and statistical methods to quantify changes in aggregation in response to experimentally induced levels of behavioral chemicals provides an ecologically sound way to assess chemical application strategies.

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