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Temporal Variation in the Spatial Dispersion Patterns of Aphids (Homoptera: Aphididae) Infesting Strawberries[1]

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ABSTRACT Temporal changes in spatial distribution patterns of aphids infesting winter strawberries in coastal California were determined using Green's Coefficient, C_x, Iwao's regression of mean crowding on the mean, and Lloyd's "Patchiness Index." Both C, and the Patchiness Index indicated the aphids were initially overdispersed, but became random as populations increased. Distribution remained random following population collapse, suggesting that density-independent mortality factors suppressed populations. Iwao's regression method provided analogous results when populations were temporarily stratified.

Aphids are occasional but important pests of strawberries in central and southern California (Oatman and Platner 1972). Economic losses result primarily from host feeding, virus transmission, honeydew production, and insect contamination (Allen 1959, Kono and Papp 1977). Such damage, which results in lower yields and unmarketable products, occurs in response to aphid density; increased density causes increased damage.

Information on the spatial dispersion of aphids in strawberries is crucial for developing sampling plans which are statistically adequate for estimation of population density. Unfortunately, theoretical models of dispersion, such as Neyman type A, Poisson, and negative binomial, may be fitted to the same count data depending on the frequency classes chosen or method of fitting the models (Iwao 1970). Thus, the relationship of theoretical models to actual field situations varies and can be biologically inaccurate.

Myers (1978) compared a variety of dispersion indices to determine which analytical techniques allowed the separation of statistical artifacts from biologically significant effects. Analyses of computer-generated egg distributions suggested that Green's coefficient of dispersion, C_x, the standardized Morista's coefficient. I_p, and the variance/mean ratio, $S^2/\bar{x}$, were not seriously influenced by density, and were therefore suitable for estimating spatial dispersion. Although a good predictor of clumping, Lloyd's patchiness index was considered less useful because patchiness decreased with increasing density. The regression of mean crowding on the mean described by Iwao (1968) and Iwao and Kuno (1971) was not compared with the other techniques by Myers (1978) but was considered to be a valid method.

The growth and decline of aphid populations on strawberries offers an interesting system for comparing the biological significance of analyses used to determine spatial dispersion. In addition to providing base-line information for a sampling program for aphids infesting strawberries, this study was designed to provide comparisons of several dispersion indices to determine which could accurately fit count data from populations that have changing spatial dispersions over time.

Materials and Methods

Whole-plant counts of aphids were recorded in 1981 and 1982 from winter plantings of 'Tufts' strawberries at the University of California's South Coast Field Station in Orange County, Calif. The 1981 and 1982 plantings were transplanted on 6 and 2 November, respectively. Both crops were drip irrigated and mulched with transparent plastic. In 1981, the field consisted of 15 double-row beds of plants, each bed with 23 sub-beds (17 plants per sub-bed). From 15 January to 28 May, 144 plants were sampled weeekly using a stratified-random design, except on 21 May, when counts were not taken. In 1982, 118 plants per week from 12 double-row beds were sampled from 12 January to 2 March, and then 72 plants per week were counted from 9 March to 11 May. No data were collected on 16 March or 3 May.

The strawberry aphid, *Chaetosiphon fragaefolii* (Cockerell), was the dominant species (>60%) encountered in both plantings. Melon aphids, *Aphis gossypii* Glover, potato aphids, *Macrosiphum euphorbiae* (Thomas), and green peach aphids, *Myzus persicae* (Sulzer), were less common. Because these species concurrently inhabit strawberries, they were evaluated as a complex during both seasons to provide a realistic and meaningful basis for a sampling program. Additionally, no significant correlations in population density were found between aphid species in either year. Other species observed (<0.05%) did not accept strawberries as host plants and were not included in the analyses.

The acaricide cyhexatin (Plictran) was applied on 7 January and 25 February 1981, and 15 April 1982, to suppress populations of *Tetranychus urticae* Koch. Kennedy et al. (1976) demonstrated that this pesticide did not significantly reduce aphid populations on strawberries. In the absence of these acaricide treatments, spider mite populations could have increased to levels where physiology of the plants would have been altered (Sances et al. 1981) and interspecific interference could affect aphid distribution.

Statistical Analysis

The aphid count data were analyzed using three common dispersion coefficients. Green's (1966) coefficient, C_x, was determined by using the formula:

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$$\frac{[s^2/m] - 1}{\Sigma x - 1}$$

where s^2 = variance, m = mean, and Σx = total number of aphids sampled.

The regression method introduced by Iwao (1968) was calculated by solving the equation $m = \alpha + \beta m$, where α (estimated by a) = the intercept on the ordinate, and β (estimated by b) = the slope of the regression line formed when $\overset{*}{m}$ is regressed on the mean. Mean crowding, $\overset{*}{m}$, was derived by solving Lloyd's (1967) formula $\overset{*}{m} = m + (\sigma^2/m - 1)$, and substituting in the $\bar{x}$ and s^2 from our count data. Student's *t*-tests were employed to determine if a = 0 or 1, or if b = 0 or 1. The 1981 and 1982 regressions of $\overset{*}{m}$ on the mean were generated by the Proc GLM procedure of Statistical Analysis Systems (SAS) (Helwig and Council 1979).

Lloyd's "patchiness index," $\overset{*}{m}/m$, was calculated as described by Lloyd (1967). Mean crowding (m) was determined by using the procedure described for the previous test. Means, variances, and related parameters were generated by the Proc Means procedures of SAS.

Results and Discussion

Green's coefficient was suitable for analyzing changes in dispersion that occurred as aphid densities fluctuated temporally. Aphid counts, sampling dates, and Green's coefficient, C_x, are listed in Table 1. Populations were overdispersed or aggregated when $C_x = 1$, and approximated a random distribution as C_x approached 0. In both plantings, C_x decreased with increasing density but remained relatively constant as populations declined. Attempts to analyze the data with 12-unit (plant) samples (1981) or 8-unit samples (1982) obscured the initial aggregation produced when single-unit counts were utilized. Similar results were reported for pooled counts of *Diabrotica longicornis* (Say) and *D. virgifera* LeConte on corn (Steffey and Tollefson 1982).

Analysis of the single-unit data with Green's coefficient was consistent with the biology and behavior of the aphid species observed. Initial migrants larvaposited clumps of nymphs which were aggregated by the site preference of the alates, which may have been influenced by the "edge effect" reported by Lewis (1969). As populations increased, more of the available niches were filled, and dispersions became random.

Although the exact reasons for the population collapse cannot be specified, a general increase in temperature for January to May (1981, 13.6–17.7°C; 1982, 9.0–16.3°C) and a corresponding fluctuation in plant physiology were probably more important than natural enemies or interspecific competition. Parasites were not an important mortality factor (<5%) and predators were not commonly observed until several weeks after the population decline had occurred. Although alate populations increased slightly as aphid density decreased, the percentage of alates in the total population did not exceed 2%, and a density-dependent change in insect physiology leading to migrant production would not account for the decline. Interspecific competition was negligible, since, at the time of peak populations, ca. 90% (1980–1981) of the aphid population was *C. fragaefolii* and the available habitat per plant was incompletely utilized. Mutual avoidance was not apparent, as all species were observed to coexist upon the same plant even when uninfested plants were available. The relatively uniform decline in the population throughout the field supports the concept of density-independent mortality factors.

The regression of mean crowding ($\overset{*}{m}$) on the mean was not designed for characterizing dispersion of a population over time, and was consequently less meaningful

Table 1.—Spatial distribution of aphids on strawberries in Orange County, Calif., in 1981 as measured by Green's coefficients, C_x

1980–1981 Planting			1981–1982 Planting		
Date	$\bar{x}$ Aphids/plant[a]	C_x	Date	$\bar{x}$ Aphids/plant[a]	C_x
15 Jan.	0.06 ± 0.04	0.53	12 Jan.	1.74 ± 0.87	0.25
22 Jan.	0.27 ± 0.15	0.29	19 Jan.	3.87 ± 1.31	0.11
29 Jan.	0.05 ± 0.02	0.14	26 Jan.	6.03 ± 1.95	0.10
5 Feb.	0.28 ± 0.13	0.21	2 Feb.	9.07 ± 2.30	0.06
12 Feb.	1.45 ± 0.51	0.12	9 Feb.	30.54 ± 6.20	0.04
19 Feb.	1.56 ± 0.54	0.12	16 Feb.	50.86 ± 11.47	0.05
26 Feb.	1.80 ± 0.66	0.13	23 Feb.	174.33 ± 34.83	0.04
6 Mar.	1.58 ± 0.41	0.07	2 Mar.	192.48 ± 37.84	0.04
12 Mar.	18.59 ± 2.95	0.03	9 Mar.	153.58 ± 26.38	0.03
19 Mar.	13.19 ± 1.61	0.01	16 Mar.	—[b]	—
26 Mar.	25.06 ± 3.39	0.02	23 Mar.	122.55 ± 15.37	0.02
2 Apr.	4.59 ± 0.75	0.03	30 Mar.	105.90 ± 9.99	0.01
9 Apr.	3.03 ± 0.43	0.02	6 Apr.	71.76 ± 8.43	0.01
16 Apr.	2.35 ± 0.23	0.01	13 Apr.	24.11 ± 2.48	0.01
23 Apr.	2.11 ± 0.22	0.01	20 Apr.	3.21 ± 0.40	0.12
30 Apr.	1.54 ± 0.25	0.02	27 Apr.	0.43 ± 0.15	0.06
7 May	1.41 ± 0.17	0.01	3 May	—	—
14 May	1.89 ± 0.22	0.01	11 May	0.88 ± 0.23	0.05
28 May	1.72 ± 0.23	0.01			

[a] Values ± SE.

[b] —, Data not available.

as an indicator of biological activity. However, this technique was used to determine whether an individual or a group of individuals was the basic component of the population. According to Iwao (1968), the "index of basic contagion" (a) described an individual as the basic unit of a population when $a = 0$, or a group of individuals when $a > 0$. In 1981, the a value was significantly greater than 0, indicating a group of individuals as the basic component (Fig. 1a). However, in 1982, when aphid populations reached ca. eight times the 1981 levels, the a value was not significantly different from 0 (Fig. 1b).

To document whether the 1982 a value was biologically meaningful or a statistical artifact, the population was separated into two temporal classes: a rising population (from inception of sampling to peak population) and a declining population (from peak population to termination of sampling) (See Table 1 for dates and aphid counts). The index of basic contagion for both populations was significantly greater than 1, suggesting that the a value obtained from the entire data set was probably a statistical artifact (rising population; $a = 17.7$, $r^2 = 0.93$, declining population; $a = 7.8$, $r^2 = 0.96$).

The regression technique developed by Iwao (1968) also provides a "density contagiousness coefficient" (b) which distinguishes how the basic components of a population are distributed within their habitat. Distribution is random when $b = 1$, and becomes increasingly aggregated as b increases. Analysis of the complete data sets (Fig. 1) from both 1981 and 1982 plantings generated b values significantly greater than 1, suggesting that populations were aggregated. However, when populations were classified as increasing or decreasing, the density contagiousness coefficients were significantly different from 1 only for the rising populations (1981; $b = 1.62$, $r^2 = 0.85$, 1982; $b = 1.72$, $r^2 = 0.93$). Thus, when stratified into temporal-distibutional classes, Iwao's (1968) regression method agreed with results produced by the analysis suggested by Green (1966).

Conclusions from analyses of aphid counts with Lloyd's patchiness index are analogous to those from both previous techniques. Figure 2 graphically shows the changes in patchiness with density as time progresses. Initially the populations were aggregated (patchiness index > 1), but became more randomly distributed as density increased. As populations declined, distributions remained relatively constant, again indicating reductions were occurring in response to density-independent mortality factors. Although this technique may be influenced by density (Myers 1978), the close agreement with C_x substantiates the results, and suggests that for this study the conclusions are valid.

The evidence presented here emphasizes the importance of basing sampling plans on changes in spatial dispersion over time as well as on data from multiple fields during a short time period. Investigation of the

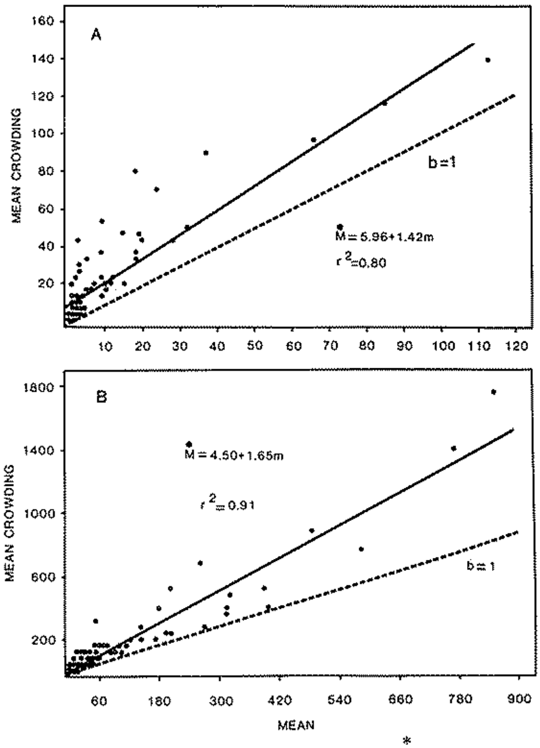

FIG. 1.—Relationship of mean crowding ($\overset{*}{m}$) to mean (m) number of aphids per strawberry plant for (A) 1980–1981 planting and (B) 1981–1982 plantings.

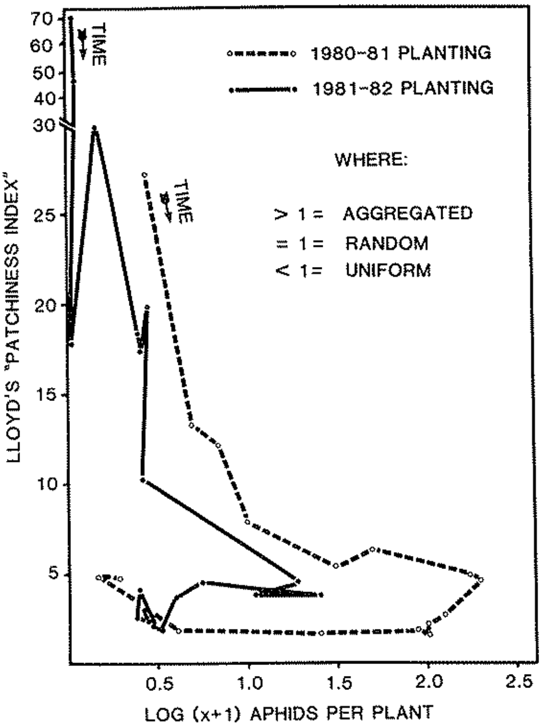

FIG. 2.—Aphid distribution in two consecutive winter plantings of strawberries in coastal California as measured by Lloyd's patchiness index. Each data point represents successive sampling dates. Aphid counts and sampling dates are reported in Table 1.

implication of changes in dispersion of insect populations over time on sampling programs have been largely ignored. The study of dispersion patterns of each larval instar of the Egyptian alfalfa weevil is a notable exception (Christensen et al. 1977).

Previous analyses of aphid dispersion by using natural immigrants or introduced reproductives indicated that dispersions changed from the Poisson to the negative binomial in less than 1 week and at densities below one aphid per plant (Sylvester and Cox 1961, Shiyomi and Nakamura 1964). Since virus transmission was of primary concern, dispersions from larger populations which would be associated with plant tolerance of aphids were not investigated. The Poisson distribution was not observed for initial populations in either of our strawberry plantings. Aphid density in the 1980–1981 planting was less than one aphid per plant for 4 weeks, but few migrants were seen. In the 1981–1982 planting, aphid population density exceeded one plant at the inception of sampling. Thus, either a low density of initial migrants or a rapid reproduction rate can result in small yet aggregated aphid populations. Similar results were reported for aphids infesting broccoli (Trumble 1982). Additional experiments that document the statistical artifacts inherent in analyzing populations that undergo changes in dispersion are critical for the production of efficient and accurate sampling strategies.

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