Population Densities and Spatial Patterns of the Aphid Tristeza Vector, *Toxoptera citricida* Kirk.

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Apart from the virulence, strain differences, and other intrinsic characters of any pathogen, there are many environmental factors which determine the course of a disease. Population densities and spatial patterns of the vector should be taken into account for vector-borne pathogens. Many research workers in ecology and epidemiology (e.g. Pielou, 1969; Kuno, 1968) have focused attention on these population characteristics to develop a full understanding of the dynamics of insect (vector) populations.

The spatial pattern of vectors is one of the basic conditions for disease spread. A vector-borne disease will not spread at a high rate if the vector population is clustered in a particular site of the field. On the other hand, alterations in the spatial pattern will undoubtedly evoke changes in the rate of spread of a disease. To assess these alterations, various distribution functions have been fitted to vector counts (Beal, 1940; Bliss and Fisher, 1953; Bliss, 1958; Bliss and Owen, 1958; Harcourt, 1961; Pielou, 1969). In our search of the conditions that underlie the spread of tristeza in Suriname, distribution functions were fitted to counts of the brown citrus aphid (*Toxoptera citricida* Kirk.) obtained from the citrus orchard of Geyersvlijt.

MATERIALS AND METHODS

In the citrus orchard of Geyersvlijt, located in the north of Paramaribo, brown citrus aphids were caught, using modified Moericke's (1951) water traps which consisted of 10-inch plastic bowls painted yellow inside and black outside. They were filled with water up to the two small outlets, below the rims and a few drops of formaldehyde were added. The outlets were covered with pieces of plastic gauze to prevent the trapped insects from draining out during heavy rains. A fixed water level was maintained in each trap by an automatic refilling device, which consisted of a 1-liter bottle, plugged with a perforated rubber stopper, fitted with a piece of plastic tubing (Schwarz, 1965*a*).

The bowls were suspended 6 feet above the ground and supported by iron rings attached to poles. Thirty traps were placed in the field and trapped insects were collected and counted weekly.

In order to characterize the aphid populations, a variate T defined as the number of traps containing X (X = 0, 1, 2, . . . 10(n)) aphids, was used.

The negative binomial distribution was fitted to this variate, since it has been shown to fit such variates very well (Bliss and Fisher, 1953). The negative binomial distribution is defined by two parameters: the arithmetic mean and a positive exponent k. It is given by the expansion of $(q-p)^{-k}$, where $p = m/k$ and $q = 1+p$. This distribution has the advantage that it converges to other biologically important distributions for limiting values of the exponent k. The distribution converges to the Poisson series when k approaches infinity (large values of k), whereas the logarithmic series appears when k approaches zero. The probability that a trap will contain 0, 1, 2, . . . n aphids is given by equation (1).

$$P(\underline{x} = x) = \frac{(k+x-1)!}{x!\,(k-1)!} \cdot \frac{R^x}{q^k} \qquad (1)$$

Where $R = p/q = m/k+m$

The parameters m and k were estimated from the frequency distributions of the samples, by the statistics $\overline{x}$ and $\hat{k}$, with

$$\overline{x} = \frac{S\,(T.x)}{N} \qquad (2)$$

The exponent k was estimated in two ways (Bliss and Fisher, 1953): 1. The method of moments, providing

$$\hat{k} = \frac{\overline{x}^2}{s^2 - \overline{x}} \qquad (3)$$

$$\text{with } s^2 = \frac{S(T.x^2) - S^2\,(T.x)/N}{N-1} \qquad (4)$$

as the sample variance.

Equation (3) is an efficient estimator of k, for 90 per cent or more, only if the following conditions are fulfilled:

a. for small values of m,k/m >6 should hold.
b. for intermediate values of m, the condition (k+m) (k+2)/m ⩾ 15 should be satisfied.
c. for large values of m, k should exceed 13.

In cases where these conditions were not satisfied, the zero class method was used to estimate k.

2. Zero class method.

This method is based on the ratio of the total number of units (traps) to the number of units (traps) with zero organisms (aphids) ($T_\circ$). By putting $P_\circ = 1/q^k$ (equation 1) equal to $T_\circ/N$, equation (5) is obtained:

$$\hat{k}\,\log\,(1+\overline{x}/\hat{k}) = \log\,(N/T_\circ) \qquad (5)$$

By iteration the required $\hat{k}$-value that balanced equation (5) was obtained.

In cases where the above-described methods did not provide a k-estimation of an acceptable efficiency, the maximum likelihood method (Haldane, 1942; and Sichel, 1951) was used (Bliss and Fisher, 1953). Here the values of k, estimated by (3) and (5), served as a first step of iterative procedure.

The probability for a given X was multiplied by the total number (N = 30) of traps to obtain the expected frequency, Ø, of traps containing X aphids. The goodness of fit was assessed by comparing the observed and the expected frequencies, using the chi-square test where

$$X^2_{n-r-1} = S\left(\frac{(T_x - Ø_x)^2}{Ø_x}\right) \qquad (6)$$

with n: the total number of ratios summed up and r: the number of parameters estimated. Here r = 2, so the degrees oi freedom were reduced by 3. For the analysis, counts of the first 19 weeks of the citrus orchard of Geyersvlijt were used.

RESULTS AND DISCUSSION

Figure 1 shows that the density of the aphid population was nearly zero during the first 6 weeks of the experiment. The highest population densities were reached from the 14th to the 18th week (December 14, 1978 to January 25, 1979). During the 18th week the density was outstanding, and it coincided with the January flush of the orange trees at Geyersvlijt. As shown in fig. 1 there is a tendency for the population density of the aphids to peak 2 weeks after heavy rainfalls. Information on the distribution of the aphids trapped is presented in table 1.

Because of the dense aphid population in the 18th week, a different grouping was used for this week. The variate T was plotted against X for the weeks 11, 15, 16, 17, and 19. A skewness typical of the negative binomial distribution was revealed (fig. 2). This distribution fitted the variate T very well during the different weeks of the experiment (table 2).

The exponent k was used as a means to characterize the flying aphid populations. Low values of k indicate pronounced clumping, and high values slight clumping (Pielou, 1969). On this basis migration was clustered during the 12th and the 18th weeks, since the lowest k-values (0.6919 and 0.9732, respectively) were found for these weeks.

There was also a considerable shift of the different k-values which does not agree with the theory that the k-value remains unaltered when a population decreases from random deaths (Pielou, 1969). One reason for different k-values was that we were collecting weekly samples of the flying aphid populations at fixed sites in the area.

A second reason is that the number of flying aphids is dependent on the population densities of the aphid on the shoots. More winged aphids will occur at high densities, so the migration pattern will undergo alterations from time to time, along with the value of k.

In addition the relative attractiveness of yellow and green to *T. citricida* differs seasonally (Schwarz, 1965*b*). In seasons when yellow and green are equally attractive, aphid trapping may best fit a Poisson distribution. Table 2 shows high k values for weeks 14, 16, and 17, and during these weeks the Poisson distribution (randomness) fitted the variate T very well.

It cannot be concluded, however, that high k values were due to a decreased attractiveness of yellow to the aphids, since such experiments were not conducted.

A final conclusion drawn from table 2 is that the negative binomial fitted the variate T well, at both high and low population densities. Even at low densities, true contagion can be expected, indicating that the presence of an individual (aphid) in a unit increases the probability that another individual will enter the same unit. This result agrees with the assessment that the habitable space of *T. citricida* is the young shoots of flushing citrus trees; a condition undoubtedly leading to contagion.

Apart from preinoculation, the contagious migration pattern encountered here for winged *T. citricida* provides an additional explanation of the patchy spread of the tristeza disease in the citrus orchard of Geyersvlijt.

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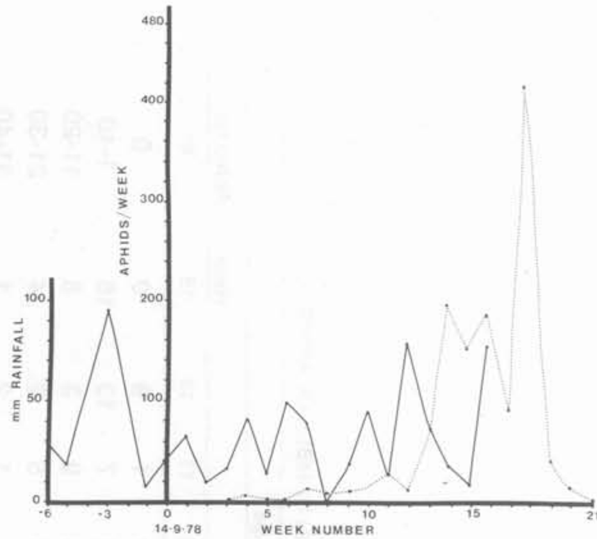

Fig. 1. Densities and spatial patterns of the tristeza aphid vector, *T. citricida* Kirk.

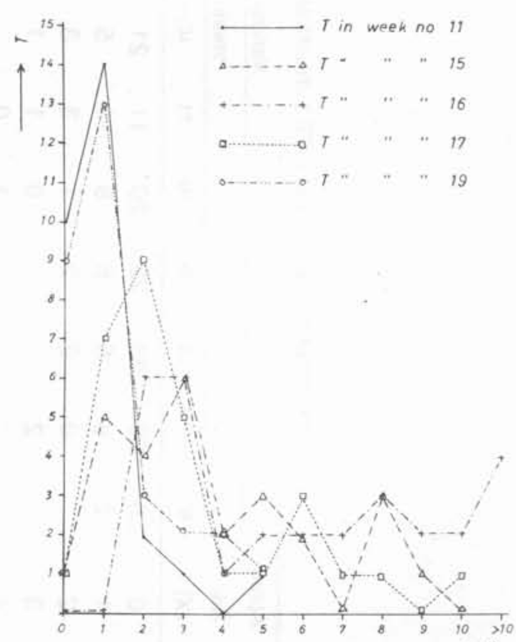

Fig. 2. The shapes of the variate T.

TABLE 1
DISTRIBUTIONS OF VARIATE T (NUMBER OF TRAPS CONTAINING (X) NUMBER OF APHIDS)

Aphid No. (X)	Variate T per weekly sample of 30 traps														
	Week													Week	Aphid no.
	6*	7	8	9	10	11	12	13	14	15	16	17	19	18	X†
0	28	20	23	22	20	11	21	4	0	1	0	1	9	0	0
1	2	8	5	6	8	14	5	10	4	5	0	7	13	16	1-10
2		0	2	2	1	3	3	6	2	4	6	9	3	8	11-20
3		2			0	1	1	3	2	6	6	5	2	4	21-30
4					1	0		2	4	2	1	1	2	1	31-40
5						1		4	2	3	2	1	1	0	41-50
6								1	4	2	2	3		0	51-60
7									1	0	2	1		0	61-70
8									2	3	3	1		1	71-80
9									2	1	2	0			
10									3	0	2	1			
>10									4	3	4				

* Week 6 started October 19, 1978.
† Different scale of X used for week 18.

TABLE 2
GOODNESS OF FIT OF THE NEGATIVE BINOMIAL DISTRIBUTION TO VARIATE T*

Week no.	m values	$\hat{k}$ values	Goodness of fit of negative binomial distribution (+/-)	Other distribution functions
7†	0.4666	1.4760	+	
8	0.3000	1.1160	+	
9	0.3333	3.2183	+	
10	0.4666	1.4755	+	
11	0.9333	5.5083	+	
12	0.4666	0.6919	+	
13	2.1666	5.3739	+	
14	2.9000	>60	-	Poisson
15	5.0666	1.1543	+	
16	6.2333	>35	-	Poisson
17	3.0666	>50	-	Poisson
18	13.6666	0.9732	+	
19	1.2666	3.0746	+	

* Variate T = number of traps containing X number of aphids.
† Week 7 started October 26, 1978.

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