Spatial and Temporal Dynamics of Tomato Mottle Geminivirus and *Bemisia tabaci* (Genn.) in Florida Tomato Fields

J. E. Polston, Gulf Coast Research and Education Center, University of Florida, 5007 60th St. E., Bradenton 34203; **D. O. Chellemi,** North Florida Research and Education Center, University of Florida, Rt. 3, Box 4370, Quincy 32351; **D. J. Schuster,** Gulf Coast Research and Education Center, University of Florida, 5007 60th St. E., Bradenton 34203; and **R. J. McGovern** and **P. A. Stansly,** Southwest Florida Research and Education Center, University of Florida, P.O. Drawer 5127, Immokolee 33934

ABSTRACT

Polston, J. E., Chellemi, D. O., Schuster, D. J., McGovern, R. J., and Stansly, P. A. 1996. Spatial and temporal dynamics of tomato mottle geminivirus and *Bemisia tabaci* (Genn.) in Florida tomato fields. Plant Dis. 80:1022-1028.

Progression of tomato mottle geminivirus (TMoV), and abundance and dispersion of adult whitefly, *Bemisia tabaci* (Gennadius) B biotype, were monitored in 1992 and 1993 in 91 experimental plots located on 10 commercial tomato farms. Prior to harvest (73 to 75 days post plant) within-row aggregation of tomato mottle–infected plants was detected by means of ordinary runs analysis in only two of 14 plots that exhibited a disease incidence greater than 5%. At harvest (95 to 107 days post plant), within-row aggregation was detected in 11 of 21 plots. Significant clustering of diseased plants occurred in only 7% of plots analyzed with Gray's two-dimensional distance class analysis. The observed pattern of disease in these plots was characterized as having numerous small clusters of symptomatic plants scattered throughout plots prior to harvest. No relationship was observed between disease incidence and the degree of aggregation. Dispersion patterns of adult *B. tabaci* fluctuated throughout the season with values of the Morisita's index ranging from less than 1 (indicating a uniform dispersion pattern) to greater than 2 (indicating an aggregated pattern). Abundant sources of immigrating viruliferous whitefly vectors, rather than secondary spread within fields, appeared to be the driving force behind epidemics of tomato mottle in this production system characterized by frequent applications of insecticides.

Additional keywords: *Bemisia argentifolii, Lycopersicon esculentum*

Symptoms of tomato mottle virus (TMoV), Geminiviridae subgroup III, were first observed in 1989 in tomato (*Lycopersicon esculentum* Mill.) in southern Florida (12,25). TMoV has a narrow host range and is found primarily in tomato plants grown in Florida (17,22). No significant virus reservoirs of weed or crop plants have been identified (17). TMoV has been detected between production periods in tomato plants found in abandoned fields, in volunteer tomato plants in ditches, pastures, and old fields, and in shoots that sprout from paraquat-treated tomato plants (23). Abandoned fields are thought to be the most important source of TMoV for newly planted spring fields, based on gradients of tomato mottle disease symptoms observed in new fields downwind of abandoned fall fields (23). Incidence of tomato mottle in tomato fields can vary from zero to 100% (23). TMoV is transmitted in a persistent manner by the adult sweet potato whitefly, *Bemisia tabaci* (Gennadius) B biotype (12). The B biotype of *B. tabaci* is an introduced whitefly pest and vector of geminiviruses that was first documented in Florida in 1986 and 1987 in greenhouse ornamentals and tomato, respectively (23). Transmission of TMoV is similar to that reported for other whitefly-transmitted geminiviruses. The minimum time required for acquisition is approximately 1 h, followed by a latent period of several hours, and a transmission feeding period of approximately 1 h (J. E. Polston, unpublished). Tomato mottle is a major concern in tomato production in Florida. It was estimated to cost the industry at least $125 million in 1991 through reduced yields and increased costs due to frequent applications of insecticides (24).

Approximately 20,240 ha in Florida each year are devoted to the production of tomatoes for the fresh market. In west-central Florida, tomatoes are grown in two seasons. Planting for the fall season begins in early August and ends in early September, with harvest from late October through early December. The spring crop is planted in late December through early March with harvest in late April through early June. Tomato seedlings, produced by the grower or by a commercial transplant producer, are planted into raised beds previously fumigated with methyl bromide and covered with plastic film, and are routinely pruned and trellised. Pesticides are applied throughout the season, with an average of two to three applications per week to control whiteflies. Pre-harvest production costs can run in excess of $15,000 per ha (27). In the production area of west-central Florida, a typical grower has five to 10 fields, approximately 3 to 8 ha in size, in close proximity to each other. At the beginning of production periods, each grower plants a field every 1 to 2 weeks. In many cases, the fields of a grower are located within 8 km of those of at least one other grower.

Relatively few studies on the movement of whitefly-transmitted geminiviruses into and within fields have been reported. Incidence of African cassava mosaic virus (ACMV) in cassava was determined to be highly dependent on wind direction and time of planting, with the highest incidences found in the upwind sides of fields (7). Primary spread accounted for the largest proportion of infected plants (6,9,13). The virus has few hosts in the agroecosystem, and these play a very minor role, if any, in its epidemiology (7). ACMV-diseased cassava plants in neighboring fields served as the most important source of inoculum for new plantings, though diseased stem cuttings accounted for some disease (6,7). In contrast, tomato yellow leaf curl virus (TYLCV), which is a pathogen of fresh-market tomato, was found to have at least two weed hosts in Israel that serve as a bridge between tomato production cycles (4). Infections of TYLCV in Israel are reported to be from primary spread at the beginning of the season, and from secondary spread as the season progresses, although the proportion of plant infections due to each type of spread has not been reported.

Understanding the epidemiology of TMoV is essential to the development of an effective pest-management program. For example, significant correlations between vector abundance and disease inci-

Corresponding author: J. E. Polston
E-mail: jep@gnv.ifas.ufl.edu

This work was supported in part by grants from the Florida Tomato Committee and the USDA Cooperative Extension Service.

Florida Agricultural Experiment Station Journal Series Number R-04492.

Accepted for publication 14 May 1996.

Publication no. D-1996-0607-07R

dence can be used to forecast outbreaks of the virus. Analysis of spatial patterns can provide information concerning secondary spread and infection gradients, information that also affects the selection of specific disease-management tactics.

In this study, the spatial and temporal dynamics of TMoV and its whitefly vector were examined to ascertain the contribution of inoculum sources within tomato-production fields to epidemics caused by TMoV. Specific objectives were to describe the spatial pattern and incidence of TMoV-diseased tomato plants in spring fields, characterize the abundance and dispersion patterns of adult *B. tabaci*, and determine if there was a correlation between the abundance of *B. tabaci* and the incidence of tomato mottle. The results of this study will enable us to better understand epidemics of whitefly-transmitted geminiviruses and will be used in the development of recommendations for managing tomato mottle disease.

MATERIALS AND METHODS

Location and design. Experimental plots were located within commercial tomato farms in west-central and southwest Florida during the spring production seasons (January through May) of 1992 and 1993. Six fields were selected in Manatee and Collier counties in 1992 and four in Manatee and Hillsborough counties in 1993, for a total of 10 fields. A 3- to 4.5-ha field at each field was divided into 0.4-ha sections and one plot was positioned at random within each section. Plots consisted of 144 plants arranged in a 12 × 12 grid consisting of 12 rows and 12 plants per row. Plant spacing was 180 cm between rows and 60 to 70 cm within rows. Seedlings of tomato (cvs. Sunny, Agriset, or Sunbeam) were transplanted into the fields between 20 and 28 January in 1992 and 1993. Plants were maintained by the commercial growers with standard production practices, including frequent applications of insecticides. Each field was managed by a different grower, and was subjected to a unique combination of insecticide applications. The following insecticides were registered for use on tomatoes in Florida at the time of this study: chlorpyrifos, endosulfan, esfenvalerate, fenpropathrin, methamidophos, methomyl, mineral oils, permethrin, and potassium salts of fatty acids (insecticidal soap).

Data collection. All plants within each plot were examined at weekly intervals for visual symptoms of tomato mottle beginning 1 to 2 weeks after transplanting. The location and disease status of each plant was recorded on each sample date. In spring, the onset of symptoms of tomato mottle was seen 5 to 6 weeks after transplant. During the season, symptom expression occurs 1 to 2 weeks after infection. Characteristic symptoms are chlorotic mottling and reduced size of young leaflets, chlorotic mottling and upward rolling of middle to old leaflets, and stunting of the plant. During the time this study was conducted in the two areas, this set of symptoms was diagnostic for the presence of TMoV.

During visual inspection, two plants were selected at random from within each row (before entering the field) and leaf samples analyzed for the presence of TMoV by nucleic acid spot hybridization with a TMoV-specific probe (22). In a previous study, a sample size of 10% of a plant population was sufficient to provide an estimate of the accuracy of visual assessments (data not shown). Seasonal abundance of adult *B. tabaci* was determined by means of vertical yellow sticky traps. Traps were constructed of two 4 × 4 cm yellow plastic squares (0.25 mm thickness, vinyl yellow, polished matte, Hillcor Distributors, Inc., Whittier, CA) sandwiched and stapled over the blunt end of 30-cm wooden garden stakes. A thin layer of heated adhesive (Stickem Special, Seabright Enterprises, Emeryville, CA) was applied to the two exposed sides of the plastic squares. Traps were suspended 25 cm above the beds and oriented perpendicular to the plant row. Nine traps were placed per plot, three each in row numbers 1, 6, and 12. Within each row, traps were placed at plants 1, 6, and 12. The distance between traps varied slightly from field to field because of the differences in plant spacing selected by individual growers. Traps were placed in the fields 7 to 14 days after transplanting. Traps were replaced at 1-week intervals, on the same days that disease incidence data were collected. After traps were removed from the field, the number of adult *B. tabaci* on each trap was counted and recorded. This was possible because adults of *B. tabaci* can be readily distinguished from those of other whitefly species found in Florida. The total number of adult *B. tabaci* per plot collected on each sample date was calculated and recorded. In addition, averages of the number of adult *B. tabaci* per trap (total whiteflies per plot/nine) were calculated for each date, as well as the cumulative number trapped per plot.

Data analysis. Ordinary runs analysis was used to determine the nonrandomness of TMoV-diseased plants within rows (16). Rows were combined to form a single row with length equal to the total number of plants in each plot. A row was considered to have a nonrandom sequence of diseased and healthy plants if the standardized variable Z_u was more negative than –1.64 (3). Ordinary runs analysis was performed for all dates in all plots with a disease incidence of 5% or greater.

Gray's two-dimensional distance class analysis (10) was used to characterize the spatial arrangement of tomato mottle–diseased plants in each plot. Only plots with a disease incidence of 15% or greater were analyzed (10). The location of plants within plots was described in terms of [*X*,*Y*] distance values with all pairs of diseased plants assigned a corresponding [*X*, *Y*] distance class. The number of diseased plants at each distance class was divided by the total number of plants at the same distance class to obtain a standardized count frequency (SCF). Expected SCFs for each distance class were generated with the BASIC program 2DCLASS (21), under the assumption that the pattern of TMoV-diseased plants in the field was random. Four hundred simulations were used to obtain an expected SCF for each distance class. Comparisons of observed to expected SCFs at each distance class were used to quantify the randomness of pairs of diseased plants and their orientation within the field. Using an overall value of $\alpha = 0.10$, the observed SCFs were considered to be significantly greater than expected

Table 1. Final incidence of tomato mottle virus (TMoV)-diseased plants and number of adult *Bemisia tabaci* collected from ten commercial tomato fields over two production seasons.

			Incidence of TMoV		No. of adult *Bemisia tabaci* trapped	
Year	Field[a]	No. of plots[b]	Range[c]	Mean[d]	Range[e]	Mean[f]
1992	M1	7	1.4 to 23.6	6.7	212 to 295	247.5
	M2	11	0 to 6.9	2.1	172 to 317	256.5
	M3	8	0 to 3.5	1.2	526 to 1,254	797.4
	M4	11	1.4 to 12.5	4.4	503 to 851	663.8
	C1	10	0 to 1.4	0.2	96 to 329	163.0
	C2	10	0 to 0.7	0.2	105 to 137	126.0
1993	H1	8	10.4 to 34.7	22.6	59 to 192	116.1
	M5	9	2.8 to 12.5	8.1	171 to 272	223.2
	M6	9	0 to 4.9	0.9	92 to 127	113.4
	M7	8	0 to 11.8	2.1	216 to 414	332.1

[a] C = Collier County, H = Hillsborough County, and M = Manatee County.

[b] Fields ranged in size from 3.0 to 4.5 ha and were divided into 0.4-ha sections, with each section containing one plot consisting of 144 plants in a 12 plant × 12 row grid.

[c] Range of final incidences of tomato mottle–diseased plants from individual plots within each field as determined by visual inspection at harvest (15 weeks post-transplant).

[d] Mean of the final incidences of tomato mottle from all plots within each field.

[e] Range of the total number of adult *B. tabaci* collected per plot over the season.

[f] Mean number of adult *B. tabaci* collected per plot during the season.

SCFs under the null hypothesis of a random pattern at $P \leq 0.05$ and less than expected at $P \geq 0.95$.

Data sets for each plot were interpreted as having a nonrandom spatial pattern if the percentage of significant SCFs was equal to or greater than 10% of the total number of distance classes, or 14.3% (10% of 143). The core cluster size was defined as the number of significant distances classes that formed a discrete contiguous group in the lower left-hand corner of the distance class analysis matrix (20). Reflected core cluster size was defined as the number of significant [*X,Y*] distance classes that formed discrete contiguous groups elsewhere in the matrix. Both ordinary runs analysis and two-dimensional distance class analysis were performed prior to harvest (73 to 75 days after transplanting) and at the time of the first harvest (95 to 107 days after transplanting).

Correlation analysis was used to measure the level of association between cumulative numbers of adult *B. tabaci* collected over each sample period and changes in the incidence of tomato mottle during the same period. Changes in the incidence of TMoV-diseased plants and the number of adult *B. tabaci* collected were compared over the production season within each plot with a final disease incidence of 5% or greater. To compensate for the latent period of TMoV, correlation analysis was also performed using 1- and 2-week lag periods between cumulative numbers of adult *B. tabaci* collected per plot and incidence of TMoV-diseased plants. The nonparametric Spearman rank correlation coefficient was employed, since the data failed to satisfy assumptions of normality (15,28,29). Spearman's rank correlation coefficient was calculated with the BASIC program SPCOVAR.BAS (16), and was used to test the null hypothesis that there was no association between the number of adult *B. tabaci* collected and the incidence of TMoV-diseased plants.

The spatial pattern of adult *B. tabaci* collected within each field was determined by using Morisita's index of dispersion (18). This index was chosen over the more commonly used *b* parameter from Taylor's power law (30) because it is independent of quadrant size, sample size, and sample mean, and thus would not be affected by the low populations of whiteflies in fields following applications of insecticides. Morisita's index varies continuously from 0, which represents a regular pattern, to infinity, which represents a highly aggregated pattern. A value of 1 indicates a random pattern. For computational purposes, each plot was considered to be an individual sample unit. The number of whiteflies per sample unit was determined by adding the numbers collected in each of the nine traps placed within each plot. The Morisita index was calculated for individual fields over each sampling interval to provide an indication of seasonal changes in dispersion patterns of adult *B. tabaci* collected, by means of the formula $I = Q \; \Sigma \; x_i(x_i - 1)/N(N - 1)$ (1), where Q is the number of plots in each field, x_i is the number of adult whitefly trapped per week in plot *i*, and N is the total number of adult *B. tabaci* collected per week in the entire field.

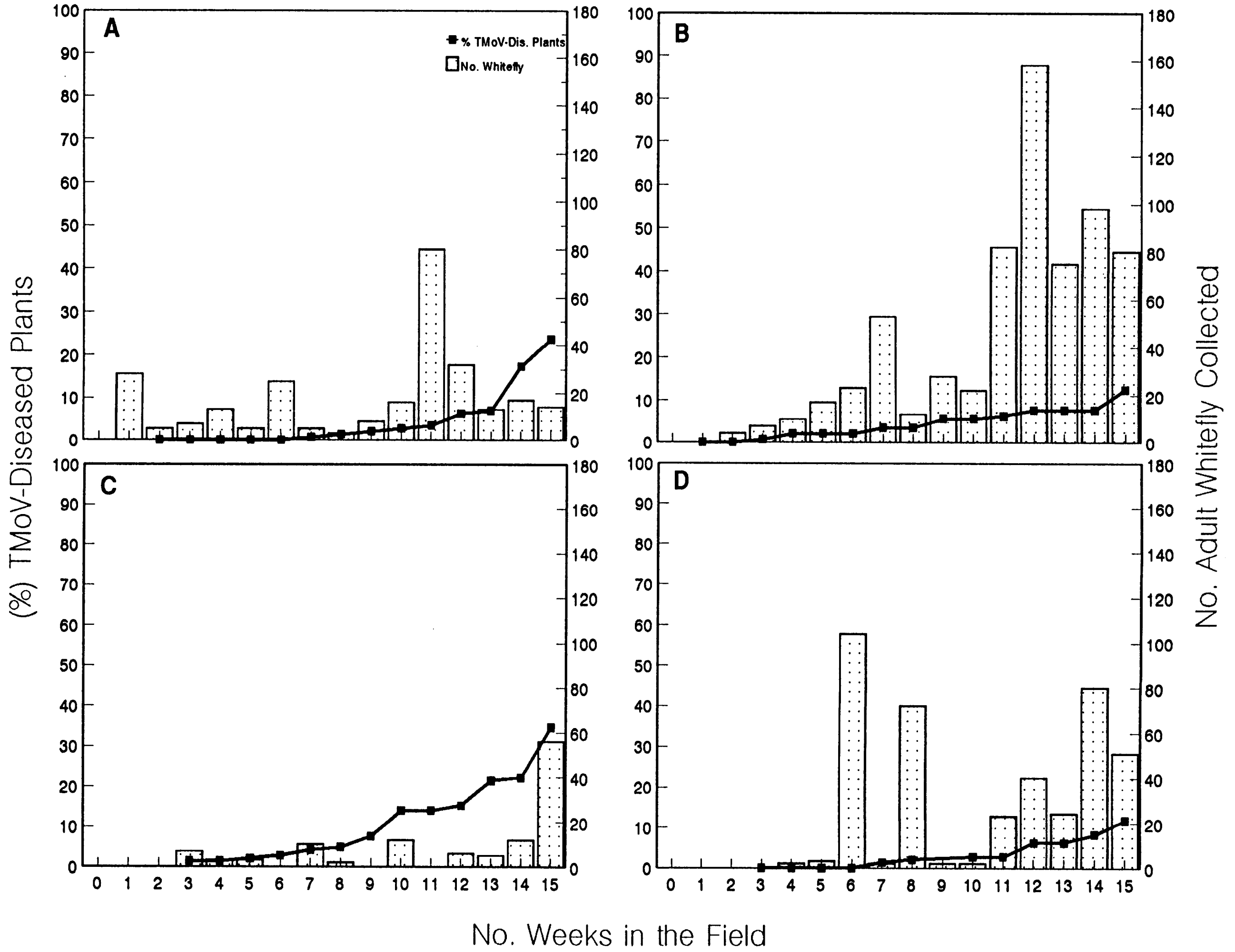

Fig. 1. Disease progress curves of tomato mottle and the number of adult *B. tabaci* collected each week in each of four plots. (**A**) 1992 field M1, plot B, planted 20 January 1992, (**B**) 1992 field M4, plot I, planted 28 January 1992, (**C**) field H1, plot D, planted 23 January 1993, and (**D**) 1993 field M7, plot A, planted 5 February 1993. Each plot had 144 plants, 12 rows of 12 plants. Incidence of tomato mottle virus–diseased plants was determined visually each week beginning 3 weeks after transplant, which is 2 weeks before symptoms can usually be seen in the spring. Adult *B. tabaci* = the averages of whiteflies trapped on nine 4 cm x 4 cm yellow sticky cards in each plot per week.

RESULTS

Incidence of TMoV-diseased plants and abundance of adult whitefly. A total of 91 plots were surveyed over two seasons. The final incidence of TMoV-diseased plants in plots ranged from 0 to 23.6% in 1992 and 0 to 34.7% in 1993 (Table 1). These incidences were typical of other commercial tomato farms for this region during 1992 and 1993 (data not shown). Twenty-one of the plots surveyed over both years had final disease incidences greater than 5% and eight plots had values greater than 15%. Disease progress curves of the eight plots with greater than 15% incidence at the end of the season tended to be slow exponential curves, with only a gradual increase in disease incidence over the season. Disease progress curves of four plots are shown in Figure 1. The number of adult *B. tabaci* collected per plot over the entire season ranged from 96 to 1,254 in 1992 and 59 to 414 in 1993 (Table 1). Averages of the cumulative numbers of adult *B. tabaci* collected per plot in 1992 were similar to those found in a survey conducted in 16 tomato fields in Hillsborough and Manatee counties during the same period.

Spatial pattern of TMoV-diseased plants. Prior to harvest (73 to 75 days after planting), 14 of the 91 plots surveyed had a disease incidence greater than 5%. Aggregation of diseased plants within rows occurred in only two plots as determined by ordinary runs analysis (Table 2). There was no apparent relationship between the incidence of disease in plots and the degree of aggregation within rows (Fig. 2A). Six plots had a disease incidence greater than 14% and all were located within the same field. None of the plots had the minimum percentage of significant SCFs (14.3%) to indicate nonrandomness (Table 2). Core clusters ranged from 0 to 3 distance classes and were considered to be small. Several reflected clusters were detected and in general were larger in size than the core clusters. Spatial maps of disease incidence, and distance classes in which significant SCFs were detected, indicated that the level of nonrandomness was low and best explained by small clusters of diseased plants scattered throughout the plots (Fig. 3).

A second analysis was conducted at the time of harvest, 95 to 107 days after planting. The approximately 4-week period between the two assessment dates was characterized by fewer insecticide applications, in anticipation of harvest. By this time, 21 of the 91 plots had a disease incidence greater than 5%. A nonrandom distribution of diseased plants within rows was found in 11 plots by means of ordinary runs analysis (Table 3). In eight of the plots, the level of aggregation was high ($P < 0.01$). There was no apparent relationship between the incidence of disease in plots and the degree of nonrandomness within rows (Fig. 2B). Eight plots had a disease incidence greater than 15% and were analyzed by two-dimensional distance class analysis. Only one of these had the minimum percentage of significant SCFs (14.3%) to indicate nonrandomness (Table 3). Core clusters ranged from 0 to 2 distance classes and were considered to be small in size. Reflected clusters were numerous and, in general, larger in size than the core clusters. Spatial maps of disease incidence, and distance classes in which significant SCFs were detected, indicated that the level of nonrandomness was greater at harvest and was best described as small clusters of diseased plants scattered throughout the plots (Fig. 4).

Correlation of TMoV-diseased plants and numbers of adult whitefly. Significant correlations ($P < 0.05$) between cumulative numbers of adult *B. tabaci* collected and the incidence of TMoV-diseased plants were observed in only two of 21 plots (Table 4). When disease incidence was adjusted to compensate for a latent period of 1 week, no significant positive correlations were observed. However, three negative correlations, significant at $P \leq 0.05$, were observed. Adjustment of disease incidence to compensate for a latent period of 2 weeks resulted in only one negative correlation, significant at $P \leq 0.05$.

Dispersion patterns of adult whitefly. In 1992, values of the Morisita index ranged from less than 1.0, indicating a random to uniform pattern, to as high as 2.9, indicating a highly aggregated pattern (Fig. 5). Dispersion patterns tended to be more uniform late in the season. In 1993, values for the Morisita index ranged from 0.7 to 2.95 (Fig. 5). Values tended to be greater than 1.0 in the second half of the season.

Table 2. Spatial analysis of tomato mottle virus–diseased plants prior to harvest in plots with a disease incidence >5%

					Runs analysis		Gray's two-dimensional distance class analysis	
Year	Field[a]	Plot	Assessment date	Days after planting	Z_u[b]	P[c]	SCFs[d]	Core[e]/Refl[f]
1992	M4	A	April 10	73	0.31	0.62	. . .[g]	
1992	M4	I	April 10	73	1.90	0.97	. . .	
1993	H1	A	April 6	73	–1.08	0.14	. . .	
1993	H1	B	April 6	73	–3.41*	<0.01	10%	3 / 4,3
1993	H1	C	April 6	73	0.63	0.74	8%	0 / 2
1993	H1	D	April 6	73	–0.33	0.37	6%	1 / . . .
1993	H1	E	April 6	73	0.77	0.81	12%	0 / 2,3
1993	H1	F	April 6	73	–1.93*	0.03	10%	1 / 5,2,2
1993	H1	G	April 6	73	0.21	0.58	8%	0 / 2, 2
1993	H1	H	April 6	73	2.03	0.98	. . .	
1993	M5	A	April 21	75	1.92	0.97	. . .	
1993	M5	F	April 21	75	1.91	0.97	. . .	
1993	M5	H	April 21	75	–0.84	0.20	. . .	
1993	M5	I	April 21	75	0.17	0.58	. . .	

[a] C = Collier County, H = Hillsborough County, and M = Manatee County.

[b] Standardized variable: values less than –1.64 (*) indicate nonrandomness.

[c] Significance level.

[d] Percentage of [*X*,*Y*] distance classes in which the observed standardized count frequency (SCF) was significantly greater ($P < 0.05$) or less ($P > 0.95$) than expected under a random spatial pattern.

[e] The number of significant, adjacent [*X*,*Y*] distance classes that formed a discrete, contiguous group in the lower left corner of the distance class matrix.

[f] The number of significant, adjacent [*X*,*Y*] distance classes that form discrete, contiguous groups elsewhere in the two-dimensional distance class matrix. A cluster was counted if two or more SCFs were adjacent in the [*X*,*Y*] distance class matrix.

[g] SCFs were not computed in plots with a disease incidence <15%.

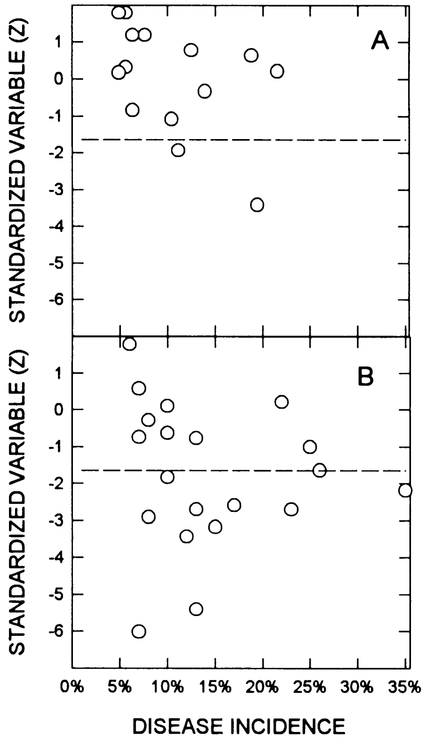

Fig. 2. Relationship between the incidence of tomato mottle virus–diseased plants in individual plots and the pattern of diseased plants within rows, as determined by ordinary runs analysis, (**A**) 73 to 75 days after transplanting and (**B**) 95 to 106 days after transplanting. Values of $Z_u < -1.64$ (dashed line) indicate significant aggregation at $P \leq 0.05$.

DISCUSSION

The epidemiology of a disease caused by a whitefly-vectored geminivirus, having no known significant crop or weed reservoirs other than tomato, is described in a Florida tomato production system. Analyses of these data using ordinary runs and two-dimensional distance class analyses suggest that primary spread rather than secondary spread played a predominant role in the increase of TMoV-diseased plants in commercial tomato fields in the spring of 1992 and 1993. Plants that become infected due to secondary spread will be clustered proximal to the primary infection sites and in this study would be expected to generate standardized variables less than −1.64 in ordinary runs analysis and medium to large size core clusters in Gray's two-dimensional distance class analysis. Prior to harvest, only 14% of plots (2 out of 14) with a disease incidence greater than 5% exhibited a nonrandom pattern of diseased plants, according to runs analysis (Table 2). The lack of significant runs was not associated with low incidences of disease (Fig. 2). By the time of the first harvest, approximately 4 weeks later, 52% of plots (11 out of 21) exhibited a nonrandom pattern (Table 3). The nonrandom pattern on both assessment dates was described as a small core cluster of symptomatic plants, usually one to three distance classes in size, both within and across rows (Table 2; Fig. 3). Several reflective clusters were also present that were larger in size (two to five distance classes) than the core clusters. This suggests that though typical secondary spread was not present, there was some type of association present.

The presence of these reflective clusters could be explained by an immigration of a swarm of viruliferous adult *B. tabaci* B biotype, which are known to migrate short distances as migratory or dispersing swarms (2). Fields that were mature, and less suitable as whitefly hosts, were present in the region and could have served as a source of viruliferous whiteflies. The increase in nonrandomness that occurred in the period between the two assessment dates could be explained by the decrease in frequency of insecticide applications, which occurred before harvest. It has been shown for several insect pests including whiteflies that insecticide applications alter the dispersion patterns of insects, usually by decreasing aggregation (14,31,32). Such alterations in the dispersion pattern of the whitefly vector could have implications for the distribution of TMoV-diseased plants. Studies are in progress to address the relevance of these possible explanations.

Our conclusions regarding the whitefly-mediated primary spread of TMoV are similar to those of two other epidemiological studies involving whitefly-vectored geminiviruses. In all three instances, primary sites of infection accounted for the largest proportion of infected plants in epidemics of ACMV in cassava in East and West Africa, and TYLCV in tomato in Cyprus (7–9,11,13). The study of ACMV was conducted in cassava, and in production systems in which no pesticides were used to manage whitefly vectors. Although whitefly vectors reproduced in the cassava, secondary spread of ACMV was minimal and primary spread was responsible for the majority of infected plants (13). Further, final incidences of TMoV were lower and disease progress curves were flatter than those of ACMV in cassava, soybean yellow mosaic geminivirus in soybean, and TYLCV in fall fields of tomato in Jordan, but were similar to those reported for TYLCV in spring plantings of tomato in Jordan (1,8,26). Final incidences of tomato mottle were similar to those of TYLCV in spring crops of tomato in Cyprus and Senegal (5,11).

Yellow sticky traps, which are commonly used to estimate the populations of adult whitefly, were not useful for estimating adult whitefly populations for studies of geminivirus epidemiology because few positive significant correlations were found between number of adult whitefly trapped and incidence of TMoV-diseased plants, even when latent periods were taken into account. Many techniques have been used to estimate whitefly populations with no standardization of trap design or placement. A recent study has shown that counts of adult whiteflies on sticky traps did not correlate well with counts of adult whiteflies on entire cotton plants (19).

Prior to this study, growers attempted to manage tomato mottle through frequent insecticide applications, through roguing of diseased plants early in the season, and through the spraying of insecticides and herbicides on ditch banks to reduce

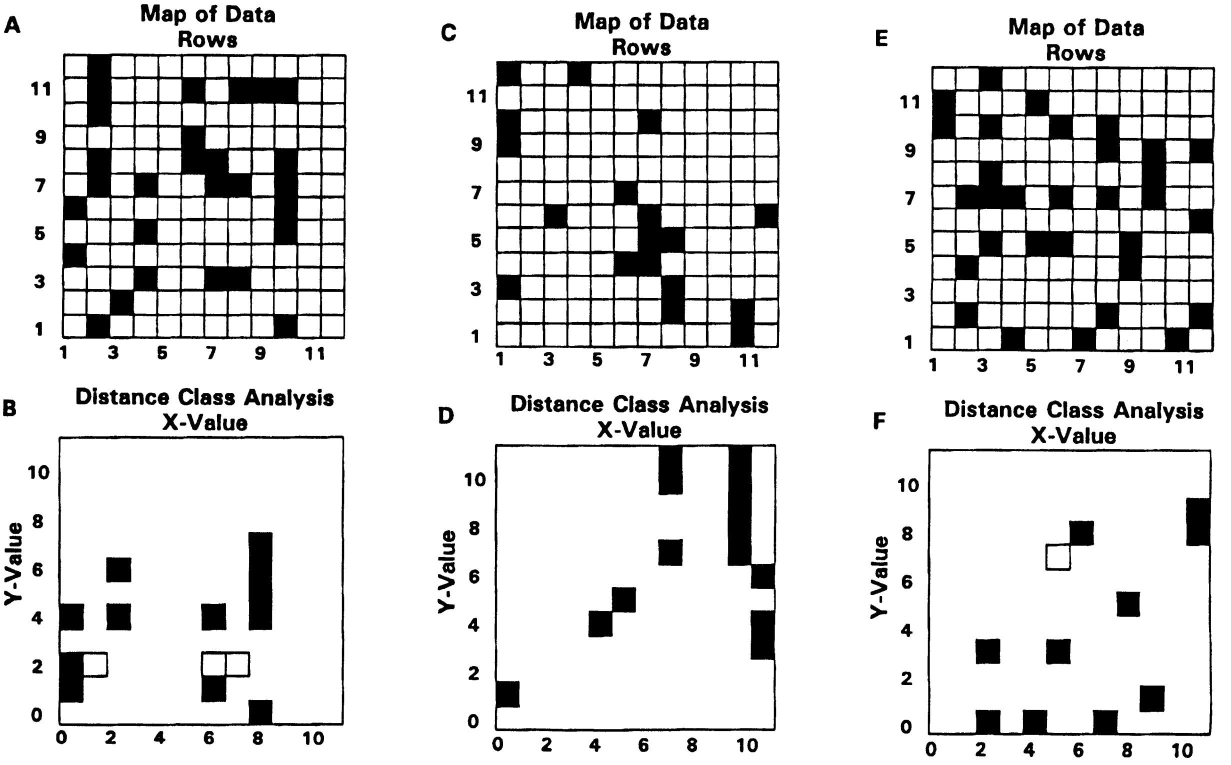

Fig 3. **(A,C,E)** Spatial pattern and **(B,D,F)** two-dimensional distance class analysis of the tomato mottle–diseased plants at 73 days after transplanting in 1993 in field H1, plots B **(A,B)**, F **(C,D)**, and G **(E, F)**. **(A,C,E)** Solid squares indicate diseased plants. **(B,D,F)** Solid squares = $[X,Y]$ distance classes with a standardized count frequency (SCF) greater than expected at $P \leq 0.05$; open squares = a SCF less than expected at $P \geq 0.95$.

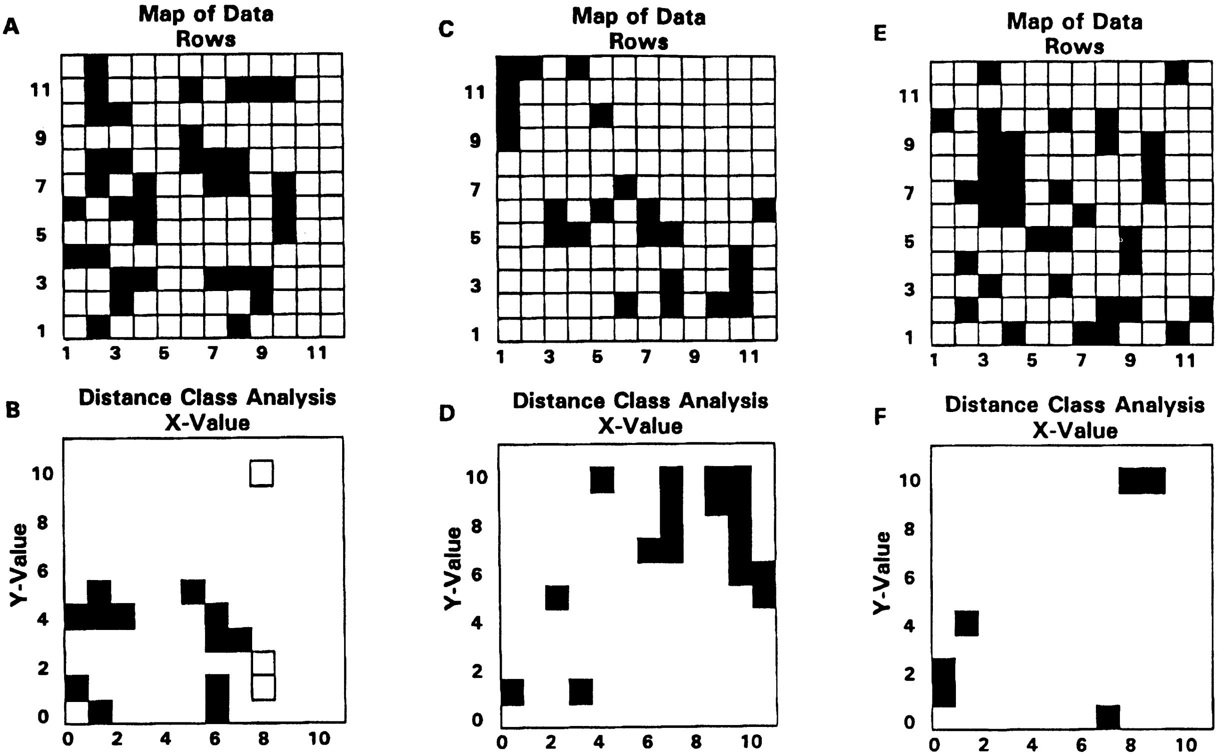

Fig 4. (A,C,E) Spatial pattern and (B,D,F) two-dimensional distance class analysis of the tomato mottle–diseased plants at 101 days after transplanting in 1993 in field H1, plots B (A,B), F (C,D), and G (E, F). (A,C,E) Solid squares indicate diseased plants. (B,D,F) Solid squares = [X,Y] distance classes with a standardized count frequency (SCF) greater than expected at $P \leq 0.05$; open squares = a SCF less than expected at $P \geq 0.95$.

Table 3. Spatial analysis of tomato mottle–diseased plants at harvest in plots with a disease incidence >5%

					Runs analysis		Gray's two-dimensional distance class analysis	
Year	Field[a]	Plot	Assessment date	Days after planting	Z_u[b]	P[c]	SCFs[d]	Core[e]/Refl[f]
1992	M1	B	May 5	106	–2.59*	<0.01	24%[*]	2 / 5,5,4,2,2
1992	M1	E	May 5	106	–0.74	0.43	. . .[g]	
1992	M2	H	April 28	96	–6.02*	<0.01	. . .	
1992	M4	A	May 14	107	–2.91*	<0.01	. . .	
1992	M4	I	May 14	107	–5.40*	<0.01	. . .	
1993	H1	A	May 4	101	–2.70*	<0.01	12%	2 / 4,4,3,2
1993	H1	B	May 4	101	–1.01	0.16	10%	2 / 4,3,2
1993	H1	C	May 4	101	–1.64*	0.05	5%	1 / 2
1993	H1	D	May 4	101	–2.18*	0.02	8%	2 / 3
1993	H1	E	May 4	101	0.21	0.58	10%	0 / 2,3
1993	H1	F	May 4	101	–3.18*	<0.01	12%	1 / 9,5
1993	H1	G	May 4	101	–1.01	0.16	4%	2 / 2
1993	H1	H	May 4	101	-0.63	0.26	. . .	
1993	M5	A	May 12	96	–2.70*	<0.01	. . .	
1993	M5	B	May 12	96	–1.83*	0.03	. . .	
1993	M5	C	May 12	96	1.91	0.97	. . .	
1993	M5	F	May 12	96	–0.77	0.22	. . .	
1993	M5	G	May 12	96	0.10	0.54	. . .	
1993	M5	H	May 12	96	–0.28	0.39	. . .	
1993	M5	I	May 12	96	0.58	0.72	. . .	
1993	M7	A	May 12	95	–3.44*	<0.01	. . .	

[a] C = Collier County, H = Hillsborough County, and M = Manatee County.

[b] Standardized variable: values less than –1.64 (*) indicate nonrandomness.

[c] Significance level.

[d] Percentage of [X,Y] distance classes in which the observed standardized count frequency (SCF) was significantly greater ($P < 0.05$) or less ($P > 0.95$) than expected under a random spatial pattern; [*] indicates nonrandom spatial pattern.

[e] The number of significant, adjacent [X,Y] distance classes that formed a discrete, contiguous group in the lower left corner of the distance class matrix.

[f] The number of significant, adjacent [X,Y] distance classes that form discrete, contiguous groups elsewhere in the two-dimensional distance class matrix. A cluster was counted if two or more SCFs were adjacent in the [X,Y] distance class matrix.

[g] SCFs were not computed in plots with a disease incidence <15%.

Table 4. Correlation between cumulative number of adult *Bemisia tabaci* trapped per plot and incidence of tomato mottle virus–diseased plants over the growing season[a]

			Time adjustment (week)[c]		
Year	Field[b]	Plot	0	1	2
1992	M1	B	0.08[d]	0.28	0.27
1992	M1	E	0.40	0.10	0.30
1992	M2	H	0.44	0.33	0.17
1992	M4	A	0.06	–0.60*	–0.55*
1992	M4	I	0.16	0.10	0.01
1993	H1	A	0.38	0.01	–0.17
1993	H1	B	0.16	–0.17	–0.48
1993	H1	C	0.15	–0.30	–0.50
1993	H1	D	0.39	–0.32	0.14
1993	H1	E	0.35	–0.32	0.38
1993	H1	F	0.10	–0.58*	–0.37
1993	H1	G	–0.05	0.01	0.06
1993	H1	H	0.48	–0.60*	0.18
1993	M5	A	0.14	0.16	–0.39
1993	M5	B	0.66*	–0.26	–0.14
1993	M5	C	0.35	0.04	0.09
1993	M5	F	0.36	–0.26	–0.34
1993	M5	G	0.48	–0.18	–0.40
1993	M5	H	0.56*	–0.23	–0.26
1993	M5	I	–0.08	–0.34	–0.55
1993	M7	A	0.32	0.11	0.08

[a] Only plots with a final incidence >5% were analyzed.

[b] C = Collier County, H = Hillsborough County, and M = Manatee County.

[c] Incidence of tomato mottle virus–diseased plants was adjusted for periods of 1 and 2 weeks after adult *B. tabaci* were collected to allow for time that would elapse between infection and symptom expression in the plants.

[d] Spearman's rank correlation coefficient, * indicates significance at $P = 0.05$.

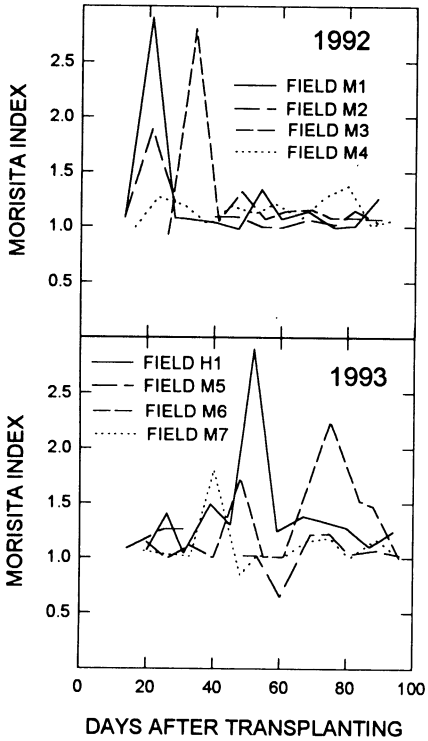

Fig. 5. Seasonal changes in the spatial dispersion of adult *B. tabaci* collected at four fields in 1992 and 1993. Values of the Morisita index indicate a random pattern at 1, a uniform pattern at less than 1, and an aggregated pattern at greater than 1.

whitefly populations. Based on the results of this study, disease management recommendations emphasize the elimination of harvested fields that can serve as virus reservoirs. Controlling vector populations on weeds in ditch banks either with insecticides or herbicides, or roguing of diseased plants, are not recommended. Growers could possibly further reduce their use of insecticides and improve regional disease management of tomato mottle by the removal of fall-planted tomato, several weeks prior to spring planting.

ACKNOWLEDGMENTS

We thank T. Austin, M. Carroll, B. Cawley, P. Hinchliff, J. Hogue, and S. Payne for their technical contributions, and an anonymous reviewer for helpful suggestions.

LITERATURE CITED

1. Al-Musa, A. 1982. Incidence, economic importance, and control of tomato yellow leaf curl in Jordan. Plant Dis. 66:561-563.
2. Byrne, D. N., Rathman, R. J., Orum, T. V., and Palumbo, J. C. 1995. Localized migration and dispersal by the sweet potato whitefly, *Bemisia tabaci*. Oecologia 105:320-328.
3. Campbell, C. L., and Madden, L. V. 1990. Introduction to Plant Disease Epidemiology. John Wiley & Sons, New York.
4. Cohen, S., Kern, J., Harpaz, I., and Ben-Joseph, R. 1988. Epidemiological studies of the tomato yellow leaf curl virus (TYLCV) in the Jordan Valley, Israel. Phytoparasitica 16: 259-270.
5. D'Hondt, M. D., and Russo, M. 1985. Tomato yellow leaf curl in Senegal. Phytopathol. Z. 112:153-160.
6. Fargette, D., Fauquet, C., Grenier, E., and Thresh, J. M. 1990. The spread of African cassava mosaic virus into and within cassava fields. J. Phytopathol. 130:289-302.
7. Fargette, D., Fauquet, C., and Thouvenel, J.-C. 1985. Field studies on the spread of African cassava mosaic. Ann. Appl. Biol. 106: 285-294.
8. Fargette, D., Jeger, M., Fauquet, C., and Fishpool, L. D. C. 1994. Analysis of temporal disease progress of African cassava mosaic virus. Phytopathology 84:91-98.
9. Fauquet, C., Fargette, D., and Thouvenel, J. C. 1988. Some aspects of the epidemiology of African cassava mosaic virus in Ivory Coast. Trop. Pest Manage. 34:92-96.
10. Gray, S. M., Moyer, J. W., and Bloomfield, P. 1986. Two-dimensional distance class model for quantitative description of virus-infected plant distribution lattices. Phytopathology 76: 243-248.
11. Ioannou, N. 1987. Cultural management of tomato yellow leaf curl disease in Cyprus. Plant Pathol. 36:367-373.
12. Kring, J. B., Schuster, D. J., Price, J. F., and Simone, G. W. 1991. Sweetpotato whitefly-vectored geminivirus on tomato in Florida. Plant Dis. 75:1186.
13. Lecoustre, R., Fargette, D., Fauquet, C., and de Reffye, P. 1989. Analysis and mapping of the spatial spread of African cassava mosaic virus using geostatistics and the kriging technique. Phytopathology 79:913-920.
14. Liu, T. S., Oetting, R. D., and Buntin, G. D. 1993. Population dynamics and distribution of *Trialeurodes vaporariorum* and *Bemisia tabaci* (Homoptera: Aleyrodidae) on poinsettia following applications of three chemical insecticides. J. Entomol. Sci. 28:126-135.
15. Ludwig, J. A., and Reynolds, J. F. 1988. Statistical Ecology. John Wiley & Sons, New York.
16. Madden, L. V., Louie, R., Abt, J. J., and Knoke, J. K. 1982. Evaluation of tests for randomness of infected plants. Phytopathology 72:195-198.
17. McGovern, R. J., Polston, J. E., Danyluk, G. M., Hiebert, E., Abouzid, A. M., and Stansly, P. A. 1994. Identification of a natural weed host of tomato mottle geminivirus in Florida. Plant Dis. 78:1102-1106.
18. Morisita, M. 1962. I-index, a measure of dispersion of individuals. Res. Popul. Ecol. (Kyoto) 4:1-7.
19. Natwick, E. T., Toscano, N. C., and Yates, L. 1995. Comparisons of adult whitefly sampling techniques in cotton with whitefly adult populations from whole plant samples. Southwest. Entomol. 20:33-41.
20. Nelson, S. C., and Campbell, C. L. 1993. Comparative spatial analysis of foliar epidemics on white clover caused by viruses, fungi, and a bacterium. Phytopathology 83: 288-301.
21. Nelson, S. C., Marsh, P. L., and Campbell. C. L. 1992. 2DCLASS, a two-dimensional distance class analysis software for the personal computer. Plant Dis. 76:427-432.
22. Polston, J. E., Hiebert, E., McGovern, R. J., Stansly, P. A., and Schuster, D. J. 1993. Host range of tomato mottle virus, a new geminivirus infecting tomato in Florida. Plant Dis. 77: 1181-1184.
23. Polston, J. E., Schuster, D. J., McGovern, R. J., and Hiebert, E. 1992. New developments in the management of tomato viruses in Florida. Pages 41-53 in: Proc. Tomato Inst. C. S. Vavrina, ed. Vegetable Crops Department, Series SS HOS 1, University of Florida, Gainesville.
24. Schuster, D. J., Funderburk, J. E., and Stansly, P. A. IPM in Tomatoes. In: Biological Control and IPM: The Florida Experience. D. Rosen, F. D. Bennett, and J. L. Capinera, eds. Intercept Ltd. Andover, UK. (In press.)
25. Simone, G. W., Brown, J. K., Hiebert, E., and Cullen, R. E. 1990. New geminivirus epidemic in Florida tomatoes and peppers. Phytopathology 80:1063.
26. Singh, H., Sandhu, G. S., and Mavi, G. S. 1971. Control of yellow mosaic virus in soybean, *Glycine max* (L.) (Merr.) by the use of granular insecticides. Indian J. Entomol. 33:272-278.
27. Smith, S. A., and Taylor, T. G. 1994. Production costs for selected Florida vegetables. Univ. Fla. Coop. Ext. Serv. Circ. 1146.
28. Sokal, R. F., and Rohlf, F. J. 1981. Biometry. W. H. Freeman and Company, San Francisco.
29. Spearman, C. 1904. The proof and measurement of association between two things. Am. J. Psychol. 15:72-101.
30. Taylor, L. R. 1961. Aggregation, variance, and mean. Nature (London) 188:732-735.
31. Tonhasca, A., Palumbo, J.C., and Byrne, D.N. 1994. Aggregation patterns of *Bemisia tabaci* in response to insecticide applications. Entomol. Exp. Appl. 72:265-272.
32. Trumble, J. T. 1985. Implications of changes in arthropod distribution following chemical application. Res. Popul. Ecol. (Kyoto) 27:277-285.