Simulating the Dynamics of *Bemisia argentifolii* (Homoptera: Aleyrodidae) in an Organic Cropping System with a Spatiotemporal Model

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ABSTRACT The dynamics of the whitefly *Bemisia argentifolii* Bellows & Perring were studied at a mixed-crop organic farm on Pine Island, FL, between September 1992 and January 1993. Whitefly populations on tomato, eggplant, zucchini, cucumber, and pepper were monitored weekly by beat-pan sampling and biweekly by visual counts, and parasitism was determined by rearing parasitoids from whitefly infested tomato and eggplant foliage. Analysis of the sampling data identified tomato and eggplant as the most attractive whitefly host plants followed by cucumber, zucchini, and pepper. Parasitism of whiteflies on tomato and eggplant reached 80% during the study. Two peaks in population numbers were observed on tomato and eggplant planted by late September, whereas only 1 peak occurred when the same crops were planted later. The suitability of a spatially explicit population model as a tool for investigating insect dynamics was demonstrated on whiteflies at the farm. Simulation experiments conducted to explain the trends in whitefly population numbers observed on early and late tomato indicated that these population peaks likely resulted from the interaction of planting date and temperature and not from the spatial heterogeneity of the crop system at the farm. Other simulation experiments showed that whitefly population levels could be lowered by grouping similar crops and maintaining barriers to whitefly movement between crops. The utility of this type of model for studying insect dynamics in systems where host plants vary spatially and temporally is illustrated.

KEY WORDS *Bemisia argentifolii*, *Bemisia tabaci*, silverleaf whitefly, spatial population model

THE DRAMATIC CHANGE in status of the sweetpotato whitefly, *Bemisia tabaci* (Gennadius), in the mid-1980s generated renewed interest in the biology and dynamics of this insect (Byrne et al. 1990, Brown et al. 1995). In Florida, this change in status was accompanied by reports of an irregular ripening disorder of tomato (Schuster et al. 1990) and a silverleaf disorder of squash (Kring et al. 1991, Schuster et al. 1991). Crop losses from whitefly attacks in Florida were estimated at $141 million in 1991 (Perring et al. 1993, Schuster 1995), and U.S. losses for the same year were over half billion dollars (Perring et al. 1993).

A new strain of *B. tabaci*, strain B, was blamed initially for the increasing infestations (Price et al. 1987, Byrne and Miller 1990). Strain B, considered to be more pestilent than the original *B. tabaci* strain (strain A), was later described as a new species of whitefly, *Bemisia argentifolii* Bellows & Perring (Perring et al. 1993, Bellows et al. 1994). Both whiteflies are highly polyphagous insects that have spread extensively throughout their ranges (Perring et al. 1992, Brown et al. 1995); however, *B. argentifolii* exploits a greater number of host plants (Perring et al. 1992, Brown et al. 1995), has slightly different oviposition preferences (Blua et al. 1995), and appears to be displacing *B. tabaci* in many regions (Perring et al. 1994, Brown et al. 1995). In spite of differences between the 2, continuing debate among entomologists suggests that the strain/species questions have not been resolved completely (see Brown et al. 1995).

Spatial movement of these whiteflies is facilitated by the existence within populations of 2 distinct dispersal morphs—a trivial flying morph and a migratory morph (Byrne and Houck 1990; Blackmer and Byrne 1993a, b). Evidence of the existence of 2 morphs was obtained in a recent study by Byrne et al. (1995) that showed the distribution of whiteflies captured from a source release to be bimodal rather than random. Adults whiteflies have the ability to move within regional crop systems and therefore their dynamics are tied closely to crop and wind patterns throughout these systems. It is difficult to study these dynamics in large spatial systems with field experiments and so simulation

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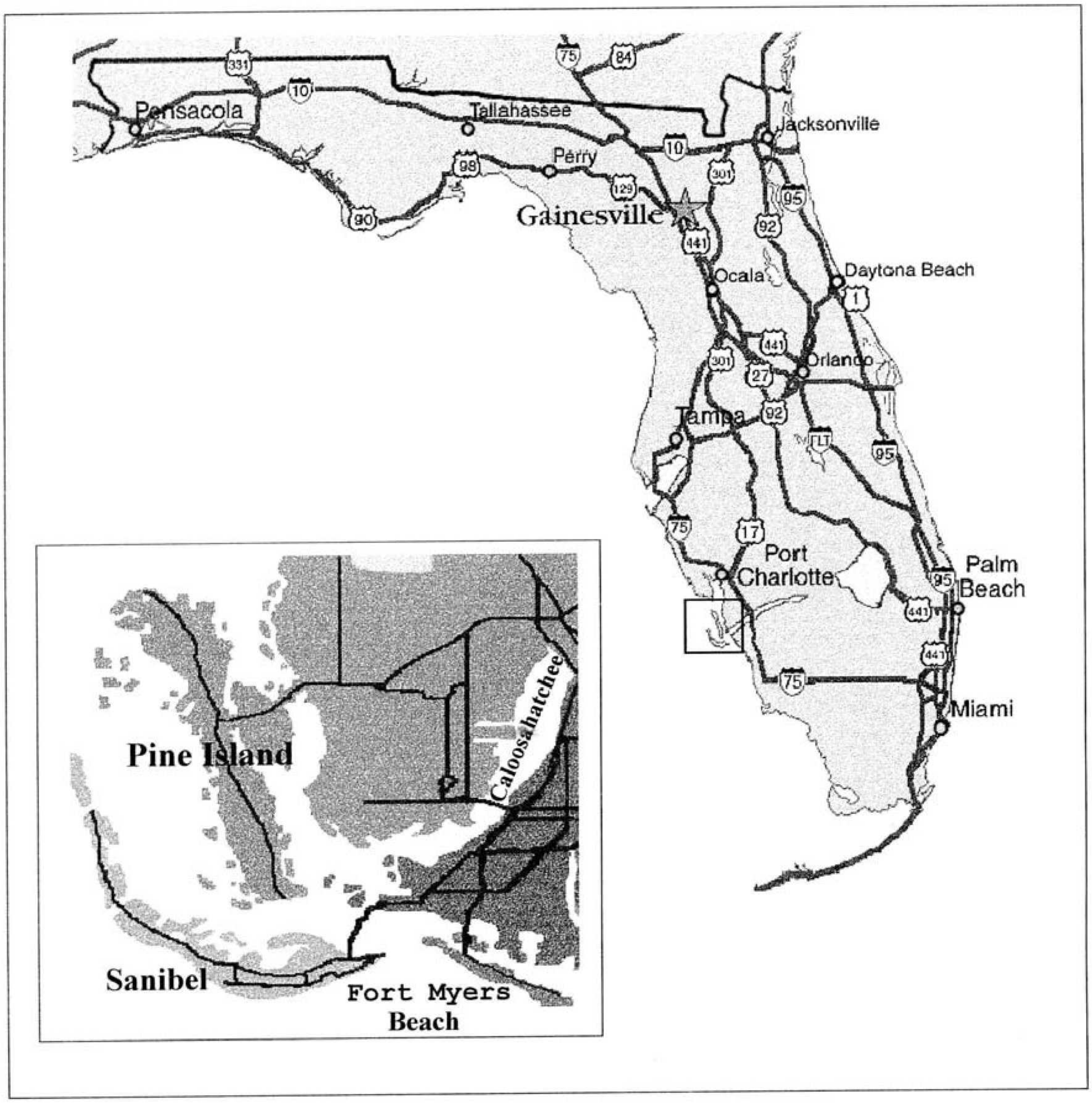


Fig. 1. Pine Island, Florida.

models are used. Most models for whiteflies however generally have been for single resource (crop) systems (von Arx et al. 1983, Baumgärtner et al. 1986, Baumgärtner and Yano 1990), although recently, a model for a regional (multicrop) system, the Imperial Valley California, was described (Wilhoit et al. 1994). There is a definite need for greater effort in this area.

The objectives of this study were 2-fold. We studied the dynamics of *B. argentifolii* (here referred to as the whitefly) in a heterogeneous cropping system with spatiotemporal variation in host plants. In addition, we demonstrated the appropriateness of a spatially explicit age-structured model (Allen et al. 1996, Brewster and Allen 1997) as a tool for studying insect dynamics in such systems. We emphasize that this is not a validation exercise per se, but one that serves to illustrate the utility of these models for studying insect dynamics in temporally and spatially varying crop systems.

Materials and Methods

Study Site. The study was conducted at a mixed-crop organic farm, Pine Island Organics, located on Pine Island, Florida. Pine Island is relatively isolated from the Florida mainland and is the largest island (27.2 by 3.2 km) of its kind on the west coast of Florida (Fig. 1). The cropping area at the farm consisted of 2 fields with 14 and 12 blocks, respectively. Each block was planted with tomato, eggplant, pepper, cucumber, or zucchini, and was separated from other blocks by a sugarcane windbreak. To facilitate insect population sampling and data collection, blocks were further divided into several plots (Fig. 2a).

Sampling and Field Data. During the period September 1992 to January 1993, adult insect samples were taken weekly from each plot by beat-pan sampling. No samples were taken from sugarcane or areas outside the boundaries of the 2 fields. In the beat-pan sampling method, the upper foliage of 5 plants from each plot was shaken vigorously over a black pan containing a thin layer of vegetable oil. Dislodged insects were identified and counted. Also, at 2-wk intervals, visual counts of insects were taken independently by commercial scouts on the same areas covered by the beat-pan sampling.

Parasitism of whiteflies was determined by taking 5 leaves from tomato and eggplant plots every 2 wk, placing them in paper cartons in the laboratory, and observing for emergence of whiteflies and their parasitoids. Percentage of parasitism was calculated by dividing the number of emerged parasitoids (×100) by the sum of the number of emerged parasitoids and whiteflies (McAuslane et al. 1994, Simmons and Minkenberg 1994).

Spatially Explicit Population Model. A spatially explicit population model was used to explore whitefly dynamics at Pine Island Organics. Spatially explicit population models combine a population model with a habitat or resource map that describes the structure (composition and spatial arrangement) of species resources within the habitat. The details of this model are given elsewhere (Allen et al. 1996, Brewster and Allen 1997), but some of its more important characteristics are restated here.

The model is a spatiotemporal age-structured Nicholsonian model (Nicholson and Bailey 1935) that uses integrodifference equations to simultaneously carry out dispersal and reproduction (Kot and Schaffer 1986, Kot 1989, Murray 1989, Andersen 1991, Hastings and Higgins 1994, Neubert et al. 1995, Kot et al. 1996). Unlike many previous studies that used 1-dimensional integrodifference equations, the spatial system in this case is 2-dimensional, so that the integrodifference equations for a simple prey–predator system with no population age-structure are

$$
\begin{aligned}
Y_{t+1}(l, m) &= \int_v \int_u K_Y(l - u, m - v) \\
&\qquad \times f[Y_t(u, v), Z_t(u, v)]\, du\, dv \\
Z_{t+1}(l, m) &= \int_v \int_u K_Z(l - u, m - v) \\
&\qquad \times g[Y_t(u, v), Z_t(u, v)]\, du\, dv \quad (1)
\end{aligned}
$$

where Y_t and Z_t are the prey and predator in generation t, and f and g are their respective interaction functions that are general and can be any of a number of Nicholsonian type interactions (e.g., Nicholson and Bailey 1935, Hassell and Varley 1969, Beddington et al. 1975) or surrogates (e.g., Kot 1989). K_Y and K_Z are redistribution (dispersal) functions for prey and predator so that $K(l - u, m - v)$ gives the probability of individuals moving from point u,v to point l,m in the spatial system. Within a time step in the model, each K is convolved separately with the respective interaction function over space creating a density surface of redistributed individuals. The convolutions are solved efficiently by taking 2-dimensional Fast Fourier transforms of the dispersal and interaction functions separately, multiplying them, and inverting the results back to the spatial domain with the inverse Fast Fourier transform. This is computationally more efficient than solving the integrals for each point in the spatial system.

Several modifications must be made to equation 1 that would allow this model to be used to explore whitefly dynamics at Pine Island Organics. First, for simulating the system, space is considered discrete and is represented by mosaic of discrete units or a grid. Double summations therefore replace the double integrals. In addition, the natural enemy complex of the whitefly is modeled as a single generic natural enemy, and each population is given 3 age-classes (egg, immature, adult) with the individuals in each age having distinct survival probabilities (S) and partial development ($1 - D$) at each time step (Brewster and Allen 1997). These modifications lead to

$$
\begin{aligned}
Y1_{t+1} &= R_t + S_{Y1}(1 - D_{Y1})Y1_t \\
Y2_{t+1} &= S_{Y1}D_{Y1}Y1_t + S_{Y2}(1 - D_{Y2})Y2_t\exp(-aP_t) \\
Y3_{t+1} &= S_{Y2}D_{Y2}Y2_t\exp(-aP_t) + S_{Y3}Y3_t \\
Z1_{t+1} &= Y2_t[1 - \exp(-aP_t)] + S_{Z1}(1 - D_{Z1})Z1_t \\
Z2_{t+1} &= S_{Z1}D_{Z1}Z1_t + S_{Z2}(1 - D_{Z2})Z2_t \\
Z3_{t+1} &= S_{Z2}D_{Z2}Z2_t + S_{Z3}Z3_t \qquad (2)
\end{aligned}
$$

where

$$R_t(l, m) = \sum_{u=1}^{n} \sum_{v=1}^{n} K_Y(l - u, m - v) f[Y3_t(u, v)]$$

(redistributed host reproduction)

$$P_t(l, m) = \sum_{u=1}^{n} \sum_{v=1}^{n} K_Z(l - u, m - v) Z3_t(u, v)$$

(redistributed natural enemy).

Ys and Zs are now spatial density $N \times N$ matrices for the whitefly and natural enemy, respectively, and the convolutions are solved with discrete Fast Fourier transforms. State variables, parameters, and functions used in the model are outlined in Table 1.

Reproductive and Attack Functions. A density-dependent Ricker function (Ricker 1954)

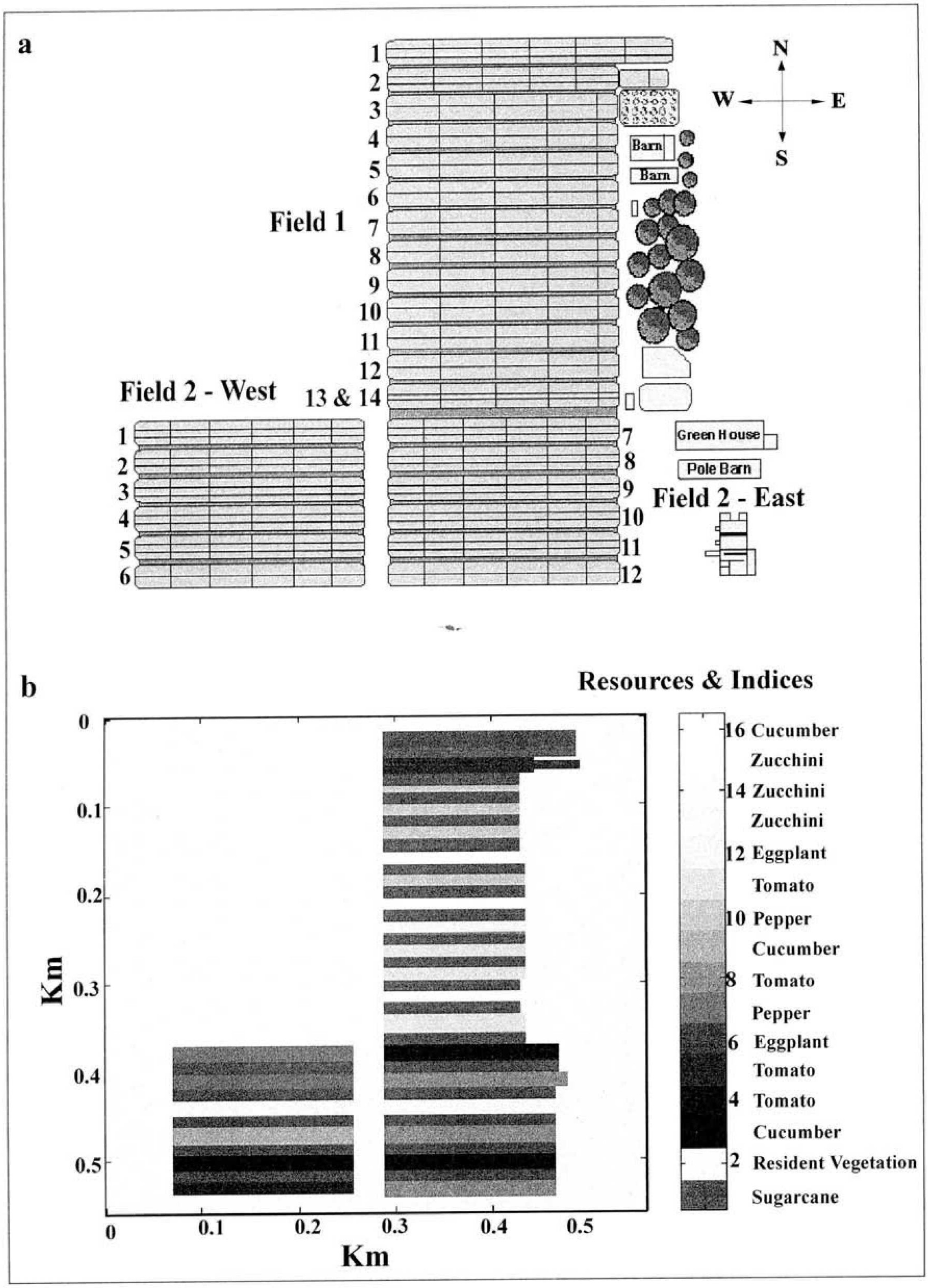


Fig. 2. Pine Island Organics. (a) Scaled map of the farm; (b) Original resource map (*X*) used in simulations.

Table 1. State variables, parameters and functions in the spatiotemporal whitefly model

Variable, parameters and functions	Description
$Y1$, $Y2$, $Y3$	Spatial matrices of whitefly egg, immature, and adult densities
S_{Y1}, S_{Y2}, S_{Y3}	Whitefly egg, immature, and adult survival probabilities
D_{Y1}, D_{Y2}	Whitefly egg and immature development probabilities
$f(Y3)$	Whitefly reproductive function (density-dependent Ricker function)
$exp(r)$	Reproductive egg production per female per period
K_Y	Whitefly dispersal function
R_t	Spatial matrix of redistributed whitefly reproduction
$Z1$, $Z2$, $Z3$	Spatial matrices of natural enemy egg, immature and adult densities
S_Z, D_Z	Natural enemy age-class survival and development probabilities
a, Q, m	Natural enemy searching efficiency, quest constant, and mutual interference constant
K_Z	Natural enemy dispersal function
P_t	Spatial matrix of redistributed natural enemy
σ_u, σ_v	Standard deviation of dispersal in the u- and v-directions
X	Spatial matrix of whitefly resources (resource map)

$$f(Y3_t) = Y3_t \exp\left[r\left(1 - \frac{Y3_t}{k}\right)\right] \qquad (3)$$

was chosen as the reproductive function of the whitefly. Natural enemy attack was assumed to be Nicholsonian with the proportion of whiteflies that survive attack equal to *exp(-aP)*, where *P* is dispersed adult natural enemy. The searching efficiency of the generic natural enemy (a) was a function of their density and was given by $a = QP_t^{-m}$ (Hassell and Varley 1969, Hassell and May 1973). The importance of mutual interference in natural enemy interactions was alluded to by Hassell and May (1973) who reported m values between 0.28 and 0.69 from laboratory studies and between 0.48 and 0.96 from field studies. These ranges were used in determining starting values for m in this study.

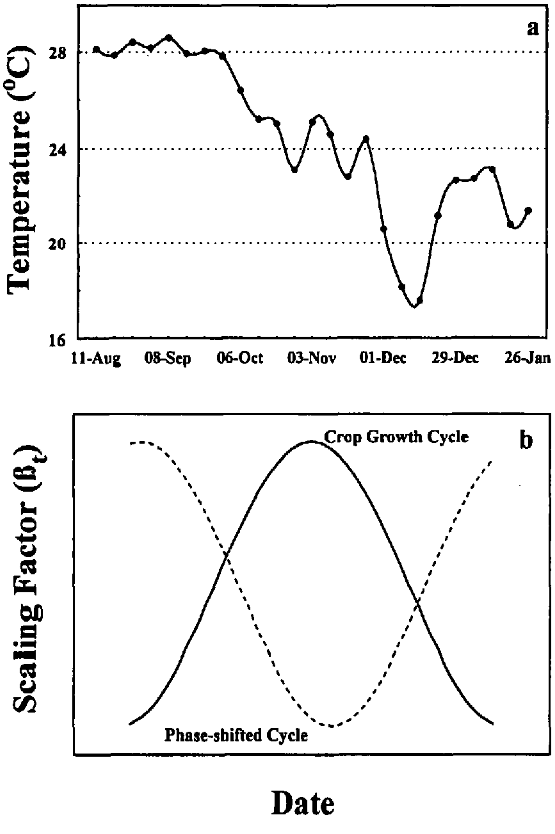


Fig. 3. Forcing functions (driving variables) for model parameters at Pine Island Organics. (a) Weekly average temperature cycle; (b) example of a crop cycle (———), and the same cycle 180° out-of-phase and shifted slightly (----) that forces the standard deviation of dispersal.

Whitefly Resource Map. The spatially explicit nature of the model comes from the inclusion of a resource or crop map that describes the structure of whitefly resources at Pine Island Organics. This map is not given explicitly in the model, but is a spatial $N \times N$ matrix (X) whose entries are integers that serve as indices to rows in a lookup table containing insect parameters for each resource in the system.

The resource map for the whitefly at Pine Island Organics was constructed by taking measurements of the cropping area and other related features, and recording the spatial arrangement of resources within fields. This information was used to create a scaled-map of the farm (Fig. 2a) onto which a 128 × 128 grid was superimposed. Whitefly resources at each location in the system were then indexed to the respective cells in the grid. The final resource map shown as a color-coded image in Fig. 2b has an extent of ≈31 ha with each grid cell ≈18.92 m^2 (4.35 by 4.35 m).

In the assignment of resource indices to crops, areas that did not contain any of the 6 main resources (tomato, eggplant, cucumber, zucchini, pepper, and sugarcane) were assumed to contain resident vegetation. Resource indices were assigned as follows: if a crop was planted in different blocks on the same date, the same resource index was assigned to these blocks and to the respective cells in the resource spatial matrix. However, if a crop was planted in different blocks on different dates, these were given different resource indices. The final resource map therefore contains 16 rather than 7 resource indices (Fig. 2b). Tomato for example, was assigned resource indices 4, 5, 8, and 11 because of different planting dates. Similarly, eggplant was assigned resource in-

Table 2. Parameter values used for *B. argentifolii* and the natural enemy complex in simulations with the model

Resources	Model parameters											
	r	S_{Y1}	S_{Y2}	S_{Y3}	D_{Y1}	D_{Y2}	Q	m	S_{ZS}	D_{ZS}	σ_u[a]	σ_v[a]
Tomato	4.4	0.90	0.60	0.30	1.0	0.60	0.08	0.35	0.50	0.50	2.0	1.0
Eggplant	4.4	0.90	0.88	0.30	1.0	0.60	0.08	0.35	0.50	0.50	2.0	1.0
Cucumber	3.8	0.90	0.50	0.30	1.0	0.54	0.08	0.35	0.50	0.50	2.0	1.0
Zucchini	3.8	0.90	0.50	0.30	1.0	0.54	0.08	0.35	0.50	0.50	2.0	1.0
Pepper	3.3	0.90	0.10	0.30	1.0	0.10	0.08	0.35	0.50	0.50	3.0	1.5
RV	4.0	0.90	0.80	0.30	1.0	0.40	0.25	0.35	0.50	0.50	6.0	3.0
Sugarcane	1.0	0.20	0.01	0.30	1.0	0.01	0.02	0.35	0.50	0.50	6.0	3.0

Values are based on a weekly time step and average temperature of 25°C. Y and Z in parameter subscript represent whitefly and natural enemy, respectively. Sources for whitefly parameters were Coudriet et al. (1985), Costa et al. (1991), Powell and Bellows (1992a, b), Wilhoit et al. (1994), Salas and Mendoza (1995), van Giessen et al. (1995), Yee and Toscano (1996), Tsai and Wang (1996). RV, resident vegetation.

[a] Values are in units of grid cells. u and v represent east-west and north-south directions, respectively. The standard deviation of dispersal for the natural enemy was assumed to be half that of the whitefly.

dices 6 and 12; cucumber, 3, 9, and 16; zucchini, 13, 14, and 15; and pepper, resource indices 7 and 10. Sugarcane and resident vegetation were assigned resource indices 1 and 2, respectively. The matrix (map) of resources was saved in ASCII file format and read by the simulation package, MATLAB (MathWorks 1994) into the spatial resource matrix, X, at the start of each simulation.

Insect Dispersal. Spatial movement of the whitefly and natural enemy was specified with dispersal density functions or redistribution kernels (K). The dispersal process was accomplished by summing the movement of individuals into each point from all other points in the spatial system at each time step. In the case of the whitefly, an integrodifference equation was used to couple dispersal with

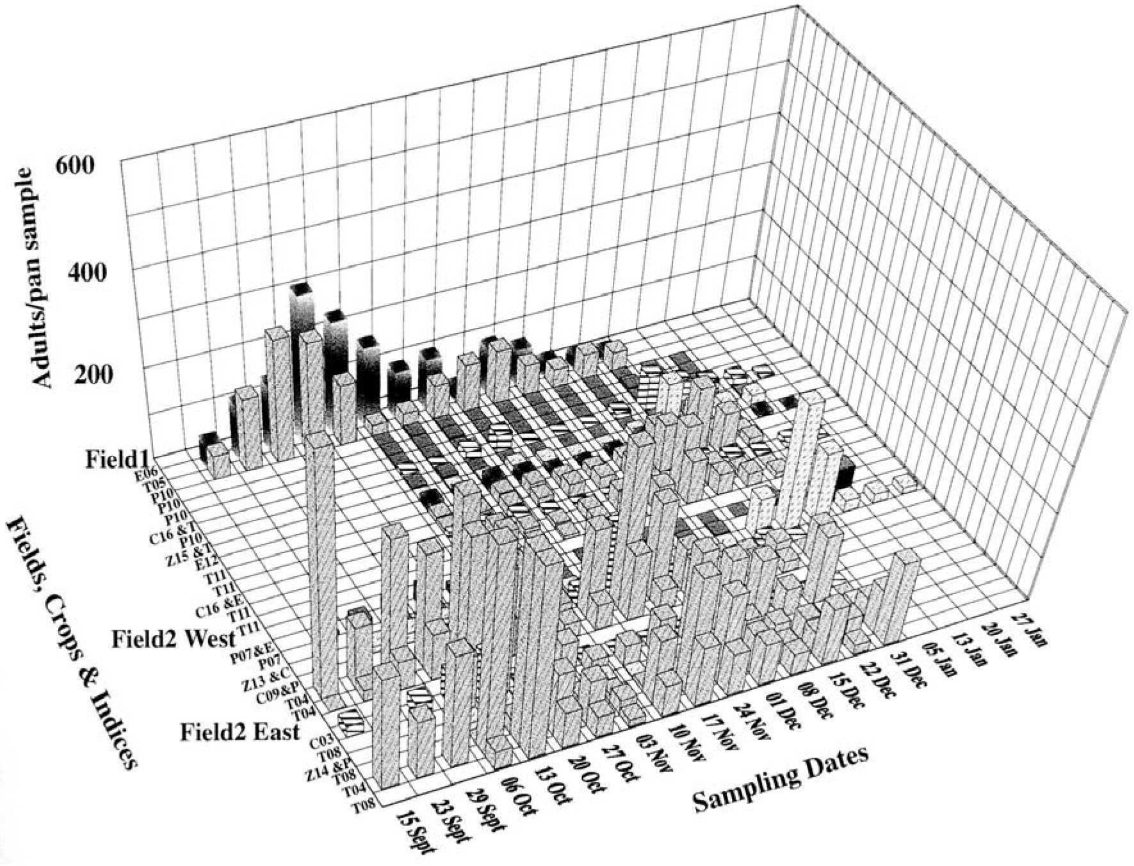


Fig. 4. Adult whiteflies collected by beat-pan sampling on various crops at Pine Island Organics. Letters and numbers in the fields, crops, and indices axis represent crop types and indices, respectively. For example, C16&T is cucumber resource 16 followed by tomato; E06 is eggplant, resource 6; Z, zucchini and P, pepper.

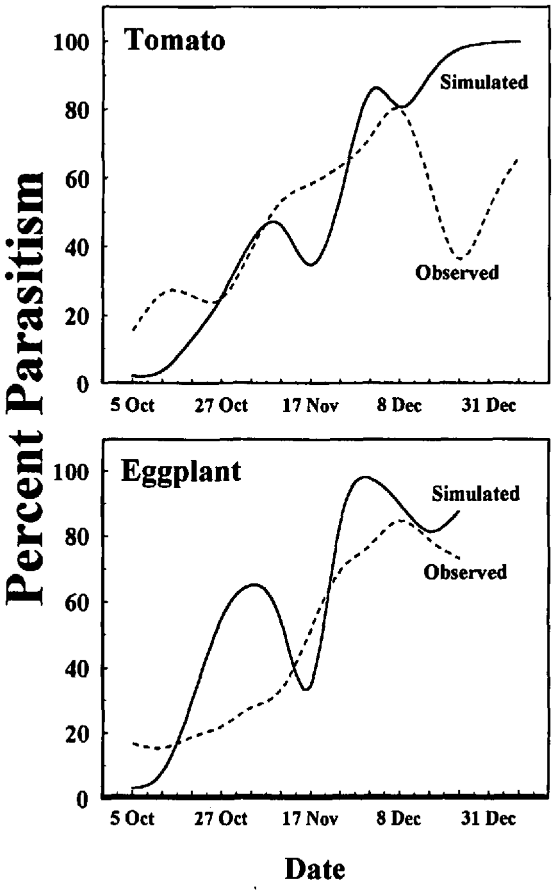


Fig. 5. Observed (----) and simulated (————) percentage parasitism of whitefly on tomato and eggplant at Pine Island Organics.

reproduction, and another integrodifference equation was used to redistribute adult natural enemies throughout the spatial system. We assumed that all dispersal was local and random and that no long-range migration occurred during the study period. The effects of wind on movement were therefore ignored. We also assumed that spatial movement to the east or west (u-direction) was greater than movement to the north or south (v-direction). These assumptions were justified because of the greater dimension of the blocks in the east-west direction, and the sugarcane barriers to movement in the north-south direction (Fig. 2). A direction-biased 2-dimensional normal density function

$$K(l, m, u, v) = \frac{1}{2\pi\sigma_u\sigma_v}\exp\left[-\frac{1}{2}\left(\frac{[l-u]^2}{\sigma_u^2} + \frac{[m-v]^2}{\sigma_v^2}\right)\right], \quad \sigma_u \neq \sigma_v \tag{4}$$

was therefore chosen as the redistribution function for both species. Because the standard deviation of dispersal per time step, σ, depends on the insect species and characteristics of the host resource at each location, it is expected to be a time-varying parameter that reaches a maximum near host plant senescence.

Model Parameters and Simulations. Estimates of parameter values for the whitefly were obtained from the literature and were mainly for female longevity, egg production, and egg and immature survival and development. Data on carrying capacity and spatial movement were limited and not crop specific. Based on the sampling data and whitefly infestation levels observed, crops were ranked and the ranking used to derive estimates for unknown parameters. Although the independently collected visual count data taken by commercial scouts were not statistically independent from the other sampling data because both were collected during the same periods, these data were nevertheless used to assist in the derivation of estimates for natural enemy parameters.

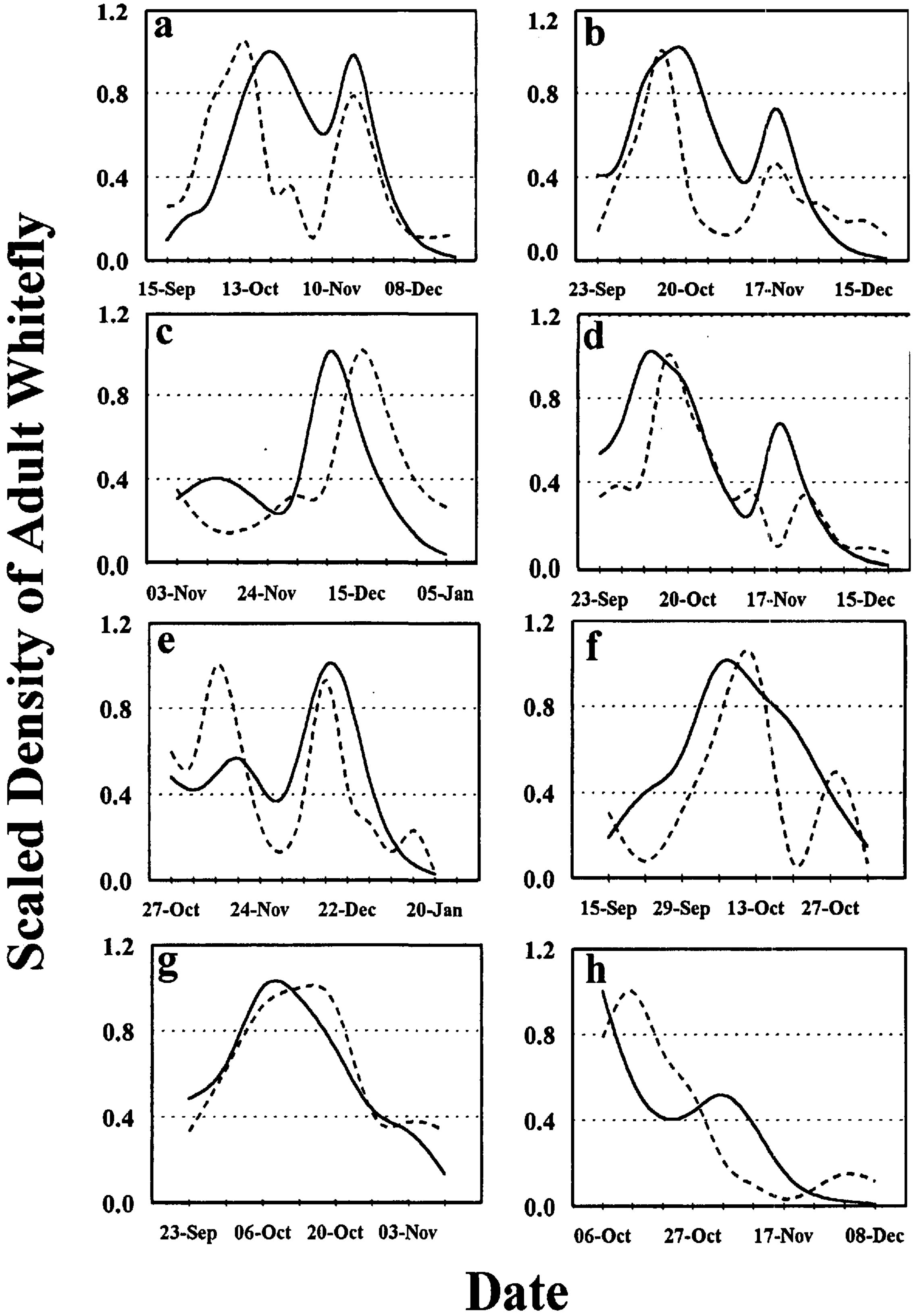
Temperature and crop growth were the driving or forcing variables on parameters in the model. Temperature thresholds of 10°C (lower) and 32.2°C (upper) have been quoted for whiteflies (Butler et al. 1983, Zalom et al. 1985). Within these limits, rate processes often tend to vary linearly with temperature (Worner 1992). Because average weekly temperature at Pine Island Organics for the period of study fell well within these established thresholds (Fig. 3a), we assumed rates were linear with temperature.

Parameters were also forced with crop growth by multiplying by a scaling factor, β_t calculated from a cosine wave

$$\beta_t = 1 + \delta \cos\left[\frac{2\pi(ST - PT)}{CP}\right] \tag{5}$$

that represented the growth cycle of the crop (Fig. 3b). In equation 5, δ ($0 < \delta > 1$) is the amplitude of the crop cycle, ST is simulation time, PT is time at peak crop growth, and CP, the growth period of the crop. Dispersal was expected to be at a maximum near crop senescence, and therefore the standard deviation of dispersal was forced by a cycle that was ≈180° out-of-phase with the crop cycle and that was also shifted to account for any lag in response time for dispersal as crop growth began to decline (Fig. 3b).

Simulations ran for 25 wk on a weekly time step. Initial population densities are always difficult to determine. Because we were interested solely in the qualitative behavior of the model and not in its ability to predict absolute whitefly densities, it was not necessary to start the simulations with actual initial densities. We therefore seeded each cell in the spatial grid with low (0–1) random densities of individuals in all whitefly age classes. An examination of the sampling data revealed that natural enemy densities at the start of sampling were much lower than those of the whitefly. We therefore seeded each cell in the natural enemy spatial matrices ($Z1$, $Z2$, $Z3$) randomly as we did for the


Scaled Density of Adult Whitefly
Date
a
1.2
0.8
0.4
0.0
15-Sep
13-Oct
10-Nov
08-Dec
b
1.2
0.8
0.4
0.0
23-Sep
20-Oct
17-Nov
15-Dec
c
1.2
0.8
0.4
0.0
03-Nov
24-Nov
15-Dec
05-Jan
d
1.2
0.8
0.4
0.0
23-Sep
20-Oct
17-Nov
15-Dec
e
1.2
0.8
0.4
0.0
27-Oct
24-Nov
22-Dec
20-Jan
f
1.2
0.8
0.4
0.0
15-Sep
29-Sep
13-Oct
27-Oct
g
1.2
0.8
0.4
0.0
23-Sep
06-Oct
20-Oct
03-Nov
h
1.2
0.8
0.4
0.0
06-Oct
27-Oct
17-Nov
08-Dec

whitefly but multiplied these densities by 0.1, 0.01, 0.001 times that for the whitefly, respectively. These density matrices were saved and reused to initialize populations at the start of simulation. In addition, we used the first 3 wk of the simulation period to allow the whitefly population to build before the natural enemy was introduced. During this period, we assumed that the resource map contained resources 1 and 2 (sugarcane and resident vegetation) only and that the natural enemy was absent. The full resource map and natural enemy were introduced into the simulation after this 3-wk initialization period. Table 2 gives the parameter values used to generate the simulation output that qualitatively matched the adult whitefly dynamics observed from the sampling data.

Comparing Model Output and Sampling Data. The sampling data were used to standardize the output of the model so that the model could be used to explore whitefly dynamics at Pine Island Organics. To determine the degree to which the sampling data and simulation results agreed, visual comparisons were made by scaling each data set to (0–1) and plotting the results on the same graph. Correlation analysis were used to quantify the visual comparisons and to compare simulated whitefly adult density maps with observed density maps. These analysis were performed using the XCORR and CORR2 functions available in the signal processing and image processing toolboxes in MATLAB (MathWorks 1994). XCORR estimates the cross-correlation coefficients between 2 equal length data sequences and also returns the correlation coefficients between the 2 sequences at various lags (Krauss et al. 1993, Stearns and David 1996). CORR2 computes the 2-dimensional correlation coefficient between 2 matrices (Thompson and Shure 1995). In the case of 2 equal length vectors, the output is a single value equivalent to the value returned by XCORR at zero lag. Correlations and significant levels for most comparisons were verified in SigmaStat (Kuo et al. 1992).

Simulation Experiments. A series of simulation experiments were conducted to explore whitefly dynamics at Pine Island Organics. One set of experiments for example was used to help explain the differences in whitefly population trends observed on early and late planted tomato. We first determined whether the trends were caused by the degree of heterogeneity within the crop system. We then replaced all crops, except sugarcane and resident vegetation, with tomato resource 4 (T04) and simulated the system. We also studied the effects of temperature on whitefly population trends by comparing whitefly dynamics on T04 with the declining temperature cycle given in Fig. 3a and these dynamics when a constant average temperature for the period of simulation was assumed. Another set of experiments compared species dynamics in simulations that used the original whitefly resource map (Fig. 2b) with those that used experimental resource maps in which the structure of the system was altered. In one experimental map, similar crop types were grouped within the same blocks so that field 1 for example contained the solanaceous crops and field 2, the cucurbits. In a variation of this map, the sugarcane barriers between blocks were removed. In another experi-

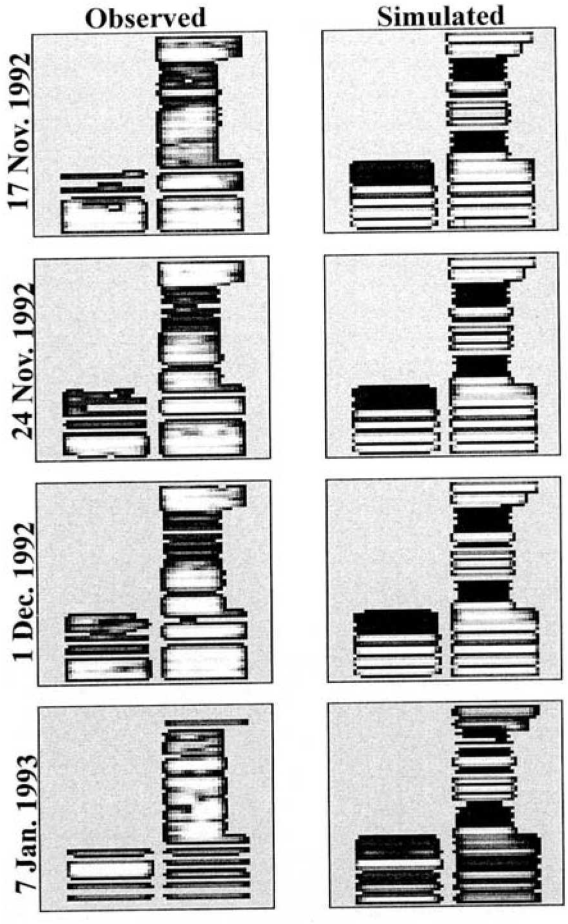


Fig. 7. Observed and simulated adult whitefly density maps at Pine Island Organics on 4 dates. The 2-dimensional correlation coefficient for each comparison was >0.70. Lighter areas indicate higher whitefly densities.

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Fig. 6. Scaled beat-pan sample data (----) and scaled simulation results (———) for adult whiteflies at Pine Island Organics. (a) tomato, resource 4 ($r = 0.85$, $P < 0.001$); (b) tomato, resource 5 ($r = 0.90$, $P < 0.001$); (c) tomato, resource 11 ($r = 0.82$, $P < 0.01$); (d) eggplant, resource 6 ($r = 0.92$, $P < 0.001$); (e) eggplant, resource 12 ($r = 0.89$, $P < 0.001$); (f) cucumber, resource 3 ($r = 0.88$, $P < 0.005$); (g) zucchini, resource 13 ($r = 0.98$, $P < 0.001$); (h) pepper, resource 7 ($r = 0.88$, $P < 0.001$).

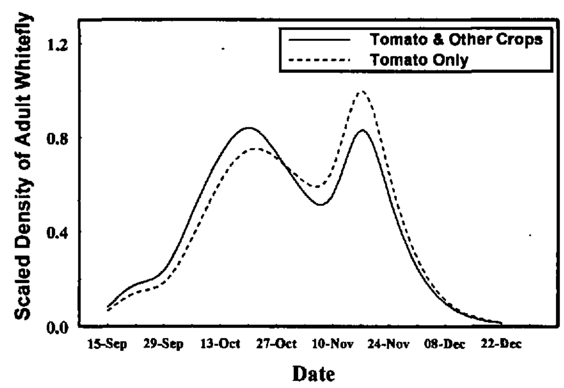

Fig. 8. Comparison of adult whitefly dynamics on tomato resource 4 (T04) in a simulation that used a resource map that contained T04 only and one that used the original resource map that contained T04 and other crops.

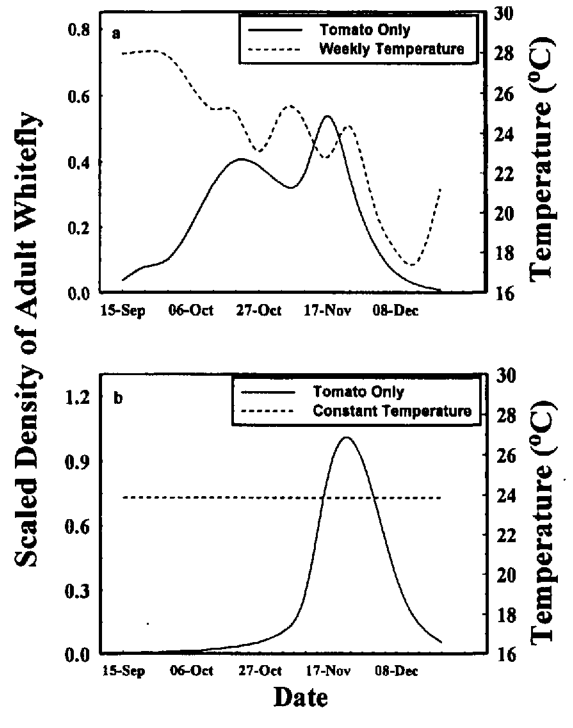

Fig. 9. Comparison of adult whitefly dynamics on tomato resource 4 (T04) in a simulation that used a resource map that contained T04 only. (a) Simulation was conducted under a declining temperature regime; (b) simulation was conducted under an average constant temperature regime for the period of crop growth.

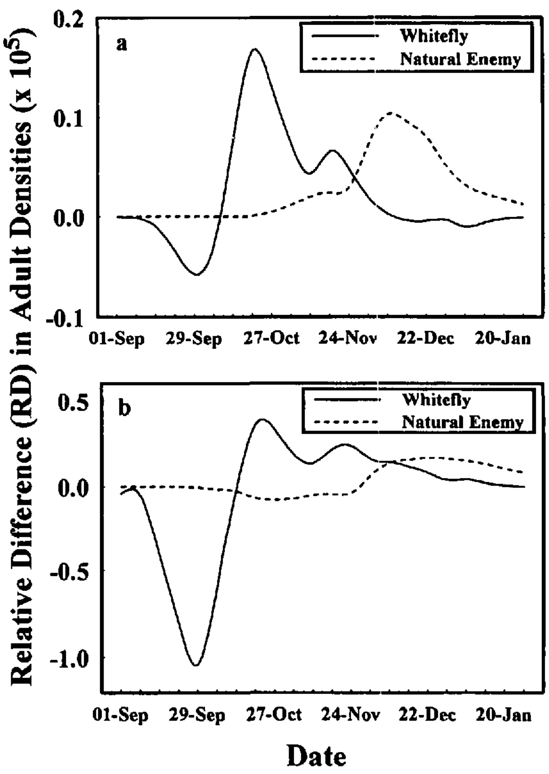

Fig. 10. Relative differences (RDs) in adult densities. (a) RDs between densities with the original resource map and an experimental map with similar resources grouped; (b) RDs in densities with the original resource map and an experimental map with the sugarcane barriers removed.

mental map, the arrangement of the resources in the original map was retained but the sugarcane barriers between blocks were removed. Comparisons were made by estimating what we called the relative differences in adult densities in simulations with these maps. At each time step during simulations, the norms of adult whitefly density ($Y3$) and adult natural enemy density ($Z3$) were computed using the NORM procedure in MATLAB (MathWorks 1994). Relative differences were computed as the differences in adult densities in simulations that used the original map and those that used the experimental map, so that

$$RD_{Y3_t} = \|OM_{Y3_t}\| - \|EM_{Y3_t}\|$$

$$RD_{Z3_t} = \|OM_{Z3_t}\| - \|EM_{Z3_t}\| \qquad (6)$$

with

$OM_{Y3_t \text{ or } Z3_t}$ = adult density with the original map,

$EM_{Y3_t \text{ or } Z3_t}$ = adult density with an experimental map

where $\|\cdot\|$ is the Frobenius norm (a measure of distance from zero) of the adult density matrix, and $Y3_t$ and $Z3_t$ are whitefly and natural enemy adults at time t. Relative differences of zero indicated no differences in adult densities between the maps. Positive relative differences meant that the original map produced relatively higher densities compared with the experimental map, and negative relative differences meant relatively lower densities compared with the experimental map. Because the removal of the sugarcane barriers allowed both species to move freely between blocks, a normal density dispersal function with no directional bias

$$K(l, m, u, v) = \frac{1}{2\pi\sigma^2}\exp\left[-\left(\frac{[l-u]^2+[m-v]^2}{2\sigma^2}\right)\right] \tag{7}$$

was used in these simulations as opposed to equation 4.

Results and Discussion

Analysis of the beat-pan sampling data taken at Pine Island Organics suggested that tomato and eggplant were the most attractive whitefly host plants followed by cucumber, zucchini, and pepper (Fig. 4). Whitefly numbers reached 529 adults per pan sample on tomato and 317 adults per pan sample on eggplant. Maxima of 160 and 35 adults per pan sample were obtained on cucumber and zucchini, respectively. On pepper, the highest number of whiteflies observed was 41 adults. Pepper was considered a poorer host than zucchini because overall whitefly numbers were lower. Sugarcane and resident vegetation were not sampled, but sugarcane was not expected to be a good whitefly host. Some resident vegetation however is known to harbor whiteflies and natural enemies (Evans 1993). Schuster et al. (1992) for example observed in west-central Florida that although low numbers of adult whiteflies normally were found on surrounding weeds, this resource tended to act as a reservoir for these insects particularly after surrounding crops had been harvested.

Natural enemies were the main agent of whitefly control at the farm because no conventional pesticides were applied. Florida is renowned for its large fauna of whitefly natural enemies (Evans 1993, Dean 1994) and under situations of limited pesticide use (as at Pine Island Organics) parasitism plays a very important role in limiting whitefly population increases. For example, in noninsecticide treated peanut fields in north-central Florida, up to 100% parasitism of whiteflies was observed (McAuslane et al. 1993, 1994). Parasitism of whiteflies on tomato and eggplant at Pine Island Organics reached as high as 80% during our study (Fig. 5).

A reasonable match was achieved between adult whitefly population trends in the sampling data and those generated by the simulation (Fig. 6) and between the adult density maps (Fig. 7). Each plot in Fig. 6 presents the collective data (after scaling) from 1 or more blocks so that Fig. 6a for example shows data obtained from all blocks containing resource 4, tomato (T04). Although the matches between the data sets were quite reasonable, cross-correlation analysis showed that in a few cases these data sets lagged each other by as much as 2 wk (e.g., Fig. 6 a and d). We feel this resulted from the manner in which crop growth was represented (equation 5; Fig. 3b). It was essential to have good agreement between the output of the model and field data (at least qualitatively) so that the model could be used to examine other scenarios that were likely to affect whitefly dynamics at the farm.

The simulations were sensitive to parameters related to the natural enemy. In particular, we found that the initial density of the natural enemy relative to the whitefly, the level of mutual interference (m) between natural enemy individuals, and the attack parameter (Q), affected the final whitefly dynamics in the system. Simulated percentage of parasitism for example fluctuated unlike observed parasitism although both showed increases (Fig. 5). Differences between the 2, we feel, are likely caused by many unknown aspects of parasite behavior and the fact that one generic natural enemy was used to represent what is actually a group of several species in the field. This might be considered by some to be a significant drawback of the model. However, at least 1 study has shown the composition of a natural enemy complex to be less important than the average searching efficiency of species within the complex (O'Neil and Stimac 1988).

Whitefly numbers on tomato planted before late September showed 2 distinct peaks (Fig. 6 a and b). The 1st peak occurred in mid-October, and the 2nd peak occurred in mid- to late November. When tomato was planted in late October, however, adult numbers were generally lower and only 1 peak, in mid- to late December, was observed (Fig. 6c). Whitefly populations on eggplant showed the same general trends as those on tomato (Fig. 6d). In Florida, Dean (1994) observed that whitefly population numbers increased exponentially on spring tomatoes, but fluctuated on fall tomatoes in a manner similar to that observed in this study. We therefore suspected that population trends on early tomato were the result of the interaction of temperature and planting date. We tested this hypothesis with the model in a series of simulation experiments with tomato, resource 4 (T04). The 1st experiment to determine the effects of the heterogeneity of the crop system indicated that no differences in population trends resulted when the system contained only T04 or when this resource was combined with the other resources grown at the farm (Fig. 8). It seemed unlikely therefore that the population peaks resulted from the presence of the other resources in the system. We also explored the effects of temperature and found that changing from a declining temperature regime to an average constant temperature regime caused the early population peak to disappear (Fig. 9 a and b.). This suggested that temperature played a key role in these trends.

Environmental temperature is considered an important determinant of whitefly population dynamics (Zalom et al. 1985; Byrne and Bellows 1991; Powell and Bellows 1992a, b). For example, in simulations of this pest in cotton, von Arx et al. (1983) found that temperature and the quality of the host plants were the most important factors controlling dynamics. At Pine Island Organics, whiteflies infesting crops planted in September were exposed initially to higher average temperatures (Fig. 3a) that most likely resulted in shorter generation times and increased female fecundity. However, whiteflies infesting crops planted in October were exposed to lower average temperatures and therefore had longer generation times and lower female fecundity.

The simulation experiments that examined the effects of changes in resource structure on whitefly dynamics served to demonstrate an inherent advantage of spatially explicit models as tools for rapidly exploring alternative habitat structures. Grouping the solanaceous resources and cucurbits in separate regions lowered the densities of both the whitefly and natural enemy relative to the original arrangement where crop types were dispersed (relative differences were positive) (Fig. 10a). This however was only so when the sugarcane barriers between blocks were maintained in both systems. The dispersed spatial arrangement provided the whitefly with varying resources that were in close proximity, whereas the grouping of similar crop types created gaps in the spatial resources at harvest and thus tended to lower overall whitefly densities. Removal of the sugarcane barriers between blocks under any arrangement improved the ability of the whitefly to move freely between resources and therefore resulted in relatively higher adult densities compared with systems that retained the barriers (Fig. 10b).

This small study on the whitefly *B. argentifolii* at Pine Island Organics has served to highlight some of the relationships between insect population dynamics and host plant spatiotemporal variations in heterogeneous systems. Whitefly dynamics are affected by the spatiotemporal arrangement of host plants and as suggested by Hirano et al. (1993), such variations may be more important than climatic factors such as temperature in determining whitefly population fluctuations. Hirano et al. (1993) pointed out that continuous cultivation of suitable whitefly host plants in time and space results in serious damage by these insects to crops that are planted later and that because these late season crops are likely to experience heavier whitefly damage earlier in their growth, they support fewer whiteflies compared with earlier planted crops. This could explain the lower densities of whiteflies on our tomato resource 11 (T11 in Fig. 4 and 6c) that was planted in late October compared with the tomato, resource 4 (T04 in Fig. 4 and 6a) that was planted in early September. Our analysis of whitefly dynamics with the model however suggested that temperature also plays an important role in these dynamics.

In a relatively small system like Pine Island Organics, it is fairly easy to test the effects of host plant arrangements on whitefly dynamics with field experiments. However, spatiotemporal models like the one used in this study open the door to simulations of crop systems of much larger extent and suggests that we could design whole crop regions to minimize pest populations.

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References Cited

Allen, J. C., C. C. Brewster, J. F. Paris, D. G. Riley, and C. G. Summers. 1996. Spatiotemporal modeling of whitefly dynamics in a regional cropping system using satellite data, pp. 111–124. *In* D. Gerling and R. T. Mayer [eds.], *Bemisia* 1995: taxonomy, biology, damage and management. Intercept, Andover, U.K.

Andersen, M. 1991. Properties of some density-dependent integrodifference equation models. Math. Bio-Sci. 104: 135–157.

Baumgärtner, J. and E. Yano. 1990. Whitefly population dynamics and modelling, pp. 123–146. *In* D. Gerling [ed.], Whiteflies: their bionomics pest status and management. Intercept, Andover, U.K.

Baumgärtner, J., V. Delucchi, R. Arx, and D. Rubli. 1986. Whitefly (*Bemisia tabaci* Genn., Stern.: Aleyrodidae) infestation patterns as influenced by cotton, weather and *Heliothis*: hypotheses testing by using simulation models. Agric. Ecosyst. Environ. 17: 49–59.

Beddington, J. R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. J. Anim. Ecol. 44: 331–340.

Bellows, T. S., T. M. Perring, R. J. Gill, and D. H. Headrick. 1994. Description of a species of *Bemisia* (Homoptera: Aleyrodidae). Ann. Entomol. Soc. Am. 87: 195–206.

Blackmer, J. L., and D. N. Byrne. 1993a. Flight behavior of *Bemisia tabaci* in a vertical flight chamber: effect of time of day, sex, age and host quality. Physiol. Entomol. 18: 223–232.

1993b. Environmental and physiological factors influencing phototactic flight of *Bemisia tabaci*. Physiol. Entomol. 18: 336–342.

Blua, M. J, H. A. Yoshida, and N. C. Toscano. 1995. Oviposition preference of two *Bemisia* species (Homoptera: Aleyrodidae). Environ. Entomol. 24: 88–93.

Brewster, C. C., and J. C. Allen. 1997. Spatiotemporal model for studying insect dynamics in large-scale cropping systems. Environ. Entomol. 26: 473–482.

Brown, J. K., D. R. Frochlich, and R. C. Rosell. 1995. The sweetpotato or silverleaf whiteflies: Biotypes of *Bemisia tabaci* or a species complex ? Annu. Rev. Entomol. 40: 511–534.

Byrne, D. N., and T. S. Bellows. 1991. Whitefly biology. Annu. Rev. Entomol. 36: 431–57.

Byrne, D. N., and M. A. Houck. 1990. Morphometric identification of wing polymorphism in *Bemisia tabaci* (Homoptera: Aleyrodidae). Ann. Entomol. Soc. Am. 83: 487–493.

Byrne, D. N., and W. B. Miller. 1990. Carbohydrate and amino acid composition of phloem sap and honeydew produced by *Bemisia tabaci*. J. Insect Physiol. 36: 433–439.

Byrne, D. N., T. S. Bellows, and M. P. Parrella. 1990. Whiteflies in agricultural systems, pp. 227–261. *In* D. Gerling [ed.], Whiteflies: their bionomics, pest status and management. Intercept, Andover, U.K.

Byrne, D. N., R. J. Rathman, T. V. Orum, and J. C. Palumbo. 1996. Localized migration and dispersal by the sweetpotato whitefly, *Bemisia tabaci*. Oecologia (Berl.) 105: 320–328.

Butler, G. D., T. J. Henneberry, and T. E. Clayton. 1983. *Bemisia tabaci* (Homoptera: Aleyrodidae): development, oviposition, and longevity in relation to temperature. Ann. Entomol. Soc. Am. 76: 310–313.

Costa, H. S., J. K. Brown, and D. N. Byrne. 1991. Life history traits of the whitefly, *Bemisia tabaci* (Homoptera: Aleyrodidae) on six virus infected or healthy plant species. Environ. Entomol. 20: 1102–1107.

Coudriet, D. L., N. Prabhaker, A. N. Kishaba, and D. E. Meyerdirk. 1985. Variation in development rate on different hosts and overwintering of the sweetpotato whitefly, *Bemisia tabaci* (Homoptera: Aleyrodidae). Environ. Entomol. 14: 516–519.

Dean, D. E. 1994. Predaceous arthropods of the sweetpotato whitefly, *Bemisia tabaci* (Gennadius) on tomatoes in Florida. Ph.D. dissertation, University of Florida, Gainesville, FL.

Evans, G. A. 1993. Systematic studies of new world *Encarsia* species and a survey of the parasitoids of *Bemisia tabaci* in Florida, the Caribbean and Latin America. Ph.D. dissertation, University of Florida, Gainesville, FL.

Hassell, M. P., and R. M. May. 1973. Stability in insect host–parasite models. J. Anim. Ecol. 42: 693–726.

Hassell, M. P., and G. C. Varley. 1969. New inductive population model for insect parasites and its bearing on biological control. Nature (Lond.) 223: 1133–1137.

Hastings, A., and K. Higgins. 1994. Persistence of transients in spatially structured ecological models. Science (Wash. D.C.) 263: 1133–1136.

Hirano, K., E. Budiyanto, and S. Winarni. 1993. Biological characteristics and forecasting outbreaks of the whitefly, *Bemisia tabaci*, a vector of virus diseases in soybean fields. Asian Studies on the Pacific Coast, Food and Fertilizer Technology Center. Technical Bull. 135.

Kot, M. 1989. Diffusion-driven period-doubling bifurcations. BioSystems. 22: 279–287.

Kot, M., and W. M. Schaffer. 1986. Discrete-time growth-dispersal models. Math. BioSci. 80: 109–136.

Kot, M, M.A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecology 77: 2027–2042.

Krauss, T. P., L. Shure, and J. N. Little. 1993. Signal processing toolbox for use with MATLAB. The MathWorks, Natick, MA.

Kring, J. B., D. J. Schuster, J. F. Price, and G. W. Simone. 1991. Sweetpotato whitefly-vectored geminivirus on tomato in Florida. Plant Dis. 75: 1186.

Kuo, J., E. Fox, and S. McDonald. 1992. SigmaStat statistical software for working scientists. User's manual. Jandel Scientific, San Rafael, CA.

MathWorks 1994. MATLAB reference guide. High-performance numeric computation and visualization software, version 4.2c.1. The MathWorks, Natick, MA.

McAuslane, H. J., F. A. Johnson, D. A. Knauft, and D. L. Colvin. 1993. Seasonal abundance and within-plant distribution of *Bemisia tabaci* (Homoptera: Aleyrodidae) in peanuts. Environ. Entomol. 22: 1043–1050.

McAuslane, H. J., F. A. Johnson, and D. A. Knauft. 1994. Population levels and parasitism of *Bemisia tabaci* (Homoptera: Aleyrodidae) on peanut cultivars. Environ. Entomol. 23: 1203–1210.

Murray, J. D. 1989. Mathematical biology. Biomathematics, vol. 19. Springer, Berlin.

Neubert. M. G., M. Kot, and M. A. Lewis. 1995. Dispersal and pattern formation in a discrete-time predator–prey model. Theor. Popul. Biol. 48: 7–43.

Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations. Proc. Zoo. Soc. Lond. 3: 551–598.

O'Neil, R. J., and J. L. Stimac. 1988. Measurement and analysis of arthropod predation on velvetbean caterpillar, *Anticarsia gemmatalis* (Lepidoptera: Noctuidae) in soybeans. Environ. Entomol. 17: 821–826.

Perring, T. M., A. Cooper, and D. J. Kazman. 1992. Identification of the poinsettia strain of *Bemisia tabaci* (Homoptera: Aleyroididae) on broccoli by electrophoresis. J. Econ. Entomol. 85: 1278–1284.

Perring, T. M., A. D. Cooper, R. J. Rodriguez, C. A. Farrar, and T. S. Bellows, Jr. 1993. Identification of a whitefly species by genomic and behavioral studies. Science (Wash. D.C.) 259: 74–77.

Perring, T. M., C. A. Farrar, and A. D. Copper. 1994. Mating behavior and competitive displacement of whiteflies, pp. 25. *In* T. J. Henneberry, N. C. Toscano, R. M. Faust, and J. R. Coppedge [eds.], Silverleaf whitefly (formerly sweetpotato whitefly, strain B) 1994 Supplement to the Five-Year National Research and Action Plan. USDA-ARS 125, Orlando, FL.

Powell, D. A., and T. S. Bellows, Jr. 1992a. Adult longevity and population growth rates for *Bemisia tabaci* (Genn.) (Hom., Aleyrodidae) on two host plant species. J. Appl. Entomol. 113: 68–78.

1992b. Preimaginal development and survival of *Bemisia tabaci* on cotton and cucumber. Environ. Entomol. 21: 359–363.

Price, J. F., D. J. Schuster, and D. E. Short. 1987. Managing sweetpotato whitefly. Greenhouse Grower 35(12): 55–57.

Ricker, W. E. 1954. Stock and recruitement. J. Fish. Res. Board. Can. 11: 559–623

Salas, J., and O. Mendoza. 1995. Biology of the sweetpotato whitefly (Homoptera: Aleyrodadae) on tomato. Fla. Entomol. 78: 154–160.

Schuster, D. J. 1995. Integration of natural enemies for management of the sweetpotato whitefly and associated disorders on mixed-cropped vegetables. Final Report of Sustainable Agriculture Research and Education(SARE)/Agriculture in Concert with the Environment (ACE) Project No. AS92-3, Gulf Coast Research and Education Center, Bradenton, FL.

Schuster, D. J., T. F. Mueller, J. B. Kring, and D. J. Price. 1990. Relationship of the sweetpotato whitefly to a new tomato fruit disorder in Florida. HortScience 25: 1618–1620.

Schuster, D. J., J. B. Kring, and J. F. Price. 1991. Association of the sweetpotato whitefly with a silverleaf disorder of squash. HortScience 26: 155–156.

Schuster, D. J., J. E. Polston, and J. F. Price. 1992. Reservoirs of the sweetpotato whitefly for tomatoes in west-central Florida. Proc. Fla. State. Hort. Soc. 105: 311–314.

Simmons, G. S., and O.P.J.M. Minkenberg. 1994. Field-cage evaluation of augmentative biological control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) in southern California cotton with the parasitoid *Eretomocerus* nr.*californicus* (Hymenoptera: Aphelinidae). Environ. Entomol. 23: 1552–1557.

Stearns, S. D., and R. A. David. 1996. Signal processing algorithms in Matlab. Prentice-Hall Englewood Cliffs, NJ.

Thompson, C. M., and L. Shure. 1995. Image processing toolbox for use with MATLAB. The MathWorks, Natick, MA.

Tsai, J. H., and K. Wang. 1996. Development and reproduction of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on five host plants. Environ. Entomol. 25: 810–816.

van Giessen, W. A., C. Mollema, and K. D. Elsey. 1995. Design and use of a simulation model to evaluate germplasm for antibiotic resistance to the greenhouse whitefly (*Trialeurodes vaporariorum*) and the sweetpotato whitefly (*Bemisia tabaci*). Entomol. Exp. Appl. 76: 271–286.

von Arx, R., J. Baumgartner, and V. Delucchi. 1983. A model to stimulate the population dynamics of *Bemisia tabaci* Genn. (Stern., Aleyrodidae) on cotton in the Sudan Gezira. Z. Angew. Entomol. 96: 341–363.

Wilhoit, L., S. Schoenig, D. Supkoff, and B. Johnson. 1994. A regional simulation model for silverleaf whitefly in the Imperial Valley. PM 94–01, Pest Management Analysis and Planning Program. State of California, Environmental Protection Agency, Sacramento, CA.

Worner, S. P. 1992. Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. Environ. Entomol. 21: 689–699.

Yee, W. L., and N. C. Toscano. 1996. Ovipositional preference and development of *Bemisia argentifolii* (Homotera: Aleyrodidae) in relaticn to alfalfa. Environ. Entomol. 89: 870–876.

Zalom, F. G., E. T. Natwick, and N. C. Toscano. 1985. Temperature regulation of *Bemisia tabaci* (Homoptera: Aleyrodidae) populations in Imperial Valley cotton. J. Econ. Entomol. 78: 61–64.

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