Differential Effects of *Toxoptera citricida* vs. *Aphis gossypii* on Temporal Increase and Spatial Patterns of Spread of Citrus Tristeza

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ABSTRACT. Data from Florida, Spain, Trinidad, Costa Rica, the Dominican Republic, and California were used to develop models for increase and spread of citrus tristeza virus (CTV). In locations where the melon aphid, *Aphis gossypii* Glover, was the predominant vector, CTV progressed from low (~5%) to high (~95%) levels in 8-15 yr. In contrast, where the brown citrus aphid, *Toxoptera citricida* (Kirkaldy), was predominant, this same increase often occurred in only 2-4 yr. Where the melon aphid was the predominant vector, new infections were diffuse and not closely associated with existing infected trees but rather with trees several tree spaces distant. Where both species coexisted, the brown citrus aphid was the dominant species. In this situation, spread to trees immediately adjacent to existing infections was common which resulted in aggregates of CTV-infected trees along with longer distance spread in some instances. CTV infections were generally diffuse or quite aggregated where the melon aphid or the brown citrus aphid was the predominant species, respectively. Thus, aphid species greatly influenced the rate and patterns of CTV epidemics, and their presence/absence was important to predict how CTV will increase in time and space.

The citrus tristeza virus (CTV) disease pathosystem is very complex and consists of a multitude of interactions among the virus, the host tree, aphid vectors, and the environment. Competitive or noncompetitive interactions may exist between any two isolates (12). Several vector species with different transmission efficiencies for individual CTV virus isolates may be present, often change over time, and possibly affect each other's population dynamics (15, 26). Weather conditions affect production of new flush, aphid populations on citrus and other vector hosts, and CTV replication. These complex interactions must be studied to determine how they affect virus incidence in the grove over time and affect spread of the virus within and between citrus plantations. One important interaction is the effect of vector species on CTV

increase and spread. The effect of vectors on increase and spread has been previously studied (2, 3, 5, 7, 8, 9, 20) but contrasts between the effects of different aphid species and populations of differing aphid species complements have on increase and spread have been examined only in a brief report (11).

The brown citrus aphid has recently spread northward from South America into the Caribbean and Central America and has recently been introduced into southeast Florida (16). As a result, the US citrus industry as well as citrus industries of other nations of the Caribbean and Central America are concerned that elevated CTV increase and spread will result in more CTV-related tree and crop losses (10, 11, 13, 24, 26, 27). Most indicated that the spatial and temporal dynamics of CTV appear to change when the brown citrus aphid, *Toxoptera citricida* (Kirkaldy) becomes part of the pathosystem (7, 11, 12, 14). To examine and elucidate the cause-effect relationship for these differences, data for this paper was accumulated from a large num-

ber of plots which were established in Florida, California, Spain, Costa Rica, the Dominican Republic and Trinidad. The plots were designed to study the temporal increase and spatial patterns of spread of CTV relative to locations of initial inoculum. Because the number of plots was large and the studies often included multiple assessments over several years, a complete presentation of all data and analyses is not possible in this paper. The purpose of this study was to analyze the effect of aphid species and biology on rates and patterns of CTV spread. To accomplish this, the large data base of plots and multiple assessments was divided into two broad categories for evaluation: 1) where increase and natural spread was associated with the melon aphid, *Aphis gossypii* Glover, and/or the spirea aphid, *Aphis spiraecola* Patch and other minor aphids and 2) where *T. citricida* was present and presumed to be the predominant aphid vector species but other species coexisted as well. The spatial and spatio-temporal relationships were then compared and contrasted for these two broad categories and the results demonstrated here through the use of specific examples.

MATERIALS AND METHODS

A large number of plots were examined over multiple years. Plot size, and cultivar/rootstock combination varied depending on location and availability of serological assays. These plots are too numerous to describe in detail but their essential characteristics are presented here divided into two major categories (Table 1).

Plot design and sampling where *A. gossypii* was the predominant vector species. In this category, data were examined from plots in Spain, California, and Florida. In Spain, data was collected from plots established within four

commercial and two experimental plantings over a 15-yr period (8, 9). The six plots varied in size from 216 to 893 trees. In Florida, data were collected from five plots established in large commercial plantings over an 8-yr period. Each plot contained ca. 1,400+ trees arranged in 14 rows of ca. 100+ trees per row. In California, data were examined from 25 large commercial blocks located in the Central Valley which were repeatedly surveyed to identify CTV-infected trees for eradication by tree removal. All data were collected prior to tree removal.

Plot design and sampling where *T. citricida* was the predominant vector species. In this category data were collected and analyzed from 11 plots, each established within commercial plantations, comprised of four in northwestern Costa Rica, six in southeastern Dominican Republic, and one in Trinidad (12). The majority of the plots within this category consisted of approximately 20 rows of trees each with 20 trees per row. Of these, eight plots were composed of sweet orange scion varieties and two located in the Dominican Republic were grapefruit.

Detection of CTV infection. CTV infections were determined by ELISA. Both double antibody sandwich (DAS), and double antibody sandwich indirect (DAS-I) procedures were used (6, 22, 23, 25). Sampling protocol varied among locations, but were consistent throughout the study at each location. Samples consisted of petioles from young flush, young leaf midribs, young twigs, and/or young fruit peduncles. Samples were collected yearly from plots where *A. gossypii* was the main vector and twice per year (in the spring and fall) from plots where *T. citricida* was the primary vector. All samples were processed individually by tree. The tissue samples were extracted by pulverizing or grinding in a small

TABLE 1

PLOT CHARACTERISTICS AND GOMPERTZ NONLINEAR TEMPORAL MODELING
RESULTS OF THE PROGRESS OF CTV WHERE DIFFERENT APHID VECTORS PREDOMI-
NATE

Plot	No. Trees	Primary Vector	k	B	r^{*2} [a]
Costa Rica 1	389	T.c.	0.349	6.721	0.957
Costa Rica 2	400	T.c.	1.218	3.435	0.985
Costa Rica 3	398	T.c.	0.481	2.177	0.982
Costa Rica 4	399	T.c.	ITD	ITD	ITD
Dominican Republic 1	396	T.c.	0.443	4.059	0.973
Dominican Republic 2	372	T.c.	0.916	1.784	0.997
Dominican Republic 3	392	T.c.	ITD	ITD	ITD
Dominican Republic 4	400	T.c.	1.270	18.977	0.970
Dominican Republic 5	320	T.c.	ITD	ITD	ITD
Dominican Republic 6	397	T.c.	ITD	ITD	ITD
Trinidad 1	400	T.c.	ITD	ITD	ITD
Spain 1	400	A.g.	0.060	1.634	0.963
Spain 2	408	A.g.	0.287	45.111	0.973
Spain 3	346	A.g.	0.072	5.397	0.977
Spain 4	893	A.g.	0.619	9.328	0.999
Spain 5	216	A.g.	0.299	15.648	0.986
Spain 6	216	A.g.	0.580	88.015	0.990
Florida 1	1,412	A.g.	0.528	94.450	0.985
Florida 2	1,414	A.g.	0.688	272.593	0.986
Florida 3	1,427	A.g.	0.704	426.060	0.995
Florida 4	1,384	A.g.	0.727	390.370	0.987
Florida 5	1,117	A.g.	0.724	381.084	0.984
California 1 to California 25	501 to 3,059	A.g.	ITD	ITD	ITD

[a]Model parameters were estimated by nonlinear regression of the integrated equation $y = \exp^{-Be \cdot kt}$
for the Gompertz model where k is the rate parameter, y is disease incidence of trees, t is time in
years, and $B = -\ln(y_o)$. Correlation coefficients of observed versus predicted values (r^{*2}) and the
presence/absence of patterns in residual plots (data not shown) were examined for the appropri-
ateness of the model.
ITD = insufficient temporal data available to estimate but included here for plot size and vector
data and because they were considered in later spatial analyses.
T.c. = predominant aphid species was *Toxoptera citricida*, although other CTV vector species
including *Aphis gossypii* were present.
A.g. = predominant aphid species was *Aphis gossypii*, although other CTV vector species were
present.

aliquot of buffer. Specific serological
methods are discussed in more
detail in recent publications (6, 7, 9,
22, 23, 25).

The incidence and spatial loca-
tion of CTV-positive trees was
mapped for each plot by assessment
date. Temporal data was fitted to a
series of linear and nonlinear models
by linear regression and/or nonlin-
ear regression (1, 18). The appropri-
ateness of the models was
determined by examination of resid-
ual plots and correlation of observed

vs. predicted values. Several spatial
analyses were performed, each to
elucidate various spatial and spatio-
temporal characteristics in the data,
two of which are discussed here.
Spatial analyses were performed by
beta-binomial distribution fitting.
This analytical technique has
recently been shown to be the most
appropriate analysis for determining
aggregation within binary (non-
quantitative estimates of +/-) data
sets (17, 19). The beta-binomial
index was calculated for data par-

celed into quadrats of various sizes and was used to test for aggregation among groups of adjacent CTV-positive trees. For spatio-temporal analyses, spatio-temporal distance class (STClass) was performed to examine the change in spatial patterns of CTV-positive trees between two consecutive assessment periods (21).

RESULTS AND DISCUSSION

Temporal increase. The data from individual CTV epidemics were analyzed and mathematical models, particularly the exponential and Gompertz nonlinear models, were used to describe disease increase over time, depending on the temporal structure of the epidemic in each plot (Table 1). Models based on data taken over multiple years in areas such as Spain and Florida, where the melon aphid is the predominant CTV vector, predicted that CTV incidence progressed from low levels (~5%) to high levels (~95%) in 8-15 yr. In contrast, when the brown citrus aphid was present, as in Costa Rica and the Dominican Republic, this same increase occurred in only 2-6 years (Fig. 1). For those data sets where multiple year data over the duration of a CTV epidemic were available, these predictions were accurate and fell within the predicted time ranges. These findings are consistent with those found previously for temporal studies associated with each predominant vector, independently (3, 5, 7, 8, 9, 14). This confirmed that CTV will increase more rapidly within an area once the brown citrus aphid is introduced.

The effect of vector species on CTV increase. In general, aphid populations in citrus occur when citrus flushes, which is also the best time for the vector to acquire the virus. Populations of *T. citricida* on citrus are quite different than those of *A. gossypii*. Citrus is the primary host of *T. citricida*, which develops very large populations on flushes of
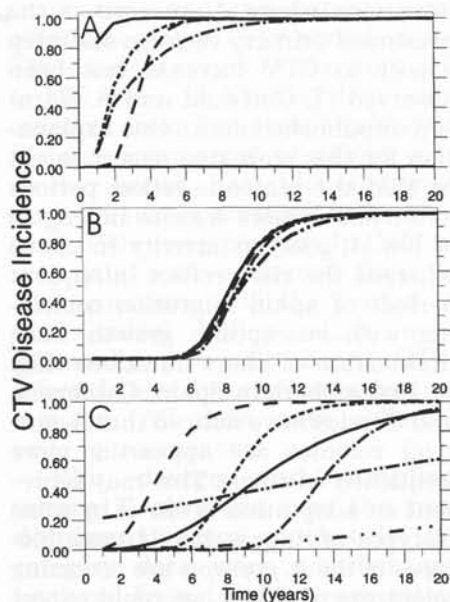

Fig. 1. Gompertz nonlinear model predictions for a 20-yr period for sample plots where A) *Toxoptera citricida* is the predominant vector in the Dominican Republic, and where *Aphis gossypii* is the predominant vector in B) Florida and C) Spain.

new growth. These large populations usually peak at least 2-3 times a year in conjunction with the new flush (13, 24, 26). The number and duration of flushes depends on the climate and horticultural conditions prevalent in each area, but significant populations of *T. citricida* will develop frequently in most areas. Virus transmission apparently occurs frequently, resulting in a rapid increase of CTV.

In contrast, citrus is not the primary host for *A. gossypii* and colony formation is infrequent. Whereas, *A. gossypii* populations build up in other crops, and tend to migrate through citrus only stopping for a brief time to feed (4). These *A. gossypii* population buildups and migrations may not coincide with growth flushes in citrus. It is sometimes difficult to find the *A. gossypii* feeding on citrus since it only sporadically colonizes citrus. In large commercial

situations where *A. gossypii* is the presumed primary vector, a stairstep aspect to CTV increase has been observed (T. Gottwald and S. Garnsey, unpublished data). One explanation for this stair-step aspect might be that the plateaus reflect periods (often one or more seasons in length) of low *A. gossypii* activity in citrus whereas the rises reflect infrequent periods of aphid migration coinciding with susceptible growth flush (most often of short duration) (Fig. 2). Researchers in Spain, California, and Corsica have noticed that *A. gossypii* colonies are appearing more frequently in citrus. This may represent an adaptation to citrus by some biotypes of *A. gossypii*. If some biotypes of the *A. gossypii* are becoming colonizers of citrus, we could expect CTV increases associated with *A. gossypii* to begin to increase at a more rapid rate.

Effect of vector species on CTV spread. Beta-binomial analysis demonstrated a contrast between situations where *A. gossypii* and *T. citricida* are the predominant vector species. Very little aggregation of

new infections was detected when *A. gossypii* was the main vector as in Spain, California, and Florida, however, aggregation was more easily detected when *T. citricida* was the predominant vector species, as in the Dominican Republic and Costa Rica (Table 2).

To examine CTV spread, the spatial position of CTV-positive trees was examined over time; individual maps were compared from one assessment to the next. For plot maps such as those shown in Fig. 3A&E, visual assessments of the associations of spatial positions of new with previously CTV-infected trees was unclear. Using spatio-temporal distance class software, hundreds of computer simulations of possible random positions for new CTV-positive trees with those positions actually determined for each plot between two consecutive assessment dates were conducted. By this method, the spatial associations among new CTV-positive trees and those previously infected were made (21). Such spatio-temporal analyses for data from California and Spain
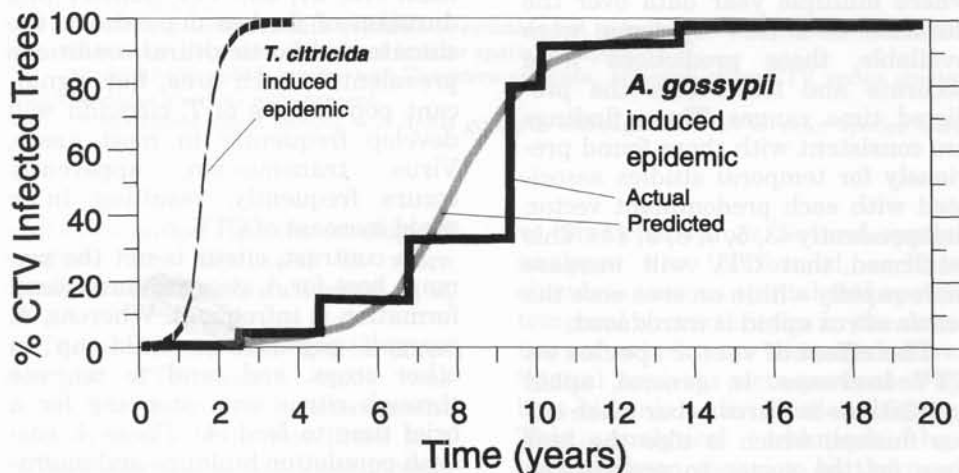

Fig. 2. Theoretical effect of aphid species on CTV temporal progress. Note the more rapid increase on CTV in the presence of *T. citricida*. The temporal models used tend to smooth out disease progress which actually consists of steps and plateaus. (A more accurate depiction of CTV progress is shown.) The steps correspond to periods of intense aphid activity and CTV transmission and the plateaus correspond to times of low aphid activity.

TABLE 2

EXAMPLES OF INDEX OF DISPERSION (I_β) ANALYSES FOR CITRUS TRISTEZA IN CITRUS ORCHARDS IN EASTERN SPAIN AND THE DOMINICAN REPUBLIC

Spanish Plots

Plot	df	Year of assessment[z]										
		1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
Spain 1	53	0.976	0.946	0.932	0.916	0.886	1.120	1.082	1.301	1.345	1.525	1.428
Spain 2	53	0.976	0.946	0.946	1.281	1.122	0.982	1.348	1.428	1.525	1.681	1.085
Spain 3	99	1.149	1.048	0.979	0.997	0.990	0.956	1.061	1.082	—[y]	—	—
Spain 4	107	0.903	0.903	1.169	1.169	1.169	1.235	1.127	1.110	1.110	1.138	1.209
Spain 5	88	—	0.858	0.882	0.882	0.890	1.101	0.961	0.935	0.976	0.953	1.559

Dominican Republic Plots

Plot	df	Year of assessment[z]					
		Sep 92	Jun 93	Dec 93	May 94	Dec 94	May 95
DR1	99	1.267	1.436	1.634	1.520	1.586	1.413
DR4	99	0.987	1.523	1.372	1.556	1.440	1.251

For all plots and assessment years, incidence of diseased trees was determined by ELISA test for CTV. Because the analysis of all plots and assessment dates is beyond the scope of this presentation, the above are selected examples showing a lack and presence of aggregation, respectively.

[z] Index of dispersion (I_β) [upper value] and associated probability (P) [lower value] values for 2×2 quadrat size by year for citrus plots in eastern Spain and Dominican Republic infected with CTV. Values presented for each assessment date are I_β (= observed variance/binomial variance) and P (=significance probability). P-values were calculated by comparison of df X I_β with the chi-squared distribution. Values of I_β not significantly different from 1 ($0.95 > P > 0.05$) indicate that the pattern of diseased trees is indistinguishable from random. A large (>1) I_β and a small P ($< = 0.05$) suggest rejection of H_0: random pattern, in favor of H_1: aggregated pattern of diseased trees. Thus aggregation was seen only occasionally during the final five assessment periods of the Spanish plots 1 and 2, whereas, aggregation was detected in the Dominican Republic for both plots and assessment periods except for the first assessment in DR4.

[y] -Indicates no assessment data available for that year or too few data points were available to allow calculation.
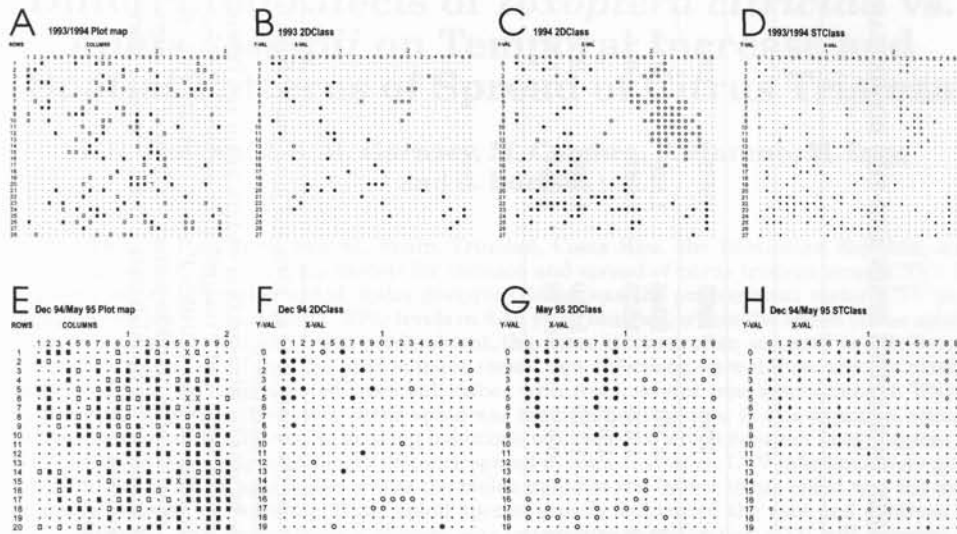
Fig. 3. Examples of spatio-temporal distance class analyses for plots in California vs. Dominican Republic where *A. gossypii* and *T. citricida* are the predominant CTV vectors, respectively. A and E) CTV plot maps for Central California and the Dominican Republic, respectively. Black and open squares denote the position of CTV-positive trees for the first and second years being compared, respectively. B-C) Two-dimensional distance class analyses of each of the years being compared for the Central California plot vs. F-G) for the Dominican Republic Plot. For two-dimensional class analyses solid and open circles represent positive and negative correlated spatial positions, respectively. D and H) Spatio-temporal distance class analyses for the comparison of two yearly assessments for the Central California and the Dominican Republic plots, respectively. For spatio-temporal distance class analyses, solid and open diamonds represent positive and negative correlated spatio-temporal positions, respectively. For both 2DClass and STClass analyses, groups of positive correlation near the origin, i.e. [x,y] position of [0,0], are indicative of aggregation of CTV-positive trees, whereas, few positive correlations near the origin are indicative of a diffuse or more random distribution and associations among CTV-positive trees. Therefore, note the random and diffuse associations among CTV-positive trees in the Central California vs. the aggregated associations in Dominican Republic plots, respectively.

indicated the spatial pattern of CTV spread usually could not be distinguished from a random situation (9) (example Fig. 3A-D), whereas for plots in the Dominican Republic and Costa Rica, considerable aggregation occurred through time (example Fig. 3E-H).

Theory to explain spatio-temporal CTV patterns associated with predominant vector species. The biology and feeding habits of aphid species that affect citrus vary by species and result in different spatial distributions of CTV. *Aphis gossypii* is a migratory species relative to citrus and only occasionally forms colonies on citrus foliage. Most often, it moves through the orchard canopy in temporal waves from surrounding crop species, i.e. melon, cotton, etc., that are primary hosts for the aphid (T. Gottwald, unpublished data). Based on patterns of CTV spread, when it picks up virus inoculum from CTV-infected trees it then apparently moves on to feed on other trees which are not necessarily close to one another (Fig. 4). Also based on our findings concerning patterns of CTV spread, it is apparently rare that a foraging viruliferous aphid would choose to fly to an adjacent tree when it decides to move. This results in an apparently random spread of CTV (Fig. 5). However, there may be a common range of
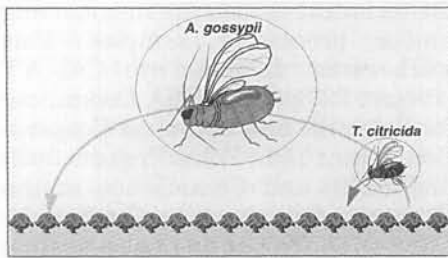
Fig. 4. Differences in spatial patterns of CTV can be explained by the predominant vector species. Based on analyses of patterns of CTV spread, when stimulated to fly, viruliferous *A. gossypii* are migrating vectors and preferentially move several trees away, whereas viruliferous *T. citricida*, which are colonizers of citrus, tend to move to immediately adjacent or nearby trees.

flight distances which may be repeated. From a study of a very large citrus plantation in south Florida, this range of movement based on the position of newly CTV-infected trees appears to be ca. 100-200 m (M. Irey and T. Gottwald, unpublished data). There was also a long and diffuse gradient of CTV infection in this plantation indicating that other factors such as wind might have affected viruliferous aphid movement.

Conversely, *T. citricida* is a citrus colonizer. When it is the predominant species, CTV- infected trees at first appear diffuse or only loosely aggregated when CTV is first introduced but soon become more tightly aggregated as viruliferous *T. citricida* move and transmit CTV to adjacent or nearby trees rather than trees further away (Figs. 4 & 5). Interestingly, *A. gossypii* infestations can also result in aggregated spatial patterns under some conditions. In Florida and Israel (M. Irey, unpublished data and M. Bar-Joseph, pers. comm.), when *A. gossypii* is the predominant vector species and when the tree canopy begins to close within the row due to growth of trees closely spaced within row, we see a change in the spatial pattern of disease from a random to an aggre-
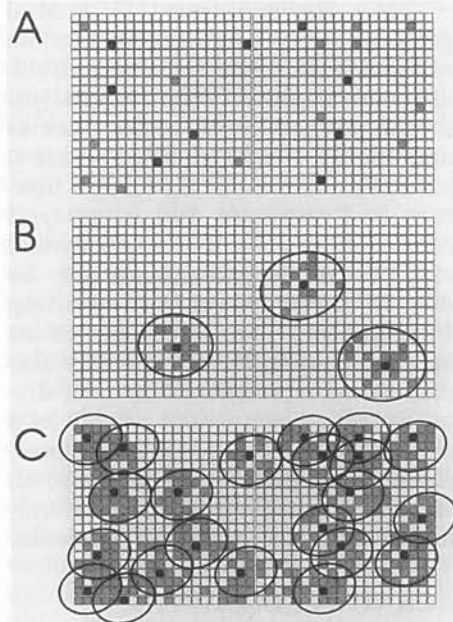

Fig. 5. Theoretical explanation for observed patterns of CTV spread. A) *Aphis gossypii* alone causes diffuse infections which are apparently random covering large distances. B) *T. citricida* alone causes aggregated infections due to spread predominantly to adjacent and nearby trees. C) A combination of the two aphid species results in diffuse spread over long distances by both species but especially *A. gossypii*, then highly efficient spread by *T. citricida* resulting in rapid coverage. Black squares represent initial aphid-transmitted CTV infections. Gray squares indicate secondary spread of CTV to new trees.

gated condition along rows of trees. Reasons for this are not entirely clear and more than one explanation could be considered. CTV aggregation could be due to the movement of viruliferous aphids crawling the continuous canopy of citrus branches. We also cannot assume that *A. gossypii* is the only vector contributing to CTV spread in this case. Other aphid species such as *Aphis spiraecola* and *Toxoptera aurantii*, which are less efficient vectors but do colonize citrus, could contribute to this aggregated pattern of CTV spread because of the large populations that can build up in citrus.

Thus, the resulting CTV spatial patterns are predominately random at least within the scale of individual plots or groves where *A. gossypii* is the predominant vector species and highly clustered when *T. citricida* is predominant or when a mixture of *T. citricida* and *A. gossypii* coexist in an area. The rapid spread of CTV over long distances may be due to virus movement resulting from the contribution of both vector species. That is, *T. citricida* may also contribute a considerable long-distance spread component as well as a short-distance component. However, rapid development and increase in clusters is apparently due predominantly to the influence of *T. citricida*.

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