Comparative effects of aphid vector species on increase and spread of citrus tristeza virus

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ABSTRACT

INTRODUCTION. The effects of different aphid species on the increase and spread of the citrus tristeza virus (CTV) have not previously been studied. Prior experiences indicated that the dynamics of CTV appear to change when the brown citrus aphid (BCA), *Toxoptera citricidus* (Kirkaldy), was introduced. To evaluate the effects of aphid population composition on CTV increase and spread, data accumulated from a large number of plots established in various countries were divided into two broad categories: where the melon aphid (MA) existed in the absence of BCA and where BCA was the predominant vector species. **MATERIALS AND METHODS**. Forty-seven plots, in commercial or experimental plantings, and with MA or BCA as the predominant vector species, were examined over multiple years. CTV infections were determined by specific ELISA methods. Temporal and spatial analyses were performed, to elucidate the CTV increase over time and its spatial patterns. **RESULTS AND DISCUSSION**. CTV increased more rapidly in areas where BCA was introduced than locations where MA was predominant. Aggregation of infected trees was detected when BCA was the main vector, but not when MA was predominant. Aphid biology can explain these results: citrus is the primary host of BCA and not of MA. Moreover, BCA is a colonizer species whereas MA is a migrator species. These characteristics affect the distribution patterns of CTV during an epidemic. The effect of vector populations should be taken into account in order to better control the ingress and spread of CTV in nurseries and increase blocks.

KEYWORDS

Citrus, citrus tristeza closterovirus, vectors, *Toxoptera citricidus*, *Aphis gossypii,* population dynamics.

Influence de l'insecte vecteur sur la multiplication et la distribution du virus de la tristeza des agrumes.

RÉSUMÉ

INTRODUCTION. L'influence de l'espèce de l'aphide vecteur, sur la multiplication et la distribution du virus de la tristeza des agrumes (CTV), n'avait encore jamais été vraiment étudiée. Certains résultats antérieurs semblaient montrer que la dynamique du CTV était modifiée en présence de l'aphide brun des agrumes (BCA), *Toxoptera citricidus* (Kirkaldy). Pour étudier ce problème, des données, portant sur l'observation de nombreuses parcelles réparties dans plusieurs pays, ont été scindées en deux catégories, selon que c'était l'aphide du melon (MA) ou le BCA qui était préférentiellement associé à la propagation du CTV. **MATÉRIEL ET MÉTHODES**. Quarante-sept parcelles de plantations commerciales ou expérimentales, avec soit MA, soit avec BCA en espèce vecteur prédominante, ont été suivies sur de nombreuses années. Les infestations par le CTV ont été déterminées à l'aide de tests ELISA spécifiques. Des analyses de données adaptées ont été réalisées pour comprendre la croissance des populations de CTV et leur distribution dans l'espace. **RÉSULTATS ET DISCUSSION**. Les populations de CTV ont augmenté plus rapidement dans les parcelles où BCA avait été introduit que dans celles où MA était prédominant. Les arbres infectés ont été trouvés regroupés lorsque BCA était le vecteur principal, mais disséminés dans le cas de MA. La biologie des aphides permettrait d'expliquer ses résultats : les agrumes sont l'hôte primaire du BCA, non celui de MA. Par ailleurs, BCA est une espèce colonisatrice alors que MA est migratrice. Ces caractéristiques affectent la distribution du CTV lors d'épidémies. Ces informations devront être prises en compte pour contrôler la propagation du CTV en pépinières et dans les blocs de multiplication.

MOTS CLÉS

Citrus, closterovirus tristeza du citrus, vecteur de maladie, *Toxoptera citricidus*, *Aphis gossypii*, dynamique des populations.

introduction

The citrus tristeza virus (CTV) disease pathosystem is complex and consists of the virus, the host tree, aphid vectors, the environment, and their interactions. Several vector species with different transmission efficiencies may be present and the composition of vector populations may change over time (HERMOSO DE MENDOZA and MORENO, 1989; YOKOMI et al, 1994). Weather conditions affect production of new flush, aphid populations, and CTV replication. These complex interactions affect virus incidence over time and spread of the virus within and between citrus plantations. One important interaction is the effect of vector species on CTV increase – the number of new infected trees over time – and spread – the spatial pattern of these newly infected trees. The effect of vectors on CTV increase and spread has been previously studied (FISHMAN et al, 1983; CAMBRA et al, 1988; MORENO et al, 1988; CHELLEMI et al, 1991; GARNSEY et al, 1996; GOTTWALD et al, 1993, 1996a) but contrasts between the effects of different aphid species and the species composition of the overall vector populations on increase and spread have been examined only in a brief report (GOTTWALD et al, 1995).

The brown citrus aphid (BCA), *Toxoptera citricida* (Kirkalday), has recently spread northward from South America into the Caribbean and Central America and is now well established in South Florida (HALBERT, 1996). The US citrus industry, as well as citrus industries of other Caribbean and Central American countries, are concerned that more rapid CTV increase and spread will occur and result in more CTV-related tree and crop losses (GOTTWALD et al, 1994a, b, 1995; ROCHA-PEÑA et al, 1995; YOKOMI et al, 1994, 1996). Experiences from other countries indicate that the dynamics of CTV appear to change when BCA is introduced (GARNSEY et al, 1996; GOTTWALD et al, 1995, 1996b; GRISONI and RIVIÈRE, 1993). Data for this paper were accumulated from a large number of plots which were established in Florida, California, Spain, Costa Rica, and the Dominican Republic. Differing virus and aphid components were present in different areas; however, for this study, the data base of plots can be divided into two broad categories for evaluation: i) 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 ii) where BCA was the predominant aphid vector species in a mixed population. Specific examples are shown to illustrate contrasts between these two categories.

Knowledge of CTV increase rates and spread patterns can help to predict the need for replanting trees damaged by decline or stem pitting. Knowledge of CTV dynamics can aid the nurserymen in protecting mother trees, nursery plantings, and increase blocks from infection.

materials and methods

Forty-seven plots were examined over time. Plot size and cultivar/rootstock combination varied depending on location. These plots are too numerous to describe in detail, but their essential characteristics are presented below. In some plots studied, the initial inoculum was introduced with the nursery trees; in other cases, the trees in the plot were CTV-free at planting, but subjected to infection from nearby inoculum sources. Plots were established in CTV-decline susceptible, ie, sweet orange or grapefruit scion on sour orange rootstock, and CTV-tolerant plantings. The latter can become infected and act as a source of virus inoculum, but do not show disease symptoms. In the majority of cases, plots were CTV-free at planting.

plot design and sampling where the melon aphid was the predominant vector species

Data were examined from plots in Spain, California, and Florida.

In Spain, data was collected over a 15-year period from plots established within four commercial and two experimental plantings (GOTTWALD et al, 1993, 1996 a). The six plots varied in size from 216 to 893 trees.

In Florida, data were collected over an eight-year period from five plots established in large commercial plantings. Each plot contained about 1 400 trees arranged in 14 rows of about 100 trees per row.

In California, data were examined from 25 large commercial blocks located in the Central Valley varying in size from 501 to 3 059 trees. These blocks were surveyed repeatedly to identify CTV-infected trees for eradication by tree removal.

plot design and sampling where BCA was the predominant vector species

Data were collected and analyzed from 10 plots, each established within commercial plantations in Northwestern Costa Rica, and the Dominican Republic (GOTTWALD, et al, 1996b). Most plots consisted of 20 rows of trees with 20 trees per row. Eight plots were located in sweet orange scion plantings and two in grapefruit.

detection of CTV infection

CTV infections were determined by double sandwich indirect (DAS-I) ELISA (GARNSEY and CAMBRA, 1991). Samples consisted of petioles or leaf midribs, or, if young growth was available, terminals from young growth or young fruit peduncles. Samples were collected yearly from plots where the melon aphid was the main vector and twice per year (in the spring and fall) from plots where BCA was the primary vector. Specific ELISA methods used to give clear differentiation between CTV-infected and CTV-free trees are described in detail in recent publications (VELA et al, 1986; PERMAR et al, 1990; GARNSEY and CAMBRA, 1991; POLEK, 1995; GARNSEY et al, 1996; GOTTWALD et al, 1996a).

data analysis

The incidence and location of CTV-positive trees was mapped for each plot by assessment date. Temporal data was fitted to a series of linear and non-linear models to describe CTV increase over time (CAMPBELL and MADDEN, 1990; MADDEN, 1986). Several spatial analyses were performed, to elucidate various characteristics in the data. These included ordinary runs to determine if spread was predominantly within or across rows, beta-binomial analysis to test for aggregation within small groups of adjacent trees (HUGHES and MADDEN, 1993; MADDEN and HUGHES, 1994), and spatial autocorrelation analysis to test for aggregation among groups of trees and over larger dimensions. Conclusions concerning the CTV spatial patterns presented below were drawn for the combination of results from these spatial analyses.

results and discussion

observed CTV increase over time

The data from individual CTV epidemics were analyzed and mathematical models were used to describe disease increase over time for each plot. Models based on data taken in areas such as Spain and Florida, where the melon aphid is the predominant CTV vector, predict that when CTV incidence is low (~5%) it generally takes 8–15 years to reach high incidence levels (~95%). In contrast, when the brown citrus aphid was present, as in Costa Rica and the Dominican Republic, this same increase generally occurred in only 2–6 years, with the exception of grapefruit plots (figure 1). These findings are consistent with those found previously (FISHMAN et al, 1983; CHELLEMI et al, 1991; GRISONI and RIVIÈRE, 1993; GOTTWALD et al, 1993; 1995; GARNSEY et al, 1996) and confirmed that CTV will increase more rapidly within an area once the brown citrus aphid is introduced.

effect of vector species on spatial spread of CTV

Spatial data analysis demonstrated a contrast between situations where the melon aphid and BCA are the predominant vector species. Very little aggregation of infected trees was detected when the melon aphid was the main vector, as in Spain, California, and Florida (GOTTWALD et al, 1996a). However, aggregation was more easily detected for individual assessment dates and through time when BCA was the predominant vector species, as in the Dominican Republic and Costa Rica.

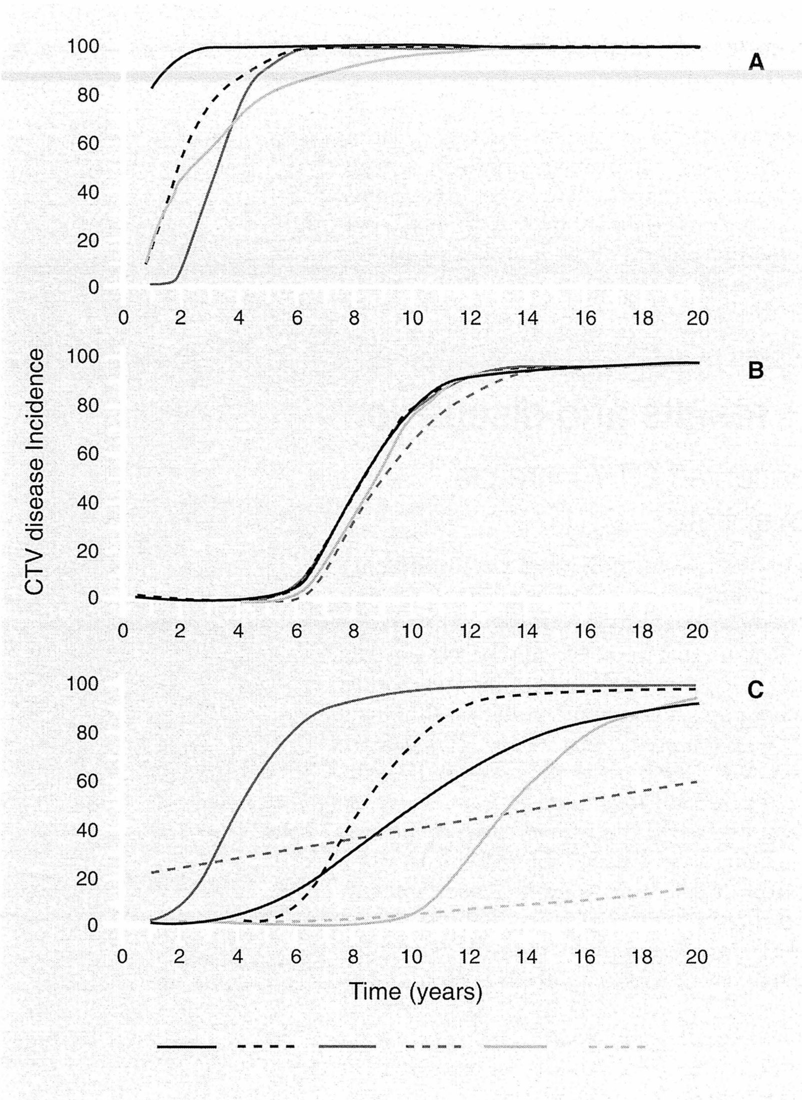

Figure 1
Model predictions for a 20-year period based on data collected in research plots where the brown citrus aphid is the predominant vector in the Dominican Republic (A), and where the melon aphid is the predominant vector in Florida (B) and Spain (C). Each line represents CTV increase in an individual test plot. All plots were orange cultivars with the exception of on grapefruit plot represented by the light gray dashed line in panel (C).

aphid biology that affects CTV increase and patterns of spread

The population dynamics of BCA and the melon aphid are quite different. Citrus is the primary host of BCA and it often develops very large populations which usually peak at least 2–3 times a year in conjunction with flushes of new growth (GOTTWALD et al, 1994b; ROCHA-PEÑA, 1995; YOKOMI et al, 1994). The number and duration of flushes depends on the climate and horticultural conditions prevalent in each area, but significant populations of BCA can be expected at least once a year. BCA is the most efficient vector of CTV and thus, virus transmission occurs frequently, resulting in a rapid increase of CTV infection.

In contrast, citrus is not the primary host for the melon aphid and formation of colonies is infrequent. However, large populations of the melon aphid build up in other crops. Citrus can be exposed to large migrating populations which stop for a brief time to feed (DICKSON et al, 1951). These melon aphid population build-ups on other crops followed by migrations through citrus may not coincide with flushes of citrus growth. Migrations during periods of unfavorable citrus flush may not result in appreciable CTV spread. In large commercial situations where the melon aphid is the presumed primary vector, a stair-step aspect to CTV increase has been observed (GOTTWALD and GARNSEY, unpublished). One explanation for this stair-step aspect might be that the plateaux reflect periods – often one or more seasons in length – when melon aphid activity in citrus was low or poorly timed, whereas the rises reflect infrequent periods of more abundant aphid migration which coincides with susceptible growth flush (figure 2).

Aphid movement also affects the spatial distribution patterns of CTV during an epidemic. Because the melon aphid is a migrator species and not a colonizer of citrus, 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. Our findings concerning patterns of CTV spread suggest that a foraging, virus-carrying melon aphid usually would not fly to an adjacent tree when it decides to move. Instead, it would land at some distance, often several trees away, from its take off point. This results in an apparently random spread of CTV (figure 3A). However, there may be a common range of 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 about 100–200 m (IREY and GOTTWALD, unpublished). There was also a long and diffuse gradient of CTV infection in this plantation indicating that other factors such as wind might have affected virus-carrying aphid movement.

In contrast to the melon aphid, BCA is a colonizer species. When it is the predominant vector, CTV-infected trees at first appear diffuse or only loosely aggregated, but soon become more tightly aggregated as virus-carrying BCA preferentially move and transmit CTV to adjacent or nearby trees rather than trees further away (figure 3B). However, when a mixture of BCA and the melon aphid 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, BCA may also contribute a considerable long-distance spread component as well as a short-distance component (figure 3C). However, rapid development and increase in clusters is apparently due predominantly to the influence of BCA.

Interestingly, the melon aphid infestations can also result in aggregated spatial patterns under some conditions. In Florida and Israel (IREY, unpublished, and BAR-JOSEPH, pers comm), when the melon aphid is the predominant vector species and when the tree canopies grow together within the row, the spatial pattern of disease changes from a random to an aggregated condition along rows of trees. Reasons for this are not entirely clear, but CTV aggregation could be due to the movement of virus-carrying aphids which crawl along the continuous canopy of citrus branches. The melon aphid may not be the only vector contributing to CTV spread in this case. Other aphid species such as the spirea aphid, *Aphis spiraecola,* and the black citrus aphid, *Toxoptera auranti*, 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. *A spiraecola* is a less efficient vector of CTV under experimental conditions compared to the melon or brown citrus aphids and its contribution to the field spread of CTV remains unknown.

relevance to citrus nurseries and increase blocks

Although the conclusions of this study were drawn primarily from young commercial plantings, they impact both nursery and increase block operations. As CTV-mediated decline increases in an area, the need for replacement trees also increases. However, propagation of CTV-free trees in heavily infected areas becomes increasingly more difficult. Nursery and budwood increase block trees are very vigorous, flush nearly continuously, and are thus attractive to aphid vectors. Therefore, when rates of CTV increase are high and nurseries and/or increase blocks are in close proximity to CTV sources, the risk of CTV ingress by virus-carrying aphids greatly increases. In the case of budwood increase blocks, which continuously produce new flush and are sometimes maintained for two or more years, aphids can also become established, multiply rapidly, acquire the virus from newly infected nursery trees, and spread it within the increase block itself. This requires more frequent virus testing and tighter nursery and increase block certification programs to maintain CTV-free trees for new plantings, and to ensure that further CTV spread does not occur due to the distribution and planting of infected plant material. Knowledge of CTV increase and patterns of spread can help nurserymen protect against CTV ingress by understanding the benefit of locating nurseries in areas where CTV is absent, in low incidence, or at considerable distance from CTV-infected plantings.

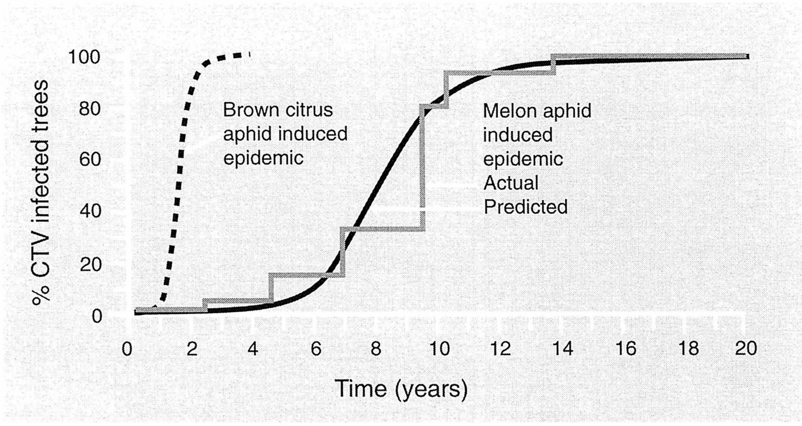

Figure 2
Theoretical effect of aphid species on citrus tristeza virus (CTV) temporal progress. Note the more rapid increase on CTV in the presence of brown citrus aphid.
The temporal models used tend to smooth out disease progress which actually consists of steps and plateau. The grey line represents a more accurate depiction of CTV progress in the presence of the melon aphid. The steps apparently correspond to periods of intense aphid activity and CTV transmission and the plateau correspond to times of low aphid activity or activity when transmission potential is low such as periods when trees have no new growth flush for aphids to feed on.

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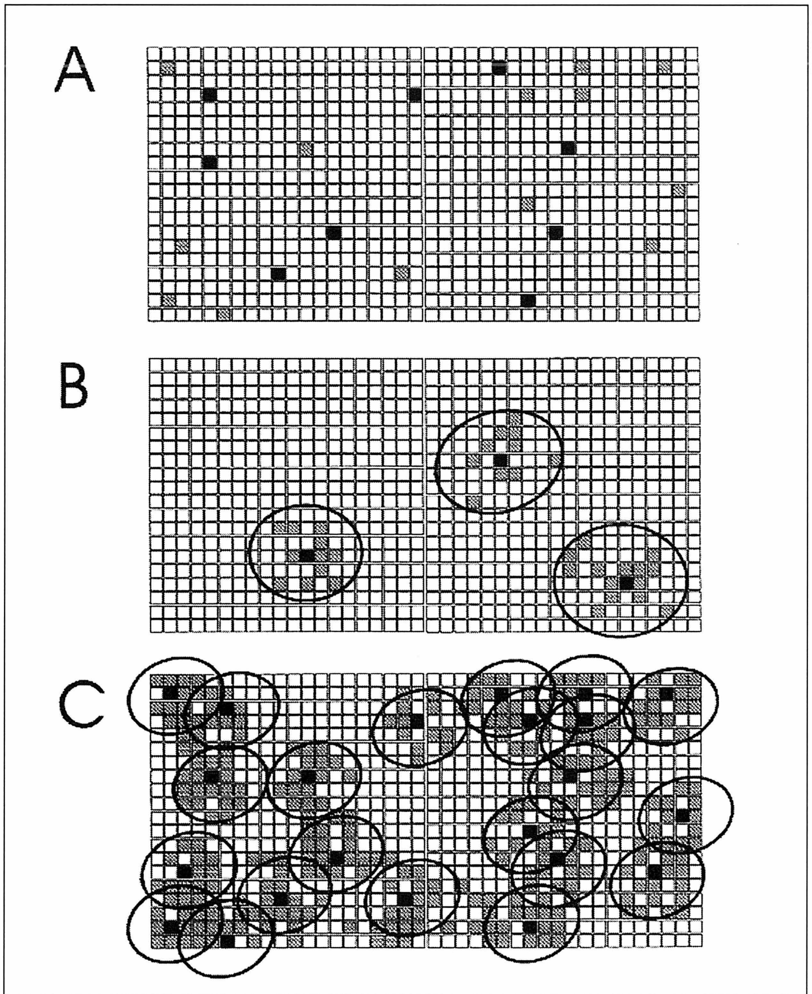

Figure 3
Theoretical explanation for observed patterns of citrus tristeza virus (CTV) spread.
A) The melon aphid alone causes diffuse infections which are apparently random, over large distances.
B) Brown citrus aphid (BCA) alone causes aggregated infections due to spread predominantly to adjacent and nearby trees.
C) A combination of the two aphid species results in diffuse spread over long distances by both species but especially the melon aphid, then highly efficient spread by BCA resulting in rapid coverage. Black squares represent initial aphid-transmitted CTV infections. Grey squares indicate secondary spread of CTV to new trees.

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Influencia del insecto vector en la multiplicación y distribución del virus de la tristeza de los agrios.

RESUMEN

INTRODUCCIÓN. La influencia de la especie del áfido vector, en la multiplicación y propagación del virus de la tristeza de los agrios (VTA), aún no había sido verdaderamente estudiada. Algunos resultados anteriores parecían indicar que la dinámica del VTA se modificaba en presencia de la *Toxoptera citricidus* (Kirkaldy). Para estudiar este problema se dividieron en dos categorías, en función del áfido (*Toxoptera citricidus* o el áfido del melón AM) asociado preferentemente a la propagación del VTA, una serie de datos referidos a la observación de numerosas parcelas distribuidas en varios países. **MATERIAL Y MÉTODOS.** Se efectuó un seguimiento, durante bastantes años, de cuarenta y siete parcelas de plantaciones, comerciales o experimentales, que tenían al

AM o a la *Toxoptera citricidus* como especie vector predominante. Las infestaciones por VTA se determinaron mediante unos tests ELISA específicos. Se realizaron una serie de análisis de datos adaptados para comprender el crecimiento de las poblaciones de VTA y su distribución espacial. **RESULTADOS Y DISCUSIÓN.** Las poblaciones de VTA aumentaron más deprisa en las parcelas en las que se introdujo la *T citricidus* que en las que el AM predominaba. Los árboles infectados se encontraron agrupados cuando la *T citricidus* era el vector principal pero diseminados en el caso del AM. La biología de los áfidos podría explicar los resultados: los cítricos son los hospedadores primarios de la *T citricidus* y no del AM. Por otro lado, la *T citricidus* es una especie colonizadora y el AM migratoria. Estas características afectan a la distribución del VTA en caso de epidemia. Habrá que tener en cuenta esta información para controlar la propagación del VTA en viveros y bloques de reproducción.

PALABRAS CLAVES
Citrus, closterovirus tristezza del citrus, vectores, *Toxoptera citricida*, *Aphis gossipii*, dinámica de la población.