PotentiaL for Spenr of Citrus tristeza Virus and its vector, The brown Citrus aphid

Tim R. Gottwald, Stephen M. Garney, and Raymond K. Yokomi
U.S. Department of Agriculture
Agricultural Research Service
U.S. Horticultural Research Laboratory
2120 Camden Rd., Orlando, FL 32803

Abstract. The recent discovery of citrus tristeza virus (CTV) and its most efficient vector, the brown citrus aphid, has heightened fears of the U.S. citrus industry that the aphid will be introduced into the continental U.S. and further CTV-related losses will occur. Florida has a high incidence of mild and decline-inducing strains of CTV, but stem-pitting strains are rare. Stem-pitting

Additional index words. epidemiology, transmission, transport, trajectory, diffusion, survival, redistribution, probability of introduction.


strains have been detected throughout South America including Colombia and Venezuela. Most infections in the Caribbean Basin can be traced to use of CTV-infected budwood from other countries including the U.S., but CTV incidence is still generally low in most locations. Importation of budwood and other propagating materials by growers, nurserymen, horticulturists, and tourists from abroad where severe CTV strains are prevalent poses a constant threat to the citrus industry. However, it is unlikely that CTV strains will spread long distances by aphid vectors. Spread of the BCA is occurring in advance of CTV infection in some areas, but CTV incidence is expected to increase once the BCA is firmly established in each new area. BCA migrates readily over short distances. However, long-range spread, i.e. between geographically separated regions, is much more likely by movement of infected plant material than by direct flight of aphids.

The recent discovery of the brown citrus aphid (BCA), Toxoptera citricida (Kirk.), and citrus tristeza virus (CTV) in many new locations and countries in Central America and the Caribbean has fostered fears of the aphid's introduction into the continental U.S. and further CTV-related losses by the U.S. citrus industry (Roistacher, 1991). Although detailed data on the distribution of these two pests is not available for some locations, BCA is present as far north as Nicaragua and in most of the Caribbean Islands including Cuba (Yokomi et al., unpublished; O'Reilly, 1993; Lee et al., 1993). CTV incidence is low in most areas, but appears to be increasing rapidly where the BCA is present. CTV has been a continual problem in Florida and California for many years and causes both losses in yields and eventual death of trees if sour orange rootstocks are used. Fortunately, indigenous aphid species in the U.S. are only moderately efficient vectors of CTV (Yokomi et al., 1989). In addition, many Florida and California CTV isolates produce no or only mild symptoms. Although losses have been high in some areas of Florida and in southern California, damage is much more severe in Asia, South Africa, Australia, and South America where the most efficient vector, the BCA, is endemic and where severe decline-producing and stem-pitting strains of CTV persist. Where the BCA and strains of CTV that cause decline are both present, tree loss on sour orange rootstocks is rapid and complete. Where stem-pitting strains of CTV are present, grapefruit trees may be severely damaged even when grown on tolerant rootstocks and even sweet oranges may be affected. The purpose of this paper is to examine the known distributions of tristeza and the brown citrus aphid in the Caribbean Basin and to explore the possibilities of their further spread by various avenues into Florida and other U.S. citrus-producing states.

Sources of Information

Information concerning the present distribution of T. citricida and CTV strains was compiled from a combination of literature, a recent survey by a team of U.S., Caribbean, and Central American scientists (Yokomi et al., unpublished), a recent survey of Cuba by IFAS scientists (Lee et al., 1993), a recent survey by Departement du Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) scientists conducted in the Caribbean Basin (Aubert et al., 1993), recent workshops in Maracay, Venezuela (Lastra et al., 1992) and Lake Alfred, Florida (anonymous, 1993) on citrus tristeza and the brown citrus aphid, reports from various Caribbean nations through United Nations Development Program, Food and Agriculture Organization (UNDP, FAO), and personal observations and confirmations by the authors. This paper also draws upon published reports and work in progress on citrus tristeza virus epidemiology (Gottwald et al., 1993; Fishman et al., 1983; Yokomi et al., 1991; Gottwald et al., unpublished), and brown citrus aphid transmission and biology (Costa and Grant, 1951; Grisoni and Riviere, 1993; Hermoso de Mendosita et al., 1984; McClean, 1975; Yokomi et al., unpublished).

The factors affecting short- and long-distance dissemination of cereal and other aphids is well documented (Isard, 1990; Taylor, 1896; Wallin and Loonana, 1971; Yokomi and Oldfield, 1991) but those affecting T. citricida are not (Seif, 1988). This paper evaluates the potential for long-range dispersal of T. citricida, examines the probabilities of dissemination of both the BCA and CTV based on information and deduction, and attempts to put the situation into proper perspective. To do this we have assembled what we know of T. citricida biology and have deduced what we don't know by extrapolating knowledge from other aphid/plant host systems.

Tristeza and the Brown Citrus Aphid: Historical and Present Distribution

The CTV distribution map (Fig. 1A) includes mild, decline, and stem-pitting strains. Data used in this figure were compiled from individual country surveys. These surveys were conducted in 1991 and later by a cooperative effort among U.S. and other scientists throughout the Caribbean Basin (Lastra et al., 1992). Recent sampling for CTV in Cuba suggests that incidence is probably low (O'Reilly, 1993; Lee et al., 1993) but nearly the entire industry is on CTV-susceptible sour orange rootstock. Incidence of CTV in Florida, Venezuela, and Colombia far exceeds that of other citrus-producing areas in the Caribbean Basin (Table 1). Stem-pitting strains occur in Colombia and Venezuela, but are rare or absent elsewhere in the Basin. Florida has a high incidence of mild and decline-inducing strains of CTV (Garnsey and Jackson, 1975; Bransky et al., 1986). CTV infection in Florida is estimated at 85 to 95 percent in commercial sweet oranges and at about 50 percent for grapefruit. Tristeza also exists in southern California where it caused severe losses in the 1950s to 1960s, and to a limited extent in the San Joaquin Valley where it is suppressed to low levels by an intensive three-county CTV-eradication program. The virus has recently been detected in low incidence in Texas and is thought to exist, at least in non-commercial citrus, in Arizona. The diversity of CTV strains elsewhere in the Caribbean Basin has not been studied, but serological tests indicate that both decline-inducing CTV strains and mild strains are present (Lastra et al., 1992).

CTV is thought to have originated in southeast Asia and to have been moved throughout the citrus-producing areas of the world, including the U.S., by introduction of CTV-infected budwood. It is likely that the original sources of infection found recently in the Caribbean Basin can be traced to importation and propagation of CTV-infected budwood or nursery trees from other countries, including the U.S. Although aphids spread CTV within citrus-grow-
Figure 1. Distribution of CTV and BCA in the Caribbean Basin. A) Generalized distribution map considering all known CTV strains. B) Distribution of the brown citrus aphid, Toxoptera citricidus, in the Caribbean Basin. Arrows indicate probable historical routes of BCA migration from the earlier infestation in northern South America.
as the brown citrus aphid, which has not yet been found in the continental U.S. (Yokomi, unpublished). Like CTV, though capable of transmitting CTV, are not as efficient in the Caribbean citrus areas (Table 1). This may change as natural spread occurs in areas where infection is now low. Currently the U.S. has a much greater reservoir of CTV than recently the Caribbean, is the major concern in Florida, but contamination of planting materials are not a new threat. How do growers, nurserymen, and backyard growers who travel abroad may encounter a desirable cultivar, and unintentionally introduce contaminated budwood from symptomless trees that carry exotic strains of CTV. Some of the most severe strains of CTV are found in Asia in cultivars which do not show symptoms. In Florida and California, where losses from CTV decline have occurred, producers have tended to replace declining trees on sour orange with scions on more tolerant rootstocks such as citrange, trifoliata, and citrumelo; however, over 20 million trees on sour orange rootstock remain in the U.S. The prevalence of CTV isolates in Florida and southern California has caused some to conclude that the introduction of CTV from other countries is not important (Table 1). Central American and Caribbean CTV isolates that originated from the U.S. via contaminated planting materials are not a new threat. However, introduction of decline isolates into central California, Arizona, and Texas is a primary concern. The introduction of exotic CTV isolates from Asia, Africa, South America, and other areas where more severe and stem-pitting isolates are endemic, either by direct introduction into the U.S. or by first establishing a foothold in Central America and/or the Caribbean, is the major concern in Florida, but loss of trees on sour orange is also a consideration. The magnitude of Caribbean Basin sources can be put into proper perspective by examining the estimated CTV incidence vs. the estimated commercial citrus acreage (Table 1). From this information it can be seen that currently the U.S. has a much greater reservoir of CTV than the Caribbean citrus areas (Table 1). This may change as natural spread occurs in areas where infection is now low. Fortunately, citrus aphids indigenous to the U.S., although capable of transmitting CTV, are not as efficient as the brown citrus aphid, which has not yet been found in the continental U.S. (Yokomi, unpublished). Like CTV, the BCA apparently originated in Asia. The BCA has spread throughout much of the world, including South America, and by the early 1970s it was found in Venezuela. However, it was detected and confirmed in Panama, Costa Rica, and Nicaragua only within the last 5 years (Lastra et al., 1992). It has been reported in nearly all islands of the Caribbean except the Bahamas within the last 2 years and in Haiti, Jamaica, and Cuba during the summer of 1993. The presumed historical routes of the aphid northward from South America through Central America and through Caribbean Islands is shown (Fig. 1B). Its apparent steady movement from northern South America toward Florida and apparent explosive movement in the Caribbean are of great concern. The current known distribution of the BCA, based on recent surveys and reports in Central America and the Caribbean Basin, is shown in Fig. 1B. The recent spread of the BCA to Cuba now places the vector within 90 miles of Florida (shore to shore) or within approximately 200 miles of Florida citrus-producing areas (area to area). BCA also occurs in Hawaii where it is believed to have been imported directly from Asia (Garnsey et al., 1991). Introduction of this efficient vector of CTV in other countries has been followed by severe losses from CTV, and many fear that the Florida industry could be heavily damaged within a few years if the BCA is introduced. Losses of more than $500 million over the next 20 years were predicted for the decline phase of CTV alone if the BCA is introduced into Florida (Behr et al., proceedings of the CTV/BCA task force meeting, Lake Alfred, Oct. 1993). The BCA is considered the most efficient vector of CTV, and recently the ability of the specific biotypes in the Caribbean Basin and Central America to transmit CTV were compared to the aphid species indigenous to the U.S. or BCA from other areas (Yokomi, unpublished). Eradication of the aphid where it now exists in the Caribbean Basin is unfeasible. Although information is available concerning CTV spread and vectoring ability of the BCA from areas in the world where CTV is widespread and the BCA is endemic (McClean, 1975), there is no information on how rapidly the virus moves into areas where there are few CTV-infected trees and/or BCA has been newly introduced. Accurate information on what happens in the first several years after the BCA arrives in new areas is essential for developing control and regulation strategies for Florida. Attempts are being made to collect this information from Caribbean research plots. Such knowledge will help the U.S. citrus industry to develop effective and practical disease and vector control strategies and to develop accurate forecasts of crop losses. For example, if we learn that initial spread is slow when only a few trees are infected, it will indicate that efforts to control further spread by identifying and removing infected trees and controlling aphid buildups could be effective in delaying or avoiding losses. If spread is extremely rapid, it will indicate that such measures are not likely to work and that efforts should be aimed at more long-term solutions such as cross-protection or use of resistant varieties. If the rate of spread varies markedly between locations, we learn what factors are associated with low rates of spread and possibly use them to our advantage in other sites.

One characteristic of the BCA is the prevalence of large colonies and the rapid proliferation of colonies and migrants within an infested grove. The viruliferous winged-adult aphid that first visits a tree and transmits CTV may

### Table 1. Estimated citrus tristeza virus incidence of various citrus-producing countries and areas.

<table>
<thead>
<tr>
<th>Citrus Area</th>
<th>Total Citrus Acreage</th>
<th>Estimated % Infection</th>
<th>Equivalent Acres Infected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bahamas</td>
<td>2,960</td>
<td>36</td>
<td>1,065</td>
</tr>
<tr>
<td>Belize</td>
<td>59,280</td>
<td>13</td>
<td>7,706</td>
</tr>
<tr>
<td>Bermuda</td>
<td>300</td>
<td>5</td>
<td>99</td>
</tr>
<tr>
<td>Costa Rica</td>
<td>42,000</td>
<td>25</td>
<td>10,500</td>
</tr>
<tr>
<td>Cuba</td>
<td>348,000</td>
<td>&lt;5</td>
<td>&lt;17,400</td>
</tr>
<tr>
<td>Dominican Republic</td>
<td>27,170</td>
<td>15</td>
<td>4,075</td>
</tr>
<tr>
<td>El Salvador</td>
<td>17,290</td>
<td>&lt;1</td>
<td>&lt;172</td>
</tr>
<tr>
<td>Guatemala</td>
<td>12,350</td>
<td>&lt;1</td>
<td>129</td>
</tr>
<tr>
<td>Hawaii</td>
<td>500</td>
<td>98</td>
<td>490</td>
</tr>
<tr>
<td>Honduras</td>
<td>29,900</td>
<td>4</td>
<td>1,200</td>
</tr>
<tr>
<td>Jamaica</td>
<td>19,760</td>
<td>2</td>
<td>395</td>
</tr>
<tr>
<td>Mexico</td>
<td>844,700</td>
<td>&lt;1</td>
<td>&lt;8,400</td>
</tr>
<tr>
<td>Nicaragua</td>
<td>55,000</td>
<td>4</td>
<td>1,400</td>
</tr>
<tr>
<td>Panama</td>
<td>14,820</td>
<td>16</td>
<td>2,371</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>13,585</td>
<td>10</td>
<td>1,358</td>
</tr>
<tr>
<td>Florida</td>
<td>791,000</td>
<td>85</td>
<td>672,350</td>
</tr>
<tr>
<td>California</td>
<td>250,000</td>
<td>15</td>
<td>37,500</td>
</tr>
<tr>
<td>Texas</td>
<td>25,000</td>
<td>17</td>
<td>2,507</td>
</tr>
<tr>
<td>Trinidad</td>
<td>14,820</td>
<td>11</td>
<td>1,630</td>
</tr>
<tr>
<td>Venezuela</td>
<td>150,000</td>
<td>99</td>
<td>148,500</td>
</tr>
</tbody>
</table>
deposit young on this tree and then move to several other trees in the area within 24 hours and do likewise. Thus, transmission of CTV by the BCA is favored by numbers of aphids and by efficiency of transmission by individual aphids. BCA will migrate more rapidly than CTV in new areas.

It is very unlikely that the progeny from the aphid that first infected a tree will spread the virus further to surrounding trees. While aphid migrants can be produced within a few days, CTV usually requires 6 to 12 months after aphid transmission for the virus to become systemic throughout the tree (Garnsey et al., 1987). For spread to occur, a new colony must be established in this same tree after the virus becomes systemic, the virus must be acquired by the aphids feeding, and the virus must be carried by new winged-adult aphids to the next tree.

**Indications of CTV Increase Over Time and Aphid Movement Within Groves**

Where the BCA is absent, CTV epidemics normally require several years before all trees in a grove are infected (Cambra et al., 1988; Fishman et al., 1983; Grisoni and Riviere, 1993; Moreno et al., 1988). Normally, CTV-infected trees on sour orange rootstock are removed soon after they decline and become nonproductive. Epidemics of CTV have only rarely been followed closely enough to develop forecasts of tree loss since rapid serological diagnostic tests have been developed only in the last decade (Bar-Joseph et al., 1979; Cambra et al., 1979; Garnsey and Cambra, 1991; Permar et al., 1990; Vela et al., 1986). CTV increase in sweet orange on Troyer due to spread by the cotton aphid, Aphis gossypii, has been monitored for 12 years in Spain (Gottwald et al., 1993) (Fig. 2A,B). In Spain, CTV incidence reached 50% in 8 to 15 years. Data from CTV epidemiology plots in South Florida are demonstrating similar rates of virus infection over time (Gottwald, Garnsey and Irey, unpublished data).

Greenhouse transmission tests have demonstrated that T. citricida is 6 to 25 times more efficient at vectoring most CTV strains compared to A. gossypii (Yokomi, unpublished data). Extrapolation of these data to U.S. conditions in the presence of the BCA is tenuous. However, because the BCA is a much more efficient vector of CTV compared to the cotton aphid, we assume that the epidemic would progress much faster, rendering individual groves on sour orange commercially inefficient or completely destroyed in a few years time after first infection. This is especially true in Florida where up to 20 percent of the trees in some areas are already infected with severe CTV isolates, and provide a high initial inoculum level. Where the BCA is present, 60 to 80 percent of the trees in a grove can become infected with CTV in 1 to 2 years (Grisoni and Riviere, 1993).

The movement of CTV within a grove was also examined (Gottwald et al., 1993). Based on CTV distribution during the initial stages of epidemics, inferences concerning aphid vector movement were made. One would guess that once an aphid migrates into a grove and begins feeding on a virus-infected tree, the aphid would establish a colony and winged adults from this first colony would move into immediately adjacent trees transmitting the virus and establishing a clumped or aggregated CTV distribution pattern due to vector movement to adjacent trees (Fig. 3a). This pattern can sometimes be elongated along rows due to some horticultural factor that influences the insects to move primarily in one direction, directional vector movement, leading to an elongated clump of diseased trees (Fig. 3b). Both of these situations and resulting patterns of disease are quite common for insectvectored virus diseases in many horticultural crops. However, data from the early stages of CTV epidemics in young groves indicated that patterns of CTV incidence were different. CTV infections associated with aphid movement were diffuse or nonadjacent (Fig. 3c). This nonadjacent pattern can best be explained by aphids normally moving several trees (8-24) away rather than to immediately adjacent trees in an ap-

![Figure 2](image-url)
among insect-vectored virus diseases which form groups of infected trees. C) Nonadjacent movement of citrus aphids in Spain, however, gives rise to apparently random CTV spread patterns. Arrows indicate probable scenarios for introduction, primary spread, and secondary spread that could have given rise to each of the indicated patterns.

The following factors contribute directly to the long-distance spread of aphids: escape, transport, trajectory, diffusion, survival, deposition, and redistribution (Taylor, 1986). Each factor can be examined in terms of probabilities to determine the overall likelihood that a viable aphid from the Caribbean or Central America will arrive and reproduce on a suitable host in Florida, Texas, Arizona, and California. In this discussion we examine the probability of the BCA spreading from points in the Caribbean to Florida. Aphids normally are stimulated to form migrants when food reserves dwindle, populations become crowded, etc. Migrations of BCA follow population peaks which usually only occur 2 or at most 3 times a season (Carver, 1978).

Escape: Aphids are not strong fliers and usually take flight only under relatively calm conditions, i.e. when wind speed is less than 1.1 mph (Taylor, 1986). This condition usually occurs in early morning or evening. When an aphid takes flight, it immediately enters a boundary layer of air 15 to 30 feet thick from the ground to just over the tree tops, which passes through the grove (Isard et al., 1990; Taylor, 1986; Kennedy and Ludlow, 1974). Many aphids never escape from this layer and are carried passively by air currents to new locations in the area. For longer distance spread the aphid must escape from the boundary layer to upper air layers. To accomplish this, aphids fly strongly toward the light (the sky), which consumes consid-

Factors Affecting Long-Distance Movement of Aphids

Long-distance movement of aphids most often involves humans unintentionally transporting the insects to new areas. Natural long-distance spread also occurs, but is less likely than other means. Cereal aphids and certain other aphids have been caught in the upper levels of the atmosphere and are thought to have carried cereal and other viruses with them to new locations (Taylor, 1986). In those cases where viruliferous aphids were apparently spread by wind currents, it was usually over land and always in the direction of the prevailing winds (Wallin and Loonan, 1971; Isard et al., 1990). The close proximity of BCA in areas in the Caribbean to Florida has made long-distance natural movement of BCA a topic of concern, especially considering the reports of spread of other aphids by wind. Therefore, the factors involved in long-distance movement of aphids were examined more closely to put the airborne mode of aphid spread and introduction in proper perspective.

parent random movement over larger distances (Gottwald et al., 1993; Sief and Islam, 1988; Gottwald and Garnsey, unpublished). Movement in older groves having trees with interlocking branches has not been studied, but presumably, non-winged aphids could simply crawl from tree to tree along the branches and down a row further accelerating the spread of CTV.

Figure 5. Distribution patterns for aphid spread of CTV. Gray squares indicate CTV-positive trees. White squares represent CTV-free trees. A) Random and B) directional vector movement to immediately adjacent trees resulting in clumped or aggregated patterns of disease are common among insect-vectored virus diseases which form groups of infected trees. C) Nonadjacent movement of citrus aphids in Spain, however, gives rise to apparently random CTV spread patterns. Arrows indicate probable scenarios for introduction, primary spread, and secondary spread that could have given rise to each of the indicated patterns.
erable energy reserves. When they achieve an altitude of about 50 to 200 feet, they are surrounded by light and no longer have the drive to climb. At this point they begin to hover at a lower energy consumption level (Kennedy and Booth, 1963). During this transition, many are often lost to eddies that force them to the ground or into obstructions. Therefore, very few winged aphids that are stimulated to migrate ever break free and make it into the upper air layers. For those that do begin to migrate, 4 hours of flight at 1.1 miles per hour satisfies the migration drive of an aphid and results in movement of about 4.4 miles (Kennedy and Ludlow, 1974). At the end of this time the aphid will begin to descend to the ground, air currents permitting.

Transport: Different altitude levels have quite different transport capabilities (Wallin and Loonan, 1971). Once above the boundary layer, some aphids are transported to upper levels and lost, some are again forced to the ground by further eddies, and only a proportion of the migrating population achieve the appropriate level for long-distance transport.

Trajectory: Once in the upper air layers, aphids are not in oriented flight but simply hover and drift en masse with the wind currents. Probably the most critical issue is the direction that the air mass is moving. Those that have attained the proper level must now be carried in the proper direction, for instance from Cuba due north to Florida. The probability of the proper trajectory is low, because the prevailing air masses move from west to east which would carry the aphids into the Atlantic Ocean. We estimate that only 5% or less of the time would the trajectory be in the proper direction toward Florida and this would have to coincide exactly with the high population times and stimulation of migration of the BCA.

Diffusion: Assuming that the trajectory is correct, many of the aphids in the air parcel are lost to diffusion (Taylor, 1986). Diffusion follows the inverse power law: \( y = a s^{-b} \), where \( y \) = number of aphids, \( a \) = a constant between 0 and 1.0, \( s \) = distance (in meters), and \( b \) = slope of the deposition gradient. Simply put, aerial aphid densities decrease logarithmically with distance (Taylor, 1986). From what we know about aphid gradients from other crops, and the distances between Florida and points in the Caribbean, the estimated number of aphids that would be left after the effects of diffusion and mixing of air parcels is extremely low. For instance, based on the known diffusion gradients for cereal aphids, only 6 and 2 brown citrus aphids of every 100,000 that attain the proper altitude would reach a destination 200 miles (Cuba) or 700 miles (Haiti) away, respectively (Fig. 4).

Survival: Citrus aphids can survive for up to 48 hours without feeding. Thus, some die in flight depending on the duration of the flight. Others die in flight due to the development of parasites, age, or poor health. Parasitism is often high when population levels are high and is a major stimulus for migration. Some are washed out of the aphid cloud by rainstorms, or adverse wind currents such as up or down drafts. Also depending on food reserves, aphids can only fly/hover for about 12 hours before their energy reserves are fully spent and they begin to fall out of the air layer (Cockbain, 1961).

Deposition: Once in the vicinity of citrus in Florida, the aphids must descend and alight. This requires active flight.

Figure 4. Dilution effects of diffusion, air mixing, advection, and other factors on an aphid cloud moving northward. The diagram demonstrates the worst case scenario in which the brown citrus aphid is first established in Cuba. At present the nearest known source of the aphid is eastern Cuba. The diagram also assumes a northward movement of an air mass from Cuba which is highly unusual (estimated at <5% of the time). The prevailing winds are from west to east. The aphid cloud broadens over distance due to the factors indicated in the text such that only a small portion of the aphid cloud would come in contact with Florida.


91
and further expenditure of energy. However, even in moderate winds they are subject to up and down drafts such that they will only rarely make landfall where they wish. Of the 17,594,846 acres in central and south Florida only 791,290 acres or 4.5% are in citrus and usually less than 30% is citrus canopy. Therefore, when the aphids alight in Florida, only 4.5% will encounter citrus acreage and 1.4% will contact citrus foliage.

Redistribution: Once the aphids make landfall, few will encounter citrus. Thus, for those that do not alight on citrus foliage, further movement or flights will be necessary in search of citrus trees before their food reserves run out completely and they die. If the aphid alights in or very near a grove but misses a tree, redistribution is very likely, whereas an exhausted aphid with little or no food reserves is unlikely to be able to search far if citrus is not in the immediate vicinity. In addition, trees encountered must have new flush to sustain the aphids.

Probability calculation: Based on the above factors, the probability is given as \( p = \frac{\text{no. of aphids that leave source}}{\text{rate of escape}} \times \frac{\text{transport capacity}}{\text{trajectory}} \times \frac{\text{diffusion}}{\text{survival}} \times \frac{\text{deposition rate}}{\text{redistribution success}} \).

Considerations for Long Distance Movement of BCA From Caribbean and Central American Sources

The tremendous amount of human traffic in the form of tourism and trade between the Caribbean Islands and U.S. citrus-producing states make chance introduction of the BCA more likely as the vector populations continue to increase in the Caribbean and Central America. The North American Free Trade Agreement (NAFTA), which includes Mexico, may provide additional potential channels for introduction from Central America if and when the BCA makes its way into Mexico. Accurate knowledge of the proximity of this efficient vector of CTV, the potential damage that might occur, if and when it is introduced, and how fast spread of CTV can be expected upon introduction of the BCA is extremely important.

Long distance aerial dispersion of the BCA into Florida has been suggested as an important hazard; however, the probability of windborne entry is negligible when compared to the likelihood of other means of entry into the U.S. If we make some highly conservative assumptions for each of the factors affecting aerial dispersion of BCA, i.e., allowing all factors to have the minimal influence possible (thus the best possible chance for aphid spread is assumed), we can begin to estimate the probabilities of natural spread from various points in the Caribbean basin to commercial citrus regions in Florida.

The probability of an aphid that takes flight from various points in the Caribbean arriving in Florida and landing on a citrus tree are extremely remote. Most of these factors are undetermined for the BCA. Calculations based on conservative best guess estimates and data from cereal aphid spread indicate that only one out of every 10 million to 10 billion aphids that take flight will make it to Florida depending on where they originate. Cuba is the nearest confirmed location of the BCA to the U.S. and is thus taken as a worst case scenario. Nicaragua is the nearest confirmed location in Central America, but the prevailing winds in Central America are rarely toward the north. Since the probabilities of windborne aphids entering the U.S. are extremely low, we should be much more concerned with other more likely modes of spread, principally unintentional introduction by humans. The continued northward migration of the BCA through the Central American land bridge toward points in the U.S. is quite probable. The large volume of human traffic traveling the Pan American highway from BCA-infested areas in Central America into Mexico and then into California, Arizona, and Texas, presents numerous opportunities for the BCA to move continually up the Central American isthmus and become established in new locations even closer to the U.S.

There is extensive commercial and tourist traffic among locations within the Caribbean Basin and between U.S. citrus-producing states and points in the Caribbean and Central America. Commercial shipping by air and water is also on the rise in the region. Numerous confiscations of plant materials, including citrus, are made by U.S. agricultural inspectors at international airports, land borders, shipping docks, and other points of entry. Because of restrictions for moving plant materials by commercial shippers, judicious inspections by agricultural inspectors at ports of entry, and awareness of insects by growers, the probability of introduction of BCA by commercial means is probably low. Lack of knowledge of plant introduction quarantines, restrictions, and of pests and diseases by tourists and the large number of tourists who pass by agricultural inspectors either intentionally or unintentionally without declaring plant materials, makes this mode of introduction more probable. BCA has not yet been found in the Bahamas, but is likely to become established soon. If that happens, private boat traffic between Florida and the Bahamas will become another important potential avenue for introduction.

We have ranked the relative probabilities of different modes of introduction of the CTV and BCA into Florida and other citrus-producing states based on the above discussion and calculations (please see Table 2). The probability of introduction of CTV by natural spread is considered none for Florida and remote for Texas and California from Mexico; whereas the probabilities of spread by commercial, tourist, pleasure, and noncommercial traffic, and by growers and horticulturists is more likely. For the BCA the relative probability of natural spread is extremely low, whereas, spread by commercial traffic, and by tourist, pleasure, and noncommercial traffic is considered much more likely.

In Cuba where the BCA was recently found and Mexico where the BCA is presently absent, CTV incidence is very

Table 2. Relative probabilities of different modes of introduction of CTV and the BCA into Florida and other citrus-producing states.

<table>
<thead>
<tr>
<th>Mode of Spread</th>
<th>CTV</th>
<th>BCA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural spread to Florida from Carribean</td>
<td>Extremely low</td>
<td>Extremely low</td>
</tr>
<tr>
<td>Natural spread to Texas and California from Mexico</td>
<td>Low</td>
<td>Extremely low</td>
</tr>
<tr>
<td>Commercial traffic</td>
<td>Low</td>
<td>Low to moderate</td>
</tr>
<tr>
<td>Tourist, pleasure, and non-commercial traffic</td>
<td>Moderate</td>
<td>Moderate to high</td>
</tr>
<tr>
<td>Growers and horticulturists</td>
<td>Moderate to high</td>
<td>Low</td>
</tr>
</tbody>
</table>

low and severe strains of CTV rare. However, the major portion of the citrus industry in both of these countries is presently on sour orange rootstock. Therefore, once the BCA becomes firmly established in Cuba or is introduced into Mexico and becomes established, epidemics of severe CTV will be slow to start due to the low initial inoculum. Unfortunately, even though the epidemics will be slow at first, the entire industries on sour orange eventually will face very large tree losses due to CTV decline similar to what happened in Venezuela and Brazil when BCA was introduced.

In Florida only ca. 20% of the citrus acreage is on sour orange, but CTV incidence is high. Because of the high initial CTV inoculum in Florida, once the BCA becomes established, epidemics will be very rapid and large tree losses on sour orange would be anticipated. Therefore, unless some control for the BCA can be instituted, 20% of the citrus acreage could be lost within a few years after the BCA is introduced.

An additional concern is the spread of stem-pitting strains of CTV that may be in very low incidence at present in plant material brought into Florida from Asia, etc. and residing in dooryards or remote locations. Stem-pitting damage is not restricted to rootstock and can cause severe production losses, especially in grapefruit. Although it is believed that there is a very low incidence of stem pitting in Florida, the BCA is an excellent vector for stem pitting. Some citrus species, including mandarin, are symptomless for stem pitting and therefore hard to detect, but still allow virus multiplication and are sources of inoculum for aphids. Stem-pitting isolates usually do not kill trees of susceptible cultivars, but severely reduce fruit yield and quality. Unfortunately, because the trees are not killed they continue to be a reservoir of inoculum unless removed. Therefore, although stem-pitting epidemics would progress slowly at first due to low initial inoculum levels, eventual additional production losses are anticipated for the Florida grapefruit industry and also for sweet oranges.

Apparently, severe CTV epidemics in other countries have been triggered by large scale propagation and distribution of infected plants. If a cultivar is introduced into Florida, propagated commercially, and widely distributed, (as was the Star Ruby grapefruit), and this cultivar is infected with CTV, initial inoculum levels would be greatly elevated. Any means which increases the initial level of CTV incidence, will accelerate the rate of CTV epidemics.

Literature Cited


Abstract. Three registered scion groves of about 1,400 trees the strain differentiating monoclonal antibody MCA-13. Trees was positive in the 1993 survey, but severe strains of CTV were positive for CB in 1992, and only one additional tree grafter inoculated into the remaining trees. No additional trees survey in 1991, and mild, cross-protecting CTV strains were removed after the initial trees were positive for CB in the 1991 survey. Trees harboring severe CTV strains in the 2-3 year old scion groves, and 3 Vela, C., M. Cambra, A. Sanz, and P. Moreno. 1986. Use of specific monoclonal antibodies for diagnosis of citrus tristeza virus, p. 55-61. In L. W. Timmer and S. M. Garnsey (eds.). Proc. 10th Conf. IOCV.}

The occurrence of severe strains of citrus tristeza virus and citrus blight in registered scion groves in the Indian River The budwood registration program in Florida (FBRP) was established in 1952 with the purpose of preventing propagation of psorosis through citrus nurseries (Norman, 1957). The program allowed for the establishment of blocks of registered budwood trees in field locations which could be used for registered budwood after they bore fruit in ensure trueness of type. Buds cut from the mother trees were used to produce budlings in nurseries.

The same year that the FBRP was established, citrus tristeza virus (CTV) was officially recognized as present in Florida from results by Grant (1952) using Mexican lime indicator plants. When the FBRP program began, CTV indexing was included as a part of the program, and trees were removed from registered status if CTV was present. However, in 1964 mother trees were no longer removed from registered status as they became CTV infected (Lee and Rocha-Peña, 1992). CTV had been recognized as present and spreading for the previous decade, but unlike California, Brazil, Argentina and other citrus areas where CTV was present, there was little indication that CTV was causing tree losses in trees on sour orange rootstock in Florida, in fact sour orange was one of the most popular rootstock being propagated (Bridges, 1974).

The complexity and severity of CTV changed in Florida in the decades following the establishment of the FBRP. In the 1950s, CTV-induced decline (CTV-ID) was noted at scattered, isolated locations in Orange county in 1956 (Knorr and Price, 1955-59), in Orange, Lake and Seminole counties (Knorr, 1957) and in the Ft. Pierce area (M. Cohen, personal communication). In the 1960s the spread of CTV-ID on sour orange was noted in the Ft. Pierce area (Bridges, 1966), but CTV did not appear to be a problem in other areas. In 1975 a destructive outbreak of tree loss due to CTV-ID occurred in western Orange and southern Lake counties (Garnsey and Jackson, 1975).

A survey conducted of budwood trees being used for propagation on sour orange rootstocks in 1979 indicated most tree loss due to CTV-ID occurred in western Orange and southern Lake counties (Knorr and Price, 1955-59), in Orange, Lake and Seminole counties (Knorr, 1957) and in the Ft. Pierce area (Bridges, 1966), but CTV did not appear to be a problem in other areas. In 1975 a destructive outbreak of tree loss due to CTV-ID occurred in western Orange and southern Lake counties (Garnsey and Jackson, 1975).

A survey conducted of budwood trees being used for propagation on sour orange rootstocks in 1979 indicated most sweet orange scion and about half of the grapefruit scions were CTV infected, but biological indexing of random samples indicated few severe CTV and/or seedling yellows.