

Transmission of Exotic Citrus Tristeza Virus Isolates by a Florida Colony of *Aphis gossypii*

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ABSTRACT

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A diverse group of citrus tristeza virus (CTV) isolates collected from 10 countries (Argentina, Brazil, China, Israel, Japan, Reunion, South Africa, Spain, Taiwan, and the United States) was tested for transmissibility by a Florida colony of the melon aphid, *Aphis gossypii*. Of 42 isolates tested, 21 were transmitted by the aphid. At least one isolate from each country was transmitted. Transmission percentages calculated for single aphid transmission ranged from 3 to 11% for some exotic isolates. Aphid-transmitted subcultures of several original source isolates that induce CTV decline, seedling yellows, and sweet orange and grapefruit stem pitting were compared for host reactions. All disease components were transmitted. Reduction of virulence of some aphid-transmitted subcultures was obtained by deliberate selection of variants in Mexican lime indicators compared with the original isolate. These results indicate that exotic CTV isolates, markedly more destructive to citrus than CTV isolates commonly found in Florida, could be spread readily by endemic *A. gossypii*, if introduced.

Many isolates of citrus tristeza virus (CTV) that vary in severity in different hosts have been described worldwide. Regional differences in isolate severity and vector transmissibility have been described. Mild CTV isolates that cause symptoms only in Mexican lime (*Citrus aurantiifolia* (Christm.) Swingle) are common in Florida (9). Isolates causing stunting or decline in sweet orange (*C. sinensis* (L.) Osbeck) or sour orange (*C. aurantium* L.) rootstock also occur in the state (4,8) and both types are transmitted by endemic populations of the melon aphid, *Aphis gossypii* Glover (13,23). Isolates of CTV that cause severe stem pitting (SP) in grapefruit (*C. paradisi* Macfad.) or sweet orange cultivars and/or a severe seedling yellows (SY) reaction in sour orange, grapefruit, and lemon (*C. limon* (L.) Burm. f.) seedling indicators (21) are rare in Florida. However, these severe SP and SY isolates are common in citrus-growing areas throughout the world where the brown citrus aphid, *Toxoptera citricidus* Kirkaldy, is endemic. This aphid is an efficient CTV vector (6), and its presence has been associated with a high incidence of severe SP isolates of CTV (17).

During the past 20 years, transmission of severe isolates of CTV by *A. gossypii* has been observed in California and

Israel and apparent increases in transmission efficiency for certain isolates by *A. gossypii* have been reported (2,14,19,20). A high rate of CTV decline in mature groves in Florida has occurred recently and has been associated with vector spread (4). These observations suggested that rapid dissemination of severe isolates of CTV may not be wholly dependent on the presence of *T. citricidus*.

An international collection of CTV isolates has been established recently under quarantine at Beltsville, MD, for comparative studies of the biological diversity of this virus and to improve isolate characterization and identification (7). As part of this effort, controlled studies were initiated on the transmissibility of numerous exotic isolates of CTV by *A. gossypii*. Included in these tests were some of the most severe SP isolates of CTV that have been described. In this paper, we report on the transmission of numerous exotic CTV isolates by a Florida colony of *A. gossypii* and discuss its basic and practical implications for the state's citrus industry.

MATERIALS AND METHODS

CTV isolates. CTV isolates were introduced under USDA APHIS quarantine permit into Beltsville, MD, as CTV-infected citrus budwood and were graft-inoculated into healthy Mexican lime and cultivars Madam Vinous or Pineapple sweet orange. After several months, systemic infection was confirmed by enzyme-linked immunosorbent assays (ELISA) (1,3). These primary source plants, maintained in a quarantine greenhouse at Beltsville, were the virus

acquisition plants for all aphid-transmission tests.

Forty-two CTV isolates from 10 different countries (Argentina, Brazil, China, Israel, Japan, Reunion, South Africa, Spain, Taiwan, and the United States) were tested and are described briefly in Table 1. In most cases, the isolate description is from the cooperator who provided the sample. A range of isolates differing considerably in the type of symptoms induced was included in this study. All caused symptoms in Mexican lime, but these varied from mild to extremely severe. At least 23 isolates caused decline or stunting in sweet orange, grapefruit, mandarin orange (*C. reticulata* Blanco), or sour orange rootstock, whereas 22 isolates caused either SY or SP symptoms. Some isolates, such as B6 and B14, were severe for all of the disease symptoms, whereas others caused only one or two of the disease symptoms. Isolates from Florida (B2, B3, and B27), California (B4 and B6), Israel (B23, B24, and B26), and Spain (B53) with known histories of *A. gossypii* transmissibility were included for reference.

Aphid vectors. The test colony of *A. gossypii* was started from a single parthenogenetic aphid from a field colony found on citrus in Winter Garden, FL. The colony was reared on kenaf (*Hibiscus cannabinus* L.) under laboratory conditions previously described (23). Aphids were transported on intact leaves from Orlando, FL, to Beltsville, MD, for vector tests.

Vector transmission. Methods for CTV vector transmission were generally as described previously (19,23). Donor plants were cut back several weeks before acquisition feeding to stimulate flushes of new growth. Aphids were established on new flushes of the acquisition host by placing heavily infested kenaf leaves in screen cages that were placed over new growth. Aphids moved to the acquisition host as the kenaf leaf dried. Aphids were transferred from acquisition hosts to receptor plants by camel's-hair brush. Healthy young Mexican lime seedlings were greenhouse-grown in Orlando, FL, transported to Beltsville, MD, and used as receptor plants in vector tests. These plants were 7-15 cm tall and had new flushes of growth favorable for aphid colonization.

Virus acquisition access periods and

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inoculation access periods were 24 hr each in an air-conditioned headhouse with supplemental 24-hr fluorescent lights. Two types of transmission tests were conducted. The first was a preliminary attempt to obtain aphid-transmitted cultures free of other pathogens from primary isolates. These tests were done using 20 aphids per receptor plant. Replications varied according to the donor tissue available. The second was a more precise test, using 10 aphids per receptor plant and 10 or 20 replications to obtain comparative transmission data. In both types of tests, plants were sprayed with malathion immediately following the inoculation access period to eliminate the vector and were returned to an aphid-free greenhouse. All vector tests were conducted from October through May when greenhouse temperatures were most favorable for CTV disease development. Isolates were tested for aphid transmissibility only if the donor flush was in good condition for virus acquisition.

Transmission efficiency was calculated as the probability of a single aphid transmission expressed as a percentage and was determined by the formula $([1-I]^{1/K}) \times 100$, where I = proportion of test plants infected and K = number of vectors per test plant (10).

ELISA. Double-antibody sandwich ELISA (1) was used to confirm CTV infection and to determine relative serological titer of CTV in donor hosts. After transferring aphids from the donor to receptor plants, leaf midribs and bark from shoots where aphids had fed on the donor were harvested, diluted 1/100 in grinding buffer, and homogenized. The source of IgG for coating and preparation of alkaline phosphatase conjugates was a polyclonal antiserum to whole, unfixed CTV isolate T4 (3). This antiserum has reacted to all isolates of CTV tested from many different areas (1), including the 42 isolates used in the present report.

CTV indexing. A profile of the biological host reaction of selected CTV isolates and an aphid-transmitted subculture of each of these isolates was determined in a set of five indicator hosts, including Mexican lime grafted on *C. macrophylla* Wester rootstock, sweet on sour orange rootstock, seedlings of sour orange, Duncan grapefruit, and Madam Vinous, as previously described (7,22). Healthy indicator plants were grown in Orlando, FL, or Riverside, CA, and were transported to Beltsville, MD, where they were graft-inoculated with test isolates when the basal stem diameter was 5–10 mm. Three replications per host were used. Inoculations were performed during the cooler periods of the year and symptoms were read between October and May after an incubation period ranging from 6 to 12 mo. Infection was verified by ELISA where virus symptoms

were not clear.

Foliar symptoms were evaluated visually, and stunting was determined by measuring and/or weighing shoot growth 10–12 mo after inoculation. Stem

pitting was determined by peeling the bark from the main stem and examining the wood for pits. Disease severity was rated for each host on a scale from 0 to 3 (using 0.5 unit increments), where

Table 1. Transmission of *Aphis gossypii* of citrus tristeza virus (CTV) isolates collected from 10 different countries

Origin and donor identification ^a	BARC code ^b	Host reaction ^c			Aphid transmission ^d
		Decline	SY	SP	
Argentina					
AMC-declinamiento	B76	+ ^e	+	+	+
Brazil					
1743/82 Mild CTV/Pera	B12	+	+	+	+
1743/89 Common CTV/Pera	B13	+	+	+	+
1932/534 Capão Bonito	B14	+	+	+	+
1932/1266 Capão Bonito	B15	+	+	+	+
Galego mild	B16	—	—	—	—
1932/435 Capão Bonito	B17	+	+	+	+
Standard common CTV	B18	+	+	+	—
Satsuma, stem pitting	B77	—	—	+	+
China					
Stem pitting	B65	+	+	+	+
Israel					
127T	B22	—	—	—	—
MOR 4-8	B23	—	—	—	+
HED 11-14	B24	ND	+	—	+
ST	B25	—	—	—	—
HT	B26	—	—	—	+
Japan					
HM-55	B29	—	—	—	—
No. 1513	B30	+	+	+	+
HS-34, Hassaku dwarf	B31	—	—	+	+
Reunion					
Severe	B1	+	+	+	+
South Africa					
Nartia	B7	—	—	—	—
7K6, stem pitting	B8	+	—	+	—
Bolton, stem pitting	B46	+	—	+	+
SR4 Bedlane, stem pitting	B47	+	—	+	+
Field	B48	ND	ND	ND	—
Sweet orange, stem pitting	B58	+	+	+	+
Spain					
T-300	B32	—	—	—	—
T-308	B34	ND	ND	ND	—
T-385	B35	—	—	—	—
T-388	B53	+	+	+	+
Taiwan					
Field	B37	+	+	+	+
Field	B38	ND	ND	ND	—
Field	B42	+	+	+	+
Field	B44	ND	ND	ND	—
United States					
California					
T514	B4	—	—	—	—
T516	B5	—	—	—	—
SY568	B6	+	+	+	—
Florida					
T30a	B2	—	—	—	—
T36	B3	+	—	—	—
T66a	B27	+	—	—	—
T68	B28	+	+	ND	+
Hawaii					
Pera, stem pitting	B10	+	+	+	+
Lyman no. 2	B11	+	—	—	—

^aIdentification is from cooperator and represents isolate characterization according to local standards.

^bCode number assigned to isolate housed in CTV collection under quarantine at the Beltsville Agricultural Research Center (BARC).

^cGeneral reaction of isolate on diagnostic economic indicators based on information from cooperators and data from assays at Beltsville. Decline in sweet orange or sour orange rootstock; seedling yellows (SY) in sour orange; stem pitting (SP) in Duncan grapefruit; and/or cv. Madam Vinous sweet orange.

^dTransmission test conducted with either 10 or 20 aphids (*Aphis gossypii*) per Mexican lime receptor plant. Donor host was sweet orange or Mexican lime. Tests were conducted in the greenhouse in Beltsville, MD, at least two different times for each of these isolates.

^e+ = Very strong reaction observed in this diagnostic indicator host, — = negative to mild reaction, ND = no data available. All isolates react in Mexican lime with varying intensities.

3 is severe. A weighted cumulative score, as described by Garnsey et al (7), was used to estimate overall economic significance of the isolate.

RESULTS

Of 42 CTV isolates tested, 21 were transmitted by *A. gossypii* (Table 1). At least 19 of the transmitted isolates were from known SY and/or SP sources. In contrast, only four of the 21 nontransmitted isolates were from SY or SP isolates. Transmitted isolates included at least one from each of the 10 countries represented in our tests.

The high proportion of CTV isolates transmitted indicated that *A. gossypii* was a good vector of the diverse collection of CTV isolates (Table 2). The highest transmission rates (determined by the probability of single aphid transmission) were obtained with isolates B77 from Brazil (11%) and B58 from South Africa (9%). Transmission of most of the other isolates ranged from 3 to 7%. Serological tests conducted on selected isolates showed no correlation between antigen titer in donor acquisition tissue and rate of vector transmission (*data not shown*). Isolates B23 from Israel and B53 from Spain were previously reported to be transmitted by the melon aphid and were transmitted efficiently in our tests. Isolate B27, a Florida decline isolate also known to be readily transmitted by *A.*

gossypii in Florida, and isolate B11, a mild isolate of unknown transmissibility from Hawaii, were not transmitted in this particular study.

Examination of the host reaction of aphid-transmitted subcultures clearly indicated that all the disease components of the exotic CTV isolates were transmitted (Table 3). Isolate B14, a severe Capão Bonito isolate from Brazil, was transmitted without any change of virulence. The severe SY reaction of this isolate in contrast to the symptomless response of isolate B2, a mild Florida isolate, is shown in sour orange (Fig. 1A).

The severe vein-corking symptom induced by the aphid-transmitted source of isolate B14 is shown in Mexican lime (Fig. 1B). Individual disease ratings of the aphid-transmitted subculture of B10, B13, B30, and B31 were milder than those for the original isolate, as indicated by the overall weighted cumulative scores (Table 3).

DISCUSSION

These results indicated that Florida *A. gossypii* can transmit a number of exotic isolates of CTV. A high proportion of these isolates were SY or SP isolates.

Table 2. Comparative transmissibility of *Aphis gossypii* of selected citrus tristeza virus (CTV) isolates collected from different countries

BARC code ^a	No. infected/ no. inoculated	Calculated transmission percentage for single aphids ^b
B10	7/20	4
B11	0/10	0
B12	4/10	5
B14	10/20	7
B23	6/20	4
B27	0/20	0
B30	5/20	3
B31	3/10	4
B42	2/20	1
B47	5/9	6
B53	4/10	5
B58	5/8	9
B65	2/9	3
B76	3/10	4
B77	7/10	11

^aCode number assigned to isolate housed in CTV collection under quarantine at the Beltsville Agricultural Research Center (BARC).

^bTen aphids per receptor plant were used. In several cases, *Fusarium* wilt in the Mexican lime receptor reduced the number of replications from that described in the text. Transmission efficiency calculated as the probability (expressed as a percentage) of transmission by a single aphid, and determined by the formula $[(1 - I)^{1/K}] \times 100$, where I = proportion of test plants infected and K = number of vectors per test plant (10).

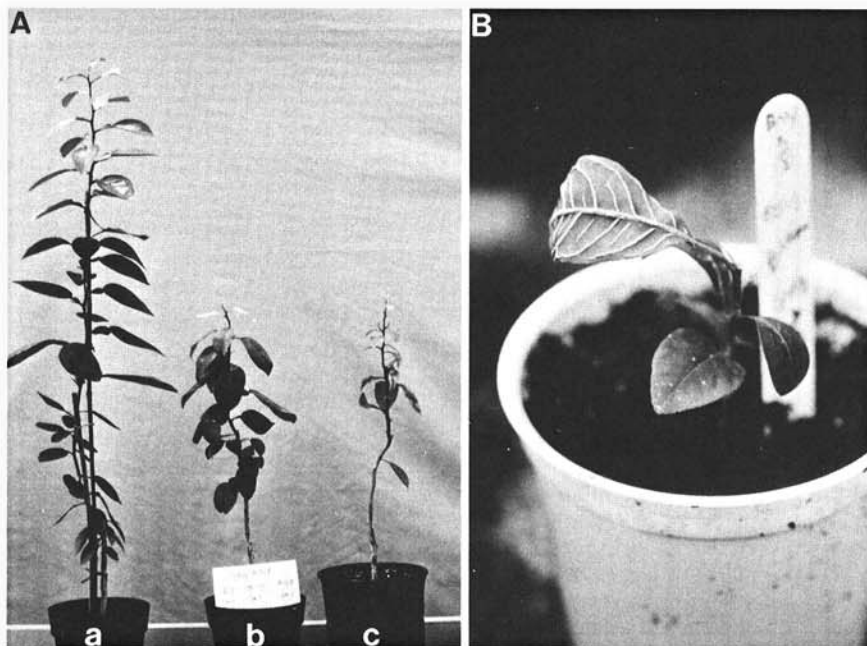


Fig. 1. Symptoms induced by a subculture transmitted by *Aphis gossypii* of severe citrus tristeza virus isolate B14 from Brazil. (A) Symptoms in sour orange seedlings inoculated with a) B2, a mild Florida isolate (symptomless in this host), b) B14 original source isolate, and c) aphid-transmitted subculture of isolate B14. (B) B14 aphid-transmitted subculture in Mexican lime showing vein corking, one of the most severe symptoms caused by the virus.

Table 3. Comparison of host reactions of aphid-transmitted subcultures of citrus tristeza virus (CTV) with the corresponding original source

BARC code ^a	Inoculum source	Host reaction ^b					Weighted cumulative score ^c
		ML	Decline	SY	SP-DG	SP-MV	
B10	Original source	2.5	3.0	3.0	2.5	2.0	37.5
	Aphid transmission	2.0	2.5	2.0	1.5	1.0	24.0
B13	Original source	2.0	3.0	3.0	2.0	2.0	35.0
	Aphid transmission	1.5	3.0	2.0	1.5	1.0	24.5
B14	Original source	3.0	3.0	3.0	3.0	3.0	45.0
	Aphid transmission	3.0	3.0	3.0	3.0	3.0	45.0
B30	Original source	2.0	3.0	ND	3.0	2.0	30.0 ^d
	Aphid transmission	2.0	1.5	ND	1.0	0	9.0 ^d
B31	Original source	2.0	0	0	3.0	1.5	21.5
	Aphid transmission	2.0	0	0	3.0	ND	14.0 ^e

^aCode number assigned to isolate housed in CTV collection under quarantine at the Beltsville Agricultural Research Center (BARC).

^bMexican lime (ML) on *Citrus macrophylla* rootstock; decline in sweet orange on sour orange rootstock; seedling yellows (SY) in sour orange; stem pitting in Duncan grapefruit (SP-DG); and stem pitting in cv. Madam Vinous sweet orange (SP-MV). Rating of severity on 0-3 scale (using 0.5 unit increments), where 0 = no symptoms and 3 = most severe; ND = no data.

^cWeighted cumulative score for an isolate calculated by multiplying the individual host severity score of ML \times 1, decline \times 2, SY \times 3, SP-DG \times 4, and SP-MV \times 5 and adding the products (9).

^dScore without SY factor.

^eScore without SP-MV factor.

Roistacher and Bar-Joseph (16) had also observed a higher transmission efficiency with more virulent CTV isolates. No relation was found between serological titer of CTV isolates and their aphid transmissibilities in our tests. This agrees with a previous report with Florida isolates (23) and with observations of Bar-Joseph and Loebenstein (2), who found no differences in CTV particle counts in donor extracts and vector transmission.

The transmission efficiencies for many of the exotic isolates (Table 2) are particularly noteworthy because experimental conditions were not always optimum. The greenhouse lacked a controlled cooling system, which resulted in variable temperatures. Temperatures were generally tolerable for CTV infection and replication during the duration of the experiments, but occasionally greenhouse temperatures exceeded 40 C for at least several hours during the day. The failure of *A. gossypii* to transmit California and Florida isolates such as B2, B3, B4, B6, and B27 (Tables 1 and 2), normally transmissible by *A. gossypii* (19,23), was more likely due to the limited attempts performed or suboptimal conditions. However, the comparatively high transmission rates that did occur for some isolates (Table 2) suggest that some exotic CTV isolates may be transmitted more efficiently than endemic Florida isolates such as B27.

Bioassays of aphid-transmitted subcultures showed that the decline, SY, and SP symptoms caused by the severe CTV isolates were also induced by the subculture. This was most evident with isolate B14 (Table 3). The apparent reduction in virulence of some aphid-transmitted subcultures was not surprising because we deliberately chose to index those subcultures of isolates B10, B13, B30, and B31 that appeared milder than the original isolate, based on symptoms in the primary Mexican lime seedling receptor plant.

Whereas many economically destructive isolates of CTV cause strong symptoms for CTV decline, SY, and SP, some isolates cause only one or two of these disease symptoms (Table 1). Furthermore, it is well known that different isolates can vary in severity in different indicator hosts (7). Our findings, that aphid passage can change symptom severity from that observed in the original source isolate, agree with earlier reports. McClean (12) observed that SP symptoms were caused by more than one strain of CTV. Martinez and Wallace (11) found that *A. gossypii* can transmit to receptor plants the complete CTV complex present in the original host as well as non-SY CTV from SY-infected source plants. Raccach et al (15) demonstrated that a field citrus tree can contain several CTV isolates that differ in their aphid transmissibilities. Host passage of

CTV through *Passiflora* spp. by using the vector *A. gossypii* has been reported to attenuate SY isolates (18). The decrease in CTV severity observed in the aphid-transmitted subcultures of B10, B13, B30, and B31 probably resulted from separation from a mixture of isolates in the donor plant rather than modification by aphid passage by the vector. The donor and receptor plants used were not selective hosts of CTV isolates (12). Additional tests of the entire population of aphid-transmitted subcultures, along with more subtransmissions, are needed to clarify this issue.

Our data indicate that if exotic CTV isolates were brought into Florida they would likely be transmissible by endemic *A. gossypii* and could be readily spread in commercial citrus groves. Because CTV is already widely distributed in sweet oranges in Florida (9), the presence of existing isolates could affect the field spread of the exotic isolate in this host. However, superinfection by decline isolates of CTV in sweet orange on sour orange trees containing nondecline isolates has occurred (4). Many Florida grapefruit trees are still free of CTV and would certainly be susceptible to infection by exotic isolates. It is widely assumed that the introduction of *T. citricidus* would dramatically increase natural spread of severe isolates of CTV, especially into grapefruit. However, it is clear that exotic CTV isolates already constitute a hazard with endemic Florida vectors. This has also been demonstrated in California (5), where Roistacher et al (19) showed efficient transmission of several presumed exotic CTV isolates by small populations of *A. gossypii*. Our results obtained from a more extensive survey of exotic CTV isolates confirm the probability of field spread of severe CTV isolates, and show further that this probability is not unique to a particular isolate.

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