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Tomato infectious chlorosis virus – a new clostero-like virus transmitted by *Trialeurodes vaporariorum*

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Abstract

A previously undescribed virus disease of tomato, other crops and weed hosts was found in California. Affected tomato plants exhibited interveinal yellowing, necrosis and severe yield losses. Leaf dips and purified preparations contained closterovirus-like long flexuous, filamentous particles approximately 12 × 850–900 nm. The virus, designated as tomato infectious chlorosis virus (TICV), is transmitted in a semipersistent manner by the greenhouse whitefly, *Trialeurodes vaporariorum*. The host range of the virus is moderate (26 species in 8 plant families) but includes some important crops and ornamental species including tomato, (*Lycopersicon esculentum*), tomatillo (*Physalis ixocarpa*), potato (*Solanum tuberosum*), artichoke (*Cynara scolymus*), lettuce (*Lactuca sativa*) and petunia (*Petunia hybrida*). The virus has been found in a number of different locations in California and has a number of potential vehicles of movement including greenhouse grown ornamentals, tomato transplants, artichoke cuttings and potato seed. The virus has the potential to spread to other growing regions with resident populations of the greenhouse whitefly. The host range, particle size, insect transmission, and serology clearly distinguish TICV from previously described viruses.

Introduction

During the fall of 1993, Bill Glover, Crop Production Services, Inc. (Riverside, California) brought to our attention an extremely serious disease syndrome of tomato (*Lycopersicon esculentum* Mill) in the Irvine area of Orange County, California. This disease induced interveinal yellowing, necrosis and severe crop losses in the entire region. The disease appeared to be associated with the occurrence of high populations of the greenhouse whitefly (*Trialeurodes vaporariorum* (Westwood)). Subsequent studies in our laboratory have shown that the disease is caused by a previously undescribed clostero-like virus which is transmitted by *T. vaporariorum*. The virus infects not only tomato but also other economically important crops as well as some weed hosts. The disease, on a number of hosts, closely resembles in symptoms other whitefly-transmitted yellowing diseases and is designated herein as tomato infectious chlorosis (TIC) and the virus causing the disease as tomato infectious chlorosis virus (TICV). A preliminary report of this research has been given [Duffus *et al.*, 1994c].

Materials and methods

Virus source and whitefly maintenance

The virus isolates used were obtained from several commercial tomato plants collected in the Irvine area of Orange County, California during the fall of 1993. The virus was maintained in tomato and transferred from plant to plant via inoculation with the whitefly vector.

A colony of *T. vaporariorum*, originally collected in the greenhouse in Salinas in the early 1960's, was reared on seedling *Solanum dulcamara* L. in muslin-covered cages. The cages were maintained in growth

rooms at temperatures that ranged from 26 to 32 °C or in an insectary greenhouse. *T. vaporariorum*, collected in the field on squash (*Cucurbita pepo* L.) in the fall of 1993 were also reared on squash in a similar manner as the older *T. vaporariorum* colonies.

The sweetpotato whitefly, *Bemisia tabaci* Gennadius (biotypes A and B by isozyme analysis) [Liu *et al.*, 1992], was reared on sweetpotato (*Ipomoea batatas* (L.) Lom.) in muslin-covered cages, as above. *B. tabaci*, biotype A, was originally collected on cotton, *Gossypium hirsutum* L., in 1981, and biotype B was collected from melon (*Cucumis melo* L.) in 1990. Virus sources in the various experiments were tomato plants inoculated about 30 days earlier. *Nicotiana clevelandii* Gray and/or *Physalis wrightii* Gray were used as test plants. Following inoculation with TICV via whiteflies, the plants were sprayed with resmethrin (to eliminate the vectors) and placed in greenhouses. All plants were grown in screened greenhouses fumigated at weekly intervals with dichlorvos and resmethrin.

Host range

The host range was determined by allowing whiteflies 24 h acquisition feedings on diseased tissue and then transferring 30–50 insects to each of 10 seedlings of each species tested and feeding them for 48 h. The presence of virus in each plant species tested for susceptibility was determined by whitefly transfer (30–50/plant) to *N. clevelandii* or *P. wrightii* seedlings 30–45 days after inoculation. Recovery tests from field plants gave evidence as to some of the species naturally infected with TICV. The virus was recovered by feeding nonviruliferous greenhouse whiteflies on collected field plants for 24 h and transferring the insects to healthy indicator seedlings and feeding them for 48 h.

Transmission

Attempts were made to transmit the TICV mechanically using 0.1 M sodium phosphate buffer, pH 7.0, containing 0.02 M sodium sulfite. The virus sources included tomato, *P. wrightii*, and *N. clevelandii*. The plants inoculated included these and a number of other species found to be susceptible when inoculated via the whitefly vector.

Transmission attempts with insects included *T. vaporariorum* collected in the field, *T. vaporariorum* from cultures collected in the early 1960's, *B. tabaci* (biotypes A and B), *T. abutilonea* (Haldeman), and *Myzus persicae* (Sulzer). Transmission attempts were made by confining the insects to diseased plants and transferring them to healthy indicator species as discussed under virus and vector relationships.

Virus-vector relationships

Transmission tests for different species of whiteflies were made by the leaf cage method described previously [Cohen *et al.*, 1983]. Five tests (ten plants per replication) were performed in each of the experiments for determination of the transmission by different insect species, vector efficiency, acquisition, inoculation, and transmission threshold periods. Unless otherwise stated, 30 insects per cage were used on each plant in the different tests. The ability of viruliferous whiteflies to retain TICV was determined by allowing the insects acquisition periods of 24 h on diseased plants and then transferring them in groups of 30 in daily serial transfers on healthy indicator seedlings.

Virus purification

Virions were purified using modifications of methods for lettuce infectious yellows virus (LIYV) [Duffus *et al.*, 1986; Klaassen *et al.*, 1994]. TICV-infected *N. clevelandii* plants were harvested 2–3 wk after inoculation. Plants were homogenized in a meat grinder with cold extraction buffer (0.1 M Tris-HCl, pH 7.4) plus 0.5% (w/v) Na_2SO_3 and 0.5% (v/v) 2-mercaptoethanol [Klaassen *et al.*, 1994]. The plant material was further homogenized with a ball mill for 2 h at 4 °C. The crude extract was expressed through cotton muslin. Triton X-100 was added to a final concentration of 2% (v/v) and the extract was stirred overnight at 4 °C. The mixture was centrifuged in a Sorvall GSA rotor at 10,000 g for 10 min. The supernatant was ultracentrifuged for 1 h at 118,000 g in a Beckman 70 Ti rotor over a 5-ml cushion of 20% sucrose in extraction buffer plus 2% Triton X-100. The pellets were resuspended overnight at 4 °C in TE (10 mM Tris-HCl, pH 7.4, 1 mM EDTA). Triton X-100 was added to the suspension at a final concentration of 2% (v/v) and again stirred for 1 h at 4 °C, followed by centrifugation in a Sorvall SS-34 rotor at 8,000 g for 10 min. The supernatant was layered over 4 ml of 20% (w/v) sucrose in TE and centrifuged in a Beckman 70 Ti rotor for 2 h at 90,000 g. The pellets were resuspended overnight in TE. The suspension was centrifuged in a Sorvall SS-34 rotor at 8,000 g for 10 min. The supernatant was layered on step cesium gradients prepared as described by Gumpf *et al.* [1981]. Gradients were centrifuged in a Beckman

SW 28 rotor for 7 hrs at 83,000 g at 10 °C. Fractions containing TICV virions were dialyzed at 4 °C against three changes of TE.

Antiserum production and serology

Purified TICV antigen, in aliquots of 0.5 ml, were administered, one injection subcutaneous (0.4 A_{260} OD), and 3 intramuscular (0.4, 0.8 and 1.6 A_{260} OD) into a rabbit. Each aliquot was mixed with an equal volume of Freund's complete adjuvant just prior to injection. Bleedings were initiated at the sixth week after the first injection. Enzyme-linked immunosorbent assays (ELISA) methods employed were the double antibody sandwich method [Clark and Adams, 1977] except that the coating immunoglobulin was used at 1 μg/ml and enzyme-conjugate was 1:2000.

Results

Geographical distribution

The virus was first found in 1993 in the Irvine area of Orange County, California. Initial observations by Bill Glover (Crop Productions Services – Riverside) indicated that symptoms of the disease affected virtually 100% of the plants in every field in the Irvine growing area. The following spring (1994) the area near Irvine and south to Encinitas was surveyed for occurrence of the disease. The disease was found and recoveries were made from fields and/or greenhouses in the agricultural region near Irvine, the Orange County-San Diego County line region and south to Oceanside, Carlsbad and Encinitas in San Diego County.

In July of 1994, Dr. Bryce Falk brought to our attention a symptom syndrome similar to that induced by TICV in field tomatoes being grown as part of the Sustainable Agriculture Farming Systems project at the University of California, Davis (Yolo County). TICV was isolated from field tomato plots and greenhouses on the Davis campus. The disease was subsequently found in commercial tomato breeding greenhouses 15 miles to the north of Davis and later in central California (San Benito County) in commercial greenhouses. These later occurrences are over 400 miles from the original findings.

Host range and symptoms

TICV induced severe yellowing and/or reddening symptoms, stunting, rolling, and brittleness of affected leaves in a wide range of weed and crop species. Species that naturally show red pigment tended to show intensification of red color in interveinal areas when infected.

Tomatoes initially showed bright interveinal yellowing symptoms on the older leaves. As the disease progressed, the yellowing developed acropetally. The leaves became thickened, brittle, and rolled. Bronzing and necrosis of the older leaves were accompanied by a decline in vigor and reduction in fruit yield (Fig. 1).

Plants susceptible to TICV are grouped by family

Chenopodiaceae – *Chenopodium capitatum* (L.) Asch., *C. murale* L.

Compositae –*Cynara cardunculus* L., *C. scolymus* L., *Lactuca sativa* L., *Picris echioides* L., *Senecio vulgaris* L., *Sonchus oleraceus* L., *Zinnia elegans* Jacq.

Cruciferae – *Capsella bursa-pastoris* (L.) Medic.

Geraniaceae – *Erodium cicutarium* (L.) L'Her., *Geranium dissectum* L.

Leguminosae – *Trifolium subterraneum* L.

Malvaceae – *Anoda cristata* (L.) Schlecht.

Solanaceae – *Lycopersicon esculentum* Mill., *Nicotiana benthamiana* Domin, *N. clevelandii* Gray, *N. glauca* Graham, *Petunia hybrida* Vilm., *Physalis alkekengi* L., *P. floridana* Rybd., *P. ixocarpa* Brot., *P. wrightii* Gray, *Solanum tuberosum* L.

Umbelliferae – *Conium maculatum* L.

Plants not susceptible to TICV under the conditions of this test

Aizoaceae – *Tetragonia expansa* Murr.

Amaranthaceae – *Gomphrena globosa* L.

Apocynaceae – *Vinca minor* L.

Caryophyllaceae – *Dianthus chinensis* L., *Spergula arvensis* L.

Chenopodiaceae – *Beta macrocarpa* Guss., *B. vulgaris* L., *Chenopodium amaranticolor* Coste and Reyn., *C. quinoa* Wild., *Spinacia oleracea* L.

Compositae – *Helianthus annuus* L., *Tagetes patula* L., *Taraxacum officinale* Weber

Convolvulaceae – *Convulus arvensis* L., *Ipomoea purpurea* (L.) Lam., *Dichondra repens* Forst.

Cruciferae – *Brassica oleraceae* L. var. *botrytis*, *Raphanus sativus* L., *Thlaspi arvense* L.

Cucurbitaceae – *Citrullus vulgaris* Schrad, *Cucumis sativus* L., *C. melo* L., *Cucurbita metuliferus* Naud., *C. pepo* L., *C. palmata* S. Wats.

Euphorbiaceae – *Ricinus communis* L.

Fig. 1. Field tomato showing interveinal yellowing, leaf rolling and necrosis induced by tomato infectious chlorosis virus.

Linaceae – *Linum lewisii* Pursh., *L. grandiflorum* Desf.

Leguminosae – *Ceratonia siliqua* L., *Medicago sativa* L., *Phaseolus vulgaris* L., *Pisum sativum* L.

Malvaceae – *Abutilon theophrastii* Medic., *Anoda abutiloides* A. Gray, *Gossypium hirsutum* L., *Malva* parviflora L.

Polygonaceae – *Rumex crispus* L.

Rosaceae – *Fragaria vesca* L.

Solanaceae – *Capsicum annuum* L., *Datura stramonium* L., *Nicandra physalodes* (L.) Gaertn., *Nicotiana glutinosa* L., *N. tabacum* L., *Solanum dulcamara* L., *S. elaeagnifolium* Cav., *S. melongena* L., *S. nigrum* L.

Transmission tests

Mechanical. No transmission was detected by mechanical transmission in any test.

Insects. Insect collections taken during the initial outbreak of the disease were *T. vaporariorum*. Preliminary studies indicated that TICV was readily transmitted by these insects and another culture of *T. vaporariorum* originally collected in the early 1960's. Because of the prevalence of other whitefly species in California and their role in the transmission of other yellowing-type viruses and the similarity of symptoms induced by aphid-transmitted yellowing viruses, we attempted transmission experiments with these other whiteflies and the green peach aphid, *Myzus persicae* (Sulzer). Under the conditions of these tests, TICV was not transmitted by *Bemisia tabaci* (biotype A) or *B. tabaci* (biotype B), *T. abutilonea*, or *M. persicae*.

Virus-vector relationships

Transmission efficiency. Single greenhouse whiteflies allowed a 24-h acquisition feeding on diseased plants are capable of transmitting TICV. Transmission rates established by 1, 5, 10, 20, and 40 whiteflies per plant were: 8.0, 28.0, 58.0, 68.0, and 83.0%, respectively.

Minimum acquisition access period. TICV was acquired by whiteflies in a feeding period of 1 h, but was transmitted more efficiently after longer feeding periods – 6.0, 20.0, 58.0, 88.0, and 94.0% after 1, 3, 6, 24, and 48-h acquisition feedings.

Minimum inoculation access period. Whiteflies given 24-h acquisition feeding on diseased plants transmitted TICV to 16.0, 22.0, 40.0, 68.0, and 80.0% of plants after inoculation feeding periods of 1, 3, 6, 24, and 48-h, respectively.

Table 1. Physalis seedlings infected (+) and noninfected (−) in daily serial transfers using groups of 30 viruliferous greenhouse whiteflies

Whitefly colony no.	Days after acquisition feeding[a]									
	0	1	2	3	4	5	6	7	8	9
1	+	−	−	−	−	−	−	−	−	−
2	+	−	−	−	−	−	−	−	−	−
3	+	−	−	+	−	−	−	−	−	−
4	+	+	−	−	−	−	−	−	−	−
5	−	+	−	−	−	−	−	−	−	−
6	+	+	−	−	−	−	−	−	−	−
7	+	−	+	−	−	−	−	−	−	−
8	+	−	−	−	−	−	−	−	−	−
9	+	−	−	−	−	−	−	−	−	−
10	+	−	−	−	−	−	−	−	−	−
11	+	−	−	−	−	−	−	−	−	−
12	+	−	−	−	−	−	−	−	−	−
13	+	−	−	+	−	−	−	−	−	−
14	+	+	−	−	−	−	−	−	−	−
15	−	−	+	−	−	−	−	−	−	−
16	+	−	+	−	+	−	−	−	−	−
17	+	−	−	−	−	−	−	−	−	−
18	+	−	−	−	−	−	−	−	−	−
19	+	+	−	−	−	−	−	−	−	−
20	+	−	−	−	−	−	−	−	−	−

[a] No seedlings were infected by the whitefly colonies in daily serial transfers from the 10th to the 15th day after acquisition feeding.

Persistence. The ability of viruliferous *T. vaporariorum* to retain TICV was determined by daily serial transfers to healthy plants. Most of the insects lost the virus during the first 24-h feeding period. The results (Table 1) show that one group retained the virus for 4 days.

Virus purification. A single band at 70 mm from the meniscus was observed in sucrose-Cs_2SO_4 gradients of partially purified preparations. This band was absent in gradients of healthy material subjected to the same purification technique. The band, after dialysis, had an absorption spectrum typical of viral nucleoprotein. The $A_{260/280}$ value for the purified virus was 1.25.

Electron microscopy. Purified preparations from sucrose – Cs_2SO_4 gradients showed large numbers of flexuous filamentous particles of variable lengths (Fig. 2). Measurements of over 200 particles from purified preparations indicated the modal length in the 800–850 nm range. The longest particles found were in the 1550–1600 nm range. The particles were estimated at 12 nm wide. Sap from TICV-infected leaves of *N. clevelandii* contained long flexuous rod-shaped particles with a modal length of 850–900 nm (Fig. 3).

Serology. ELISA tests demonstrated that TICV antiserum reacted with purified TICV and reacted to TICV-infected tissue from tomato, potato, *N. clevelandii*, *N. benthamiana*, *P. wrightii*, but not with healthy plants of the same species. The antiserum did not react with plant species infected with other whitefly-transmitted viruses, beet pseudo yellows, lettuce infectious yellows or cucurbit yellow stunting disorder.

Epidemiology. The disease induced by TICV, when first distinguished in 1993, occurred in epidemic proportions in the Irvine area of Orange County, California. Whitefly populations (*Trialeurodes*) were extremely high in the region. The disease first occurred

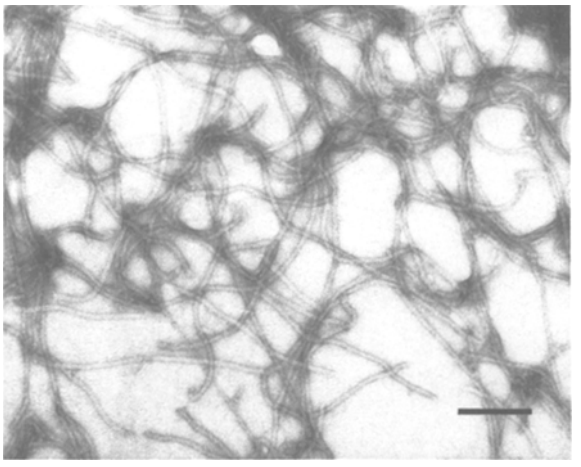

Fig. 2. Electron micrograph of purified tomato infectious chlorosis virus particles stained in 2% uranyl acetate. Bar represents 200 nm.

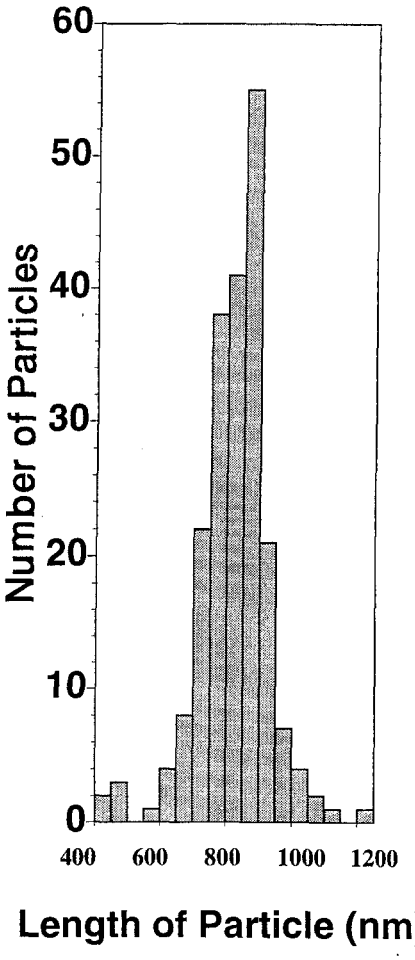

Fig. 3. The length distributions of tomato infectious chlorosis virus particles in leaf dip preparations from TICV infected *Nicotiana clevelandii* and negatively stained with 2% uranyl acetate.

in transplanted tomatoes in the foothills region in land cultivated for only one to two years. Early speculation was that the virus may have moved from native or weed populations to the transplanted tomatoes. Indeed, the virus was recovered from a number of tree tobacco (*N. glauca*) plants which are widespread in the region. Subsequently, the virus was recovered from commercial artichoke (*C. scolymus*) in the foothill area and from large patches of bristly oxtongue (*P. echioides*). Thus the virus appears to be established in naturalized weed and crop species in the southern California coast.

Artichoke thistle, or cardoon (*C. cardunculus* L.) is also widely distributed in the region. Plants of this species tested in the laboratory are hosts of TICV, although the virus was never recovered from field-collected plants.

Although the virus now seems to be established in perennial weed species in the southern coastal region of California, it is not known if the virus was in these hosts prior to the introduction of tomato.

The outbreak of TICV in northern California (over 400 miles from the Irvine area) was definitely associated with breeding programs in greenhouse grown tomatoes. The three separate occurrences in different locations in northern and central California have no apparent connection. Thus the possibility exists that the virus could be moving through greenhouse plant populations and transplant systems.

The origins of TICV in California are not known. There are, however, a number of potential vehicles for virus movement into or out of the state. The vector *T. vaporariorum* is an abundant and destructive species in greenhouses and in the field in warmer climates throughout the world. The susceptibility of several ornamentals and their movement from area to area are a potential danger. The use of transplants for tomato production is becoming more and more common. The production of transplants in greenhouses, or outdoors in warmer climates, where greenhouse whiteflies are common, could widely distribute the virus. Indeed, some evidence in southern California indicates that this has happened.

Potato was shown to be a host of TICV in these studies and, although as far as the authors are aware, no previous indications of the natural occurrence of a typical closterovirus in potato has been noted, this

plant could serve as an important means of movement of the virus throughout the world.

Commercial artichoke (*C. scolymus*) has been widely propagated by means of vegetative offshoots. Movement of infected planting material is another possible mode of movement of the TICV.

Discussion

Whitefly-transmitted clostero-like viruses are an expanding heterogenous group of plant viruses. The viruses induce interveinal yellowing, and brittleness of affected leaves, and/or vein yellowing symptoms [Duffus, 1987]. They are transmitted by their whitefly vectors in a semipersistent manner and have flexuous, filamentous virions. The whitefly-transmitted clostero-like viruses include beet pseudo yellows (BPYV) [Duffus, 1965; Liu and Duffus, 1990], lettuce infectious yellows (LIYV) [Duffus *et al.*, 1986], cucurbit yellow stunting disorder (CYSDV) [Duffus *et al.*, 1994a; Hassan and Duffus, 1991], abutilon yellows (AYV) [Duffus, 1987], Diodia vein chlorosis (DVCV) [Larsen *et al.*, 1991], lettuce chlorosis (LCV) [Duffus *et al.*, 1994b], sweetpotato sunken vein (SPSVV) [Cohen *et al.*, 1992] and the newly described TICV.

The closteroviruses have been characterized by a number of features including particle morphology, cytopathology, mode of transmission, and more recently, genome organization [Dolja *et al.*, 1994; Klaassen *et al.*, 1994]. Unfortunately, all of these features have not been characterized for any of these viruses.

Early classifications of closteroviruses were based on particle lengths; long or typical, with particles of 1200–2000 nm and short or atypical, with particles 700–800 nm [Lister and Bar-Joseph, 1981; Dolja *et al.*, 1994]. The measurements, however, were made by a number of different individuals, utilizing different techniques and/or criteria for measurement (i.e. modal lengths, average lengths, or even the longest length observable). LIYV, for instance, was reported as particles with a continuous decreasing distribution from shorter particles 400–500 nm range to 1800–2000 nm [Duffus *et al.*, 1986]. TICV has particles with an average length of 645 nm, a modal length of 850 nm and the longest particle observed was 1600 nm.

TICV appears to be more closely affiliated with BPYV than to other whitefly transmitted clostero-like viruses because of the transmission by *T. vaporariorum*. BPYV has a wide host range of crops, weeds, and ornamentals. It has caused severe losses in greenhouse grown cucurbit and lettuce crops throughout North America, Europe, and Asia. BPYV has been termed cucumber yellows virus [Yomashita *et al.*, 1979], muskmelon yellows [Lot *et al.*, 1980], cucumber infectious chlorosis [Hristova and Natskova, 1986] cucumber chlorotic spot [Woudt *et al.*, 1993] and melon yellows virus [Jorda-Gutierrez *et al.*, 1993], but these all appear to be synonyms for BPYV [Duffus, 1995].

TICV differs significantly from BPYV in serology, insect transmission biology, and host range. These two viruses have many host plants in common and induce almost identical symptoms on these hosts. However, they differ significantly in their susceptibility on tomato, potato and other Solanaceae and in the Cucurbitaceae. BPYV causes major economic losses throughout the world on cucurbits and has two important hosts, dandelion (*Taraxacum officinale* Webber) and marigold (*Tagetes patula* L.), which play significant roles in virus epidemiology. Serial transfer studies indicate that BPYV is retained in the vector significantly longer than TICV. Most insects are still viruliferous after 3 days and some can retain the virus for up to 6 days. Tomato has not been shown to be a host of any isolates of BPYV studied in the world.

TICV has now been found in a number of separate locations in California in field and greenhouse grown tomatoes. These occurrences have no known connections. Tomato breeders who have recently become aware of the disease symptoms have indicated that they have noticed symptoms for some time but have associated them with nutritional factors, water management, and other virus diseases.

The virus has the same, and perhaps even greater, potential to be disbursed than BPYV. If it is not already worldwide in distribution, it has the potential to spread to other growing regions with resident populations of the greenhouse whitefly.

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