Transmission, Host Range, and Virus-Vector Relationships of Chino del Tomate Virus, a Whitefly-Transmitted Geminivirus from Sinaloa, Mexico

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ABSTRACT

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The transmission properties, host range, and virus-vector relationships of chino del tomate virus (CdTV), a whitefly-transmitted geminivirus from Sinaloa, Mexico, are described for the first time. CdTV is transmitted by *Bemisia tabaci*, but not by seed or mechanical means. The virus, which has an apparently narrow host range within the Asclepiadaceae, Leguminosae, Malvaceae, and Solanaceae, has several characteristics in common with tomato yellow leaf curl virus (TYLCV) described in the Middle East and Africa. Tomato breeding lines *Lycopersicon pimpinellifolium* LA121 and LA1478, which showed tolerance to TYLCV, were tolerant to infection by CdTV. In virus-vector studies, the minimum acquisition-access period (AAP) and inoculation-access period were 1 hr (22% transmission) and 2 hr (8.3% transmission), respectively. A latent period of 17–22 hr was demonstrated. The virus was retained by its whitefly vector for 4.5 and 7.3 days after 24- and 72-hr AAP, respectively, which suggested a dose effect. Relative efficiencies of transmission for 1, 5, 10, and 20 *B. tabaci* were 15, 49, 84, and 100%, respectively.

The chino del tomate (CdT), or leaf curl, disease of tomato (*Lycopersicon lycopersicum* (L.) Karsten) was first reported in cultivated tomato fields in Sinaloa, Mexico, during 1970–1971 (9). Epidemics recurred during 1976–1983 and coincided with unusually high populations of *Bemisia tabaci* (Genn.) (3), the whitefly vector of the virus (3,9). The disease presently occurs in tomato production areas of the west coast of Sinaloa and may affect 100% of the plants in a field (9). All cultivars of commercial tomatoes grown in these areas are susceptible (9). The CdT disease is characterized by curling and rolling of leaves, thickening of veins, a bright to subdued yellow mosaic (which varies with time of the year), stunting, and a reduction in fruit set (9). Though CdT has been reported exclusively in Sinaloa, the disease has the potential to become a serious threat to nearby tomato production areas in Mexico and the United States. Recently, a whitefly-transmitted geminivirus, CdT virus (CdTV), was implicated as the causal agent of this disease (2,3), but information concerning biological properties of the virus is lacking. Here, we present the results of studies involving virus transmission, experimental host range, and virus-vector relationships.

MATERIALS AND METHODS

Collection and maintenance of the virus and whitefly vector. Tomato leaves with characteristic chino (leaf curl) symptoms were collected from whitefly-infested fields in Sinaloa in the fall of 1983. A virus-free colony of *B. tabaci* was established, and whiteflies were manipulated as previously described (4). Whiteflies were allowed a 24-hr acquisition-access period (AAP) on source plants and transferred to tomato cv. Pole Boy, a susceptible test species, for a 3-day inoculation-access period (IAP). Inoculated plants were maintained in the greenhouse and observed for symptom development. Plants that developed chino symptoms were transferred to a separate room and used as virus source plants for studies reported here.

Host range. Seeds of test plants were sown in 3.6-cm-diameter pots, thinned at the four-leaf stage to one or two plants per pot for host range and back-indexing inoculations, respectively, and maintained in an insect-free greenhouse as described (4). The experimental host range study included plant species previously used for identification of whitefly-transmitted diseases of tomato (1,7,8,11,12,14,15, 17–25). Seed of *L. pennellii* (Correll) D'Arcy LA716, *L. pimpinellifolium* (L.) Mill. LA722 and LA1478, *L. peruvianum* (L.) Mill. LA111, and *L. peruvianum* var. *glandulosum* LA1292 were obtained from C. M. Rick (University of California, Davis). Seed of *L. pimpinellifolium* LA121, *Cynanchum acutum* L., and *Malva nicaeensis* All. were provided by S. Cohen (Volcani Research Center, Bet Dagan, Israel). Seed of *L. peruvianum* 85LT-1308-5 and *L. hirsutum* Humb. & Bonpl. LA1777 were supplied by J. C. Watterson (Petoseed Co., Woodland, CA). Test plants were inoculated with viruliferous *B. tabaci* that were allowed a 48-hr AAP on CdTV-infected source plants and a 3-day IAP on test plants. Whiteflies were killed by fumigation (4), and plants were transferred to a separate greenhouse and observed for symptom development. After 4–6 wk, plants were tested for infection by back-indexing to Pole Boy tomato seedlings, using whiteflies and the AAPs and IAPs given above. Indicators were maintained in the greenhouse for 6 wk, after which the development of characteristic chino symptoms was considered indicative of infection of the respective test plant. At least five plants of each species, line, or accession were tested in each of four experiments.

Mechanical transmission. Mechanical inoculation experiments were conducted by rubbing sap from virus source plants on the cotyledons and/or true leaves of test plants. Sap was obtained by grinding symptomatic leaves in a mortar and pestle with 2 vol (w/v) 0.2 M potassium phosphate buffer (pH 7.4) containing 0.5% diatomaceous earth as an abrasive. Attempts were made to enhance infectivity/transmission by adding 1.0% polyvinylpyrrolidone (av. M_r 40,000 [PVP-40]), 2.0% nicotine, 0.5% 2-mercaptoethanol, or 0.02 M sodium sulfite to the inoculation buffer before grinding. At least 40 plants of *Datura stramonium* L., *Nicotiana benthamiana* L., and Pole Boy tomato were inoculated in each of five experiments over a 3-yr period.

Seed transmission. Over 200 seeds were collected from each of three CdTV-infected plants of *D. stramonium, N. benthamiana*, and Pole Boy tomato. Seeds were harvested and cleaned from the tomato fruits by grinding in 4 vol distilled water (w/v) in a blender. The mixture was stirred for 30 min with sodium hypochlorite at a final concentration of 2.7%. The seeds were separated from the debris, washed with distilled water, and planted. Seeds were sown (10 per pot) in 15-cm-diameter pots in the greenhouse, and the resulting seedlings were maintained for 8 wk in the greenhouse for observation.

Virus-vector relationships. Virus source plants, test plants, and the whitefly colony were maintained as described above. All whitefly feedings occurred in a growth chamber (32 C) using adults from the colony. Inoculation

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periods were terminated by fumigation (4), and test plants were transferred to and maintained in an insect-free greenhouse (4) for the duration of the study.

Relative efficiencies of virus transmission were determined by allowing 1, 5, 10, or 20 whiteflies a 3-day IAP on indicator plants after a 48-hr AAP on virus source plants. Fifteen plants were used in each of three trials.

The minimum AAP required for transmission (acquisition threshold) was determined by allowing whiteflies access to virus source plants for 10 min, 30 min, or 1, 2, 4, 8, 16, 24, or 48 hr before transfer to indicator plants for a 3-day IAP. Twenty whiteflies per pot and 15 plants were used in each of three trials.

To determine the minimum IAP (inoculation threshold), whiteflies were allowed either a 2- or a 24-hr AAP on virus source plants and an IAP of 10 min, 30 min, or 1, 2, 4, 8, 16, 24, or 48 hr on indicator plants. Twenty whiteflies per pot and 15 plants were used in each of three trials.

The maximum virus retention (persistence) by *B. tabaci* was determined by allowing individual whiteflies either a 24- or a 72-hr AAP on virus source plants, followed by serial transfer at 24-hr intervals to indicator plants for 12 consecutive days, or for the life of the whitefly. Fifteen whiteflies were used in each of three trials. Values reported represent data from the 10 whiteflies that survived longest in each trial.

RESULTS

Host range. The results of the experimental host range study and the symptoms associated with hosts are summarized in Table 1. A test plant was considered to be a host of CdTV when characteristic chino symptoms were observed in Pole Boy tomato indicator plants after inoculation of the test plant and back-indexing with *B. tabaci*. A test plant was considered a nonhost if typical symptoms failed to develop on Pole Boy tomato plants by back-indexing with *B. tabaci* (Table 1). The host range of CdTV included members within the Leguminosae, Malvaceae, and Solanaceae as well as a single species within the Asclepiadaceae (Table 1). Under the conditions described here, there were no CdTV hosts identified within the Amaranthaceae, Chenopodiaceae, Compositae, Cruciferae, Cucurbitaceae, Graminae, or Umbelliferae (Table 1).

Symptoms on infected plants ranged from mild to extremely severe; some hosts showed no symptoms (Table 1). In tomato, pepper (*Capsicum* spp.), and tobacco (*Nicotiana* spp.), symptoms were most prominent from September through January. In tomato, a bright yellow and green mottle-mosaic and severe leaf curling developed during this time, whereas during the spring and summer months, foliar symptoms consisted of dull yellow mottle-mosaic and mild leaf curling. Infected pepper and tobacco developed mild leaf distortion and faint mosaic symptoms from September to January but were symptomless for the remainder of the year. The CdTV could be detected serologically using its homologous antiserum and was transmissible by *B. tabaci* from infected plants, irrespective of symptom severity or time of year (*data not shown*).

Mechanical transmission. Characteristic chino symptoms did not develop on mechanically inoculated *D. stramonium, N. benthamiana*, or Pole Boy tomato. Furthermore, additives in the inoculation buffer did not result in mechanical transmission of CdTV in any case. To further substantiate these results, leaves were collected from representative test plants 8 wk after mechanical inoculation, pooled, and back-indexed using *B. tabaci*. Symptoms did not develop in any indicator plants.

Seed transmission. No symptoms were observed in any of the seedlings resulting from seed of virus-infected *D. stramonium, N. benthamiana*, or Pole Boy tomato, and no symptoms developed in indicators following back-indexing of representative plants using *B. tabaci*.

Virus-vector relationships. The development of characteristic chino symptoms on indicator plants after exposure to whiteflies was considered indicative of virus transmission by *B. tabaci*. The results for transmission

Table 1. Results of a host range study of chino del tomate virus (CdTV) by whitefly transmission using a 48-hr acquisition-access feeding on virus source plants, a 3-day inoculation-access period on test plants, and back-indexing to tomato cv. Pole Boy indicator plants

Test plant	Symptoms[a]/ back-indexing results[b]
Amaranthaceae	
Gomphrena globosa L.	NS/−
Asclepiadaceae	
Cynanchum acutum L.	M,VC/+
Chenopodiaceae	
Beta vulgaris L. 'H-9'	NS/−
Chenopodium album L.	NS/−
Compositae	
Lactuca sativa L. 'Salina'	NS/−
Zinnia elegans Jacq. 'Lilliput'	NS/−
Cruciferae	
Capsella bursa-pastoris (L.) Medic.	NS/−
Raphanus sativus L. 'Comet'	NS/−
Cucurbitaceae	
Citrullus vulgaris Schrad. 'Charleston Gray'	NS/−
Cucumis melo L. 'Topmark'	NS/−
C. sativus L. 'Bush Champion'	NS/−
Cucurbita maxima Duch. 'Big Max'	NS/−
C. pepo L. 'Early Acorn'	NS/−
Gramineae	
Zea mays L. 'Golden X Bantam'	NS/−
Leguminosae	
Cicer arietinum L. 'Kabuli Type'	NS/−
Lens culinaris Medic. 'Chilean Lentil 78'	M,Mo,VC/+
Phaseolus aureus Roxb.	M,Mo/+
P. vulgaris L. 'Red Kidney'	M,LC,Mo/+
Pisum sativum L.	NS/−
Vicia faba L.	NS/−
Vigna unguiculata subsp. *unguiculata* (L.) Walp. 'California Blackeye'	NS/−
Malvaceae	
Althaea rosea Car. 'Chater's Double Mix'	NS/−
Gossypium hirsutum L. 'Delta Pine 70'	NS/−
Hibiscus esculentus L. 'Clemson Spineless'	NS/−
Malva nicaeensis All.	M,Mo,LC/+
M. parviflora L.	S,Mo,LC/+
Sida sp. L.	NS/−
Solanaceae	
Capsicum annuum L. 'Anaheim'	M,Mo,VC/+
C. frutescens L. 'Tabasco'	M,Mo,VC/+
Datura stramonium L.	S,Mo,LC/+
D. tatula L.	M,Mo,LC/+
Lycopersicon lycopersicum (L.) Karsten 'Pole Boy'	S,Mo,LC/+
L. hirsutum Humb. & Bonpl. LA1777	M,VC/+
L. pennellii (Correll) D'Arcy LA716	M,VC/NT
L. peruvianum (L.) Mill. LA111	M,Mo/+
L. peruvianum PI126935	M,Mo/+
L. peruvianum var. *glandulosum* LA1292	M,Mo/+
L. pimpinellifolium (L.) Mill. LA1478	NS/+
L. pimpinellifolium LA722	M,Mo/+
L. pimpinellifolium LA121	M,Mo/+
Nicotiana benthamiana L.	S,Mo,LC/+
N. clevelandii Gray	S,Mo,LC/+
N. glutinosa L.	M,LC/+
N. repanda L.	M,LC/+
N. rustica L.	M,Mo,LC/+
N. tabacum L. 'Samsun'	M,Mo,LC/+
N. tabacum 'Xanthi'	M,LC/+
N. tabacum 'White Burley'	NS/+
Physalis peruviana L.	NS/−
Solanum melongena var. *esculentum* Nees. 'Black Beauty'	NS/−
S. tuberosum L. 'White Pontiac'	NS/−
Umbelliferae	
Daucus carota L. var. *sativa* 'Danvers Half Long'	NS/−

[a] NS = no symptoms, M = mild symptoms, S = severe symptoms, LC = leaf curling, Mo = mottle or mosaic, VC = veinclearing.
[b] + = Host, − = nonhost, NT = not tested.

studies are reported as the mean efficiency of transmission, which is based on the means of three trials each and 15 plants per trial. The means of the three trials were used to calculate the grand mean, followed in parentheses by the standard deviation.

The relative percent efficiencies of virus transmission for 1, 5, 10, and 20 *B. tabaci* were 15 (±4.0), 49 (±14.0), 84 (±10.1), and 100% (±0.0), respectively, after a 48-hr AAP and a 3-day IAP on indicators.

The minimum AAP required for virus transmission was 1 hr, after which 22% (±3.5) transmission occurred. AAPs of 2, 4, 8, 16, 24, and 48 hr resulted in transmission efficiencies of 26 (±6.5), 42 (±3.5), 55 (±4.04), 86 (±3.5), 91 (±10.1), and 98% (±4.0), respectively.

The minimum IAP required for virus transmission after a 2-hr AAP was 16 hr, with 15% (±6.5) transmission. With a 2-hr AAP and IAPs of 24 and 48 hr, transmission efficiencies increased to 80 (±6.5) and 98% (±4.0), respectively. The minimum IAP was reduced to 2 hr after a 24-hr AAP, however, and transmission efficiency was 8.3% (±4.3). When the 24-hr AAP was followed by increasingly longer IAPs of 4, 8, 16, 24, and 48 hr, transmission efficiencies were 31 (±3.9), 58 (±7.6), 78 (±10.2), 98 (±3.9), and 100% (±0.0), respectively. On the basis of these data, the transmission threshold of CdTV by *B. tabaci* is between 18 (2-hr AAP and 16-hr IAP minimum) and 26 hr (24-hr AAP and 2-hr IAP minimum). Furthermore, a latent period of 17 (1-hr AAP and 16-hr IAP minimum) to 26 hr (24-hr AAP and 2-hr IAP minimum) may be demonstrated. In a subsequent experiment, no latent period was detectable when the AAP was increased to 48 hr, since transmission occurred after a 10-min IAP (data not shown).

After 24- and 72-hr AAPs, whiteflies retained the ability to transmit CdTV for 4.5 (±0.1) and 7.3 (±0.3) days, respectively. The results of these experiments suggest that a dose effect exists with *B. tabaci* and CdTV, since longer AAPs resulted in the ability to retain the virus longer. The ability of *B. tabaci* to retain the CdTV for an average of 7.3 days is indicative of a persistent type (> 100 hr retention) (10) virus-vector relationship. Whiteflies survived 8.9 (±0.3) and 9.1 (±0.3) days when individual *B. tabaci* were serially transferred at 24-hr intervals after the 24- and 72-hr AAP, respectively. Therefore, the length of the AAP (amount of virus acquired) appeared to have no effect on whitefly longevity.

DISCUSSION

Chino del tomate, or leaf curl of tomato, was first recognized as a viruslike disorder in the west coast of Sinaloa, Mexico, during 1970–1971 and has been a serious threat to tomato production since then (9). Epidemics caused by CdTV are directly associated with elevated levels of whitefly vector populations, which have become increasingly prevalent in the Sonoran Desert and adjacent agricultural areas during the past several years (3,4). Although CdT has been reported exclusively in Sinaloa (3,9), the disease has the potential to become a serious problem in nearby tomato production areas in Mexico and the United States.

The lack of mechanical transmission, the symptoms in tomato, and the host range differences clearly distinguish CdTV from tomato golden mosaic virus reported from Brazil and Venezuela (8,14,15,22). In addition, differences in host range and symptomatologies suggest that CdTV is distinct from the nonmechanically transmissible geminivirus(es) causing tomato or tobacco leaf curl (TLC) in India, Japan, and Sudan (5,14,18,20,21,23–25) and tomato yellow dwarf in Ceylon and Japan (14,17,18). Among previously described whitefly-transmitted geminiviruses, CdTV appears to be similar to tomato yellow leaf curl virus (TYLCV) described in Africa (Nigeria, Senegal, Somalia, Sudan, and Tunisia) (6,14,25), Cyprus (11), and the Middle East (Israel, Jordan, Lebanon, and Saudi Arabia) (1,7,12,13,16,18). Both CdTV and TYLCV are transmitted by *B. tabaci* but not by mechanical means (7), and virus-vector relationships for the two viruses are similar but not identical. A minimum AAP of 1 hr and 15–30 min, a minimum IAP of 2 hr and 15–30 min, and an estimated latent period of 17–26 hr and 21 hr are reported for CdTV and TYLCV, respectively (7).

CdTV and TYLCV differ somewhat in geographical distribution, host range, and symptomatology, however (2,4,7). With respect to geographical distribution, CdTV has been reported exclusively in North America (Sinaloa, Mexico), whereas TYLCV has been described in numerous countries on the African and Asian continents. An attempt was made in this study to include key hosts, which would allow a direct comparison with available information on TYLCV (7; S. Cohen, *personal communication*). Hosts common to both CdTV and TYLCV are tomato and *D. stramonium*, but symptoms associated with infection by the two viruses are distinct (Table 1; 7). Both viruses also infect bean, lentil, *M. nicaeensis, M. parviflora*, and *C. acutum*. However, TYLCV causes symptomless infection, whereas CdTV incites distinct symptoms in these hosts (Table 1; S. Cohen, *personal communication*). Likewise, the two viruses infect tobacco but symptomatologies are different (Table 1; 7). An important host by which these two viruses may be distinguished is pepper, since CdTV infects the two *Capsicum* species tested (Table 1) and TYLCV does not (7; S. Cohen, *personal communication*). Earlier reports associated a leaf curl symptom of pepper with a whitefly-transmitted virus (14,17,23,24), but the disease is now believed to have been caused by the TLC virus (TLCV) (14,18).

The severe foliar symptoms and drastic reduction in fruit production caused by CdTV indicate an immediate need for effective control measures on both a short- and a long-term basis. Attempts to adequately reduce the number of whiteflies to decrease virus infection have generally been unsuccessful. The difficulties associated with placement of insecticides on the lower leaf surface where whiteflies feed, the presence of a waxy covering on immature instars that protects against insecticidal action, the development of resistance to insecticides, and the reduction of natural predators and parasites after insecticide application are in part responsible for the inability to control whiteflies and thus whitefly-transmitted viruses. The implementation of crop-free periods to deprive whiteflies of overseasoning hosts has not been feasible in the southwestern United States or Mexico to date, because of the diversity of cropping practices in most areas. Sanitation measures in which virus-infected and/or whitefly-infested materials are removed from seedling nursery greenhouses and adjacent commercial fields have been recommended.

Breeding for resistance to a number of whitefly-transmitted geminiviruses of tomato is of major concern in commercial production areas of the world (12–14,19; H. Laterrot of Montfavet and J. C. Watterson of Petoseed, *personal communications*). A selection of *L. pimpinellifolium* LA121 was reported to be resistant to TYLCV in Israel (19) and Jordan (12), whereas *L. pimpinellifolium* LA1478 showed tolerance to TYLCV infection in Sudan (C. M. Rick and H. Laterrot, *personal communications*). Inoculation of both selections with CdTV under greenhouse conditions resulted in the development of either extremely mild foliar symptoms or a symptomless infection (depending on the time of year), and virus could be recovered to indicator hosts after back-indexing (Table 1). Resistant LA121 plants tested in Israel supported only low levels of virus (19). Although no attempt was made to quantify virus titer in the experiments with CdTV, these results indicate the potential feasibility of developing tomato selections with tolerance or resistance to CdTV.

The biological evidence presented here suggests that TYLCV and CdTV are distinct viruses or possibly different strains of the same virus. Characterization of CdTV by biochemical and serological means is currently in progress. Such information should allow a more direct comparison of CdTV with TYLCV and other whitefly-transmitted geminiviruses.

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