Resistance to Tomato Yellow Mosaic Virus in Species of *Lycopersicon*

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ABSTRACT

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Diseases caused by geminiviruses are widespread in the tropical–subtropical tomato production areas. Tomato yellow mosaic geminivirus (ToYMV) is a member of the whitefly-transmitted subgroup (III), which is vectored by the whitefly *Bemisia tabaci*. Several accessions of *Lycopersicon chilense, L. hirsutum,* and *L. peruvianum* var. *glandulosum* were identified that exhibit tolerance or a high degree of resistance to a Venezuelan isolate of ToYMV in field and greenhouse studies using mechanical inoculation and viruliferous vectors. Polymerase chain reaction analysis showed that viral DNA is present in infected plants and absent in resistant ones. Mechanical and insect transmission gave different results in some species or cultivars, suggesting a distinct mechanism for resistance.

Tomato yellow mosaic geminivirus (ToYMV) has caused millions of dollars in losses over the past several years in commercial tomato (*Lycopersicon esculentum* Mill.) plantations in Venezuela. By the time of flowering, 90–100% of tomato plants typically become infected by ToYMV. Symptoms of the disease are a golden yellow mosaic and stunting, and no fruit is produced if plants are infected early. Thus, the disease negatively impacts both fruit quality and yield.

ToYMV belongs to subgroup III of the Geminiviridae and is transmitted by the whitefly *Bemisia tabaci* (Gennadius) in the family Aleyrodidae (6,11,13,25, 26). Control of ToYMV with insecticides is ineffective because the whitefly is resistant to most available compounds (9). The virus is transmissible by mechanical inoculation, but in the field it is not transmitted by contact between plants, by seeds, or by pollen (11,26).

Wild *Lycopersicon* species vary in tolerance or resistance to viruses, and some valuable traits have been transferred into cultivated tomato (17,19,20). Some wild species of *Lycopersicon* are resistant to other geminiviruses, e.g., tomato yellow leaf curl virus (TYLCV) (28), chino del tomate virus (CdTV) (2), and tomato mottle virus (TMoV) (18). The purpose of this investigation was to screen wild *Lycopersicon* species to identify sources of natural resistance to ToYMV, with the expectation of using these materials to improve cultivated tomato.

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MATERIALS AND METHODS

Plant material. Seedlings and in vitro micropropagated plantlets of different species, accessions, and cultivars of the genus *Lycopersicon, Nicotiana benthamiana* Domin., and *N. glutinosa* L. were used. Seeds of some wild species were obtained from C. Rick (Tomato Genetic Resource Center, University of California, Davis). Certificate seeds of commercial cultivars were from Sunblest Seeds and San Martin Seeds Co., USA, purchased locally.

Solid, hormone-free MS medium (1/2 macronutrients) was used for the propagation of plants (16). Seedlings and micropropagated plantlets were transferred to sterilized soil in pots and grown in a greenhouse under illumination (16-h photoperiod) at 28–32 C.

Source of virus. ToYMV-infected tomato plants (*L. esculentum* cv. Rio Grande) from agricultural zones in central Venezuela (Aragua, Guarico, and Lara) were used as a source of virus inoculum. Virus was maintained in Rio Grande by mechanical transfer approximately every 2 wk.

Virus transmission. *Mechanical inoculation.* Young tomato leaves and leaf buds from ToYMV-infected plants were collected and frozen at −20 C. Sap inoculum was produced by grinding leaves in a chilled mortar in a 1% suspension of magnesium trisilicate in 0.1 M potassium phosphate buffer (pH 8.5–9.0) (1:3, w/v) containing a small amount of Carborundum (600 mesh). Inoculum was immediately inoculated onto leaf surfaces of 12- to 15-day-old test plants or micropropagated tomato plantlets.

Back-inoculation experiments. When symptoms in test plants were mild or not obvious, indicator plants were used in back-inoculation experiments. Leaves and leaf buds collected from test plants and sap, prepared as described, was used to mechanically inoculate young seedlings of tomato cvs. Rio Grande and Marglobe, *N. benthamiana,* and *N. glutinosa.*

Whitefly transmission. B. tabaci colonies were maintained in screened insect boxes on Rio Grande showing typical ToYMV disease symptoms. Fourth and fifth generations of *B. tabaci* were used for virus transmission. Asymptomatic, healthy test plant seedlings were exposed in a growth chamber to viruliferous whiteflies for 2 wk, with approximately 50 whiteflies per plant. Whiteflies were killed by treatment with a systemic insecticide, and plants were placed in the greenhouse (16 h of light, at 25–32 C) for periodic observation until characteristic symptoms of systemic infection were observed, in approximately 14 days. Similarly, field inoculation of test plants was accomplished using naturally inoculative whiteflies and test plants grown in a field plot at the Fusagri Experimental Agricultural Station (Cagua, Aragua). Field plots were located near tomato plantations where insecticides are not regularly used.

Symptom rating system. Disease symptoms of ToYMV were rated on a scale of 0 to 4, where 0 = no symptoms, 1 = slight symptoms visible only after a careful search, 2 = slight but more visible symptoms, 3 = moderate symptoms over most of the plant, and 4 = severe symptoms over entire plant (24).

DNA preparation. Total plant DNA was prepared by macerating 1 g of leaves from infected or noninfected plants in a mortar with cold 0.1 M Tris at 2 ml/g (pH 7.0) with 0.1 M NaCl, 10 M EDTA, 0.5% SDS (w/v), and proteinase K at 100 μg/ml. The suspension was incubated for 10 min at 65 C and then centrifuged 5 min in a microfuge. The supernatant was extracted once with TE-saturated phenol and twice with chloroform:isoamyl alcohol (24:1). Nucleic acid was precipitated with 0.5 volumes of isopropanol after NaCl was adjusted to 0.3 M and centrifuged 10 min, and the pellet was washed twice with 70% ethanol and resuspended in 50 μl of TE (10:1), pH 7.4.

ToYMV detection using polymerase chain reaction (PCR). Primers MAT-1 (5′-GCATCTGCAGGCCCACATI-GTCTTICCIGT-3′) and MAT-2 (5′-AA-TACTGCAGGGCTTICTITACATIGG-3′) for the complementary strand were used. They are modifications of previously published degenerate primers for geminivirus detection (22), which amplify

a 1.1-kb fragment from the A component of geminivirus bipartite genome. To restrain the degeneracy, the ambiguity base has been changed for deoxyinosine, a neutral base that pairs in an equivalent manner with all four nucleotides (14,23). The primers were diluted in ddH_2O to 1 μg/ml. PCR reaction mixtures of 1 μg of DNA, 0.2 mM each dNTP, 1.5 mM $MgCl_2$, 2.5 u Taq, and 100 pmol of each primer in 100 μl total volume of 1× Taq buffer. Each reaction was covered with 50 μl of mineral oil. Amplification was performed in a GTC-2 Thermal Cycler with melting for 1 min at 92 C, annealing for 1 min at 50 C, and elongation for 2 min at 72 C. After 40 cycles, the extension time was increased to 10 min at 72 C and then the reaction was cooled to 4 C. Two milliliters of each reaction was used for electrophoresis in 1.4% agarose (0.5× TBE). The 1-kb ladder was used as a size standard. Gels were stained with ethidium bromide.

RESULTS

Virus cultures. ToYMV was initially mechanically transmitted from infected tomato plants cv. Rio Grande to tomato cv. Marglobe, *N. benthamiana,* and *N. glutinosa.* Virus-infected tomato plants developed a bright yellow mosaic and curling leaves, and were stunted within 10–12 days after inoculation. Chlorotic mottling and curling of leaves developed in infected *N. benthamiana,* and yellow veins were observed in *N. glutinosa* after both mechanical and insect transmissions. All *L. esculentum* plants inoculated by viruliferous *B. tabaci* developed typical ToYMV symptoms.

Susceptibility to infection and symptom development. ToYMV was transmitted mechanically and by the insect vector to various *Lycopersicon* species with different frequencies. Most infected plants developed symptoms, but the severity and intensity of symptoms varied among lines, cultivars, and accessions (Table 1). Symptoms observed in *L. esculentum, L. pimpinellifolium* (L.) Mill., and *L. hirsutum* Humb. & Bonpl. were as those described previously for ToYMV (11,26).

Lycopersicon esculentum. Tomato cv. Marglobe inoculated with sap extract showed 70.6% of ToYMV transmission, and cv. Rio Grande, 68.7%. Symptoms on Rio Grande started 14 days after mechanical inoculation. *B. tabaci* was able to transmit ToYMV from Rio Grande to 90.2% of Marglobe and to 88.8% of Rio Grande in greenhouse tests. In the field, 100% of plants were infected (Table 1). Plants of *L. esculentum* var. *cerasiforme* (Dunal) A. Gray infected mechanically and by *B. tabaci* both showed the same typical symptoms as the cultivated tomato (Fig. 1).

***Lycopersicon cheesmanii* Riley f. *minor* (F. Hook) Muller.** Seven plants were obtained from germination and propagation in vitro of 100 seeds of *L. cheesmanii* accession LA 166 from Ecuador. All seven test plants of *L. cheesmanii* were susceptible to the ToYMV after both mechanical inoculation and insect transmission (Table 2). In the field plot, all LA 166 plants exhibited striking golden yellow mosaic leaves and stunting.

***Lycopersicon chilense* Dunal.** Some plants of three different accessions of *L. chilense,* LA 1963, LA 1969, and LA 2584, (from Chile) were found to be highly resistant to ToYMV. Symptoms appeared in susceptible plants 1 mo after inoculation in the field plot, but more than 2 mo after inoculation in the greenhouse, either mechanically or with insects. Usually the leaf form was not changed, but leaf size was reduced and yellow spots were observed on leaves (Fig. 2A). Disease development was less in *L. chilense* than in other *Lycopersicon* species (Tables 1 and 2). Plants of accessions LA 1969 and LA 2584 were more susceptible to ToYMV than were those

Table 1. Disease rating for tomato yellow mosaic virus infection in different *Lycopersicon* species inoculated by *Bemisia tabaci*

Species	Cultivars, accessions	Number of plants[a]		Disease rating[b]	
		I	WS	Mean	Range
L. esculentum	Marglobe	74	74	3.8	3–4
	Rio Grande	196	196	3.5	3–4
L. esculentum var. *cerasiforme*	LA 1673	15	15	3.6	3–4
L. cheesmanii	LA 166	16	16	3.6	3–4
L. chilense	LA 1963	47	10	0.25	0–2
	LA 1969	5	3	0.7	0–2
	LA 2584	17	7	0.6	0–3
L. chmielewskii	LA 1306	12	12	3.9	3–4
L. hirsutum	LA 1353	7	2	0.3	0–2
L. hirsutum var. *glabratum*	LA 1223	47	22	0.8	0–3
L. parviflorum	LA 1326	12	11	3.36	2–4
	LA 2727	9	4	3.5	3–4
L. pennellii	LA 716	5	5	3	2–3
L. pennellii var. *puberulum*	LA 1926	6	3	3.6	3–4
L. peruvianum	LA 111	13	12	1.5	1–4
L. peruvianum var. *dentatum*	3767	68	44	1.3	0–3
	3772	16	6	1.25	0–2
L. peruvianum var. *glandulosum*	LA 1292	20	4	0.2	0–1
L. peruvianum var. *humifusum*	LA 385	7	7	2	2–3
L. pimpinellifolium	LA 2187	16	15	2.7	0–4

[a] I = inoculated, WS = with symptoms.
[b] Scale: 0 = no symptoms, 1 = slight symptoms visible only after a careful search, 2 = slight symptoms but more visible, 3 = moderate symptoms over most of plant, 4 = severe symptoms over entire plant.

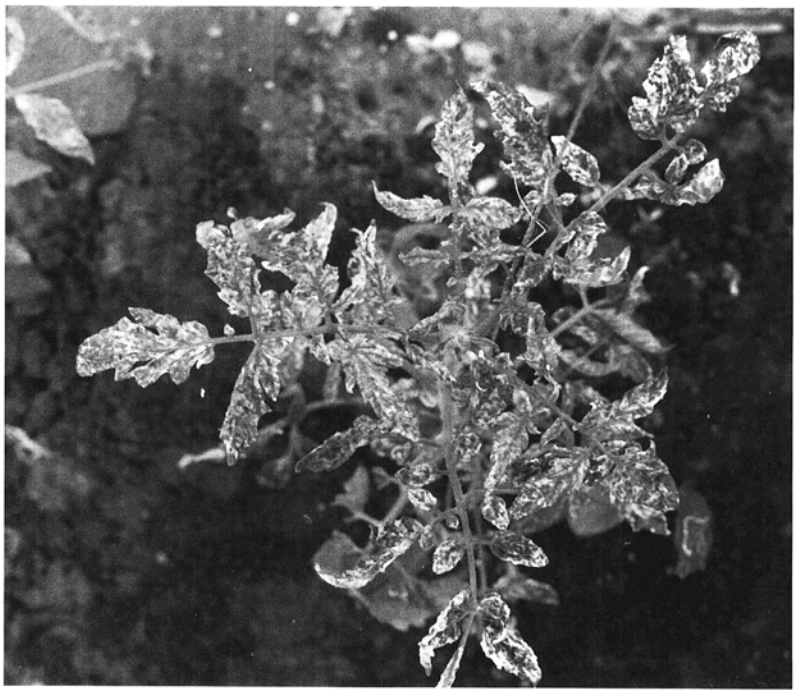

Fig. 1. Tomato plant cv. Rio Grande showing strong yellow mosaic as a result of tomato yellow mosaic geminivirus infection.

Table 2. Response of *Lycopersicon* species to inoculation of tomato yellow mosaic virus by mechanical and whitefly transmissions

Species	Cultivars, accessions	Mechanical inoculation[a]	*Bemisia tabaci* transmission[a]	Reaction to ToYMV[b]
L. esculentum	Marglobe	+	+	S
	Rio Grande	+	+	S
L. cheesmanii	LA 166	+	+	S
L. chilense	LA 1963	−	−	R
	LA 1969	+	−	R
	LA 2584	+	+	S
L. chmielewskii	LA 1306	+	+	S
L. hirsutum	LA 1353	+	−	R
L. hirsutum var. *glabratum*	LA 1223	+	+	S
L. parviflorum	LA 1326	+	+	S
	LA 2727	+	+	S
L. pennellii	LA 716	+	+	S
L. pennellii var. *puberulum*	LA 1926	+	+	S
L. peruvianum	LA 111	+	+	S,T
L. peruvianum var. *dentatum*	3767	−	+	S,T
	3772	−	+	S,T
L. peruvianum var. *glandulosum*	LA 1292	−	−	R
L. peruvianum var. *humifusum*	LA 385	−	+	S,T
L. pimpinellifolium	LA 2187	+	+	S

[a] + = ToYMV symptoms, − = no symptoms.
[b] R = Resistant, T = tolerant, S = susceptible.

of accession LA 1963 (Table 1). Within accession LA 1963, we found some tolerant and some highly resistant plants, which were without symptoms after 5 mo of cultivation in the field despite the high population of *B. tabaci* (Fig. 2B).

***Lycopersicon chmielewskii* Rick, Kes., Fob., & Holle.** Accession LA 1306 from Peru was susceptible to infection after mechanical and insect transmission of ToYMV (Table 2). The severity of disease symptoms was uniform and similar to that observed for *L. esculentum* (Table 1). Although the yellow mosaic was not as intense, severe leaf curling and stunting were observed.

Lycopersicon hirsutum. Two accessions of *L. hirsutum* var. *glabratum* LA 1223 (Ecuador) and LA 1353 (Peru) were tested. Accession LA 1223 plants developed faint yellow spots but no curling of leaves or stunting (Fig. 3A). In the field plot, all plants were symptomatic, but symptoms were mild, in that yellowing was more golden and no curling was observed (Fig. 3B). ToYMV was transmitted to accession LA 1353 by mechanical inoculation, but attempts to transmit

Fig. 2. *Lycopersicon chilense* LA 1963 grown in a field plot with a high population of *Bemisia tabaci*. **(A)** Plant with mild symptoms of tomato yellow mosaic geminivirus infection. **(B)** Plant without symptoms.

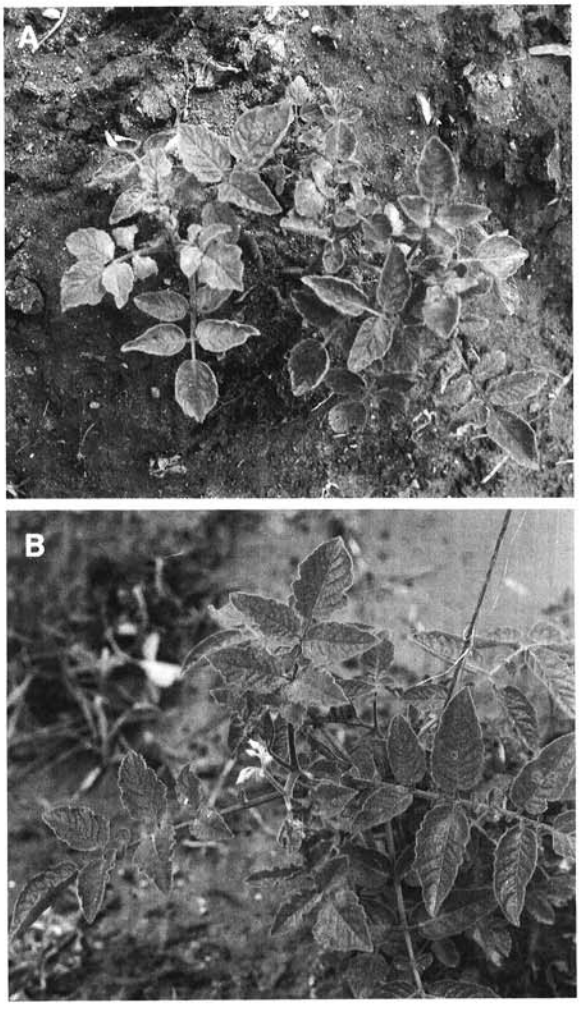

Fig. 3. *Lycopersicon hirsutum* var. *glabratum* LA 1223 in field plot: **(A)** Plant showing symptoms of tomato yellow mosaic geminivirus. **(B)** Plant with mild symptoms.

ToMYV with *B. tabaci* were not successful (Tables 1 and 2). ToYMV was transmitted mechanically or by *B. tabaci* to accession LA 1223 (Tables 1 and 2).

***Lycopersicon parviflorum* Rick, Kes., Fob., & Holle.** When accessions LA 1326 from Peru and LA 2727 from Ecuador were inoculated, disease symptoms were observed 3–4 wk after either mechanical or insect-mediated transmission (Tables 1 and 2). Both tested accessions showed severe symptoms identical to those in the *L. esculentum* control.

***Lycopersicon pennellii* (Corr.) D'Arcy.** Accessions *L. pennellii* var. *pennellii* LA 716 and *L. pennellii* var. *puberulum* LA 1926 from Peru developed symptoms after mechanical inoculation and insect transmission (Table 2). Yellow spots, reduction of leaf size, and stunting of plants were observed, indicating susceptibility of *L. pennellii* to ToYMV (Table 1).

***Lycopersicon peruvianum* (L.) Mill.** Varieties *L. peruvianum* LA 111 (Peru) and *L. peruvianum* var. *humifusum* LA 385 (Peru) were susceptible to the ToYMV infection after mechanical inoculation and insect transmission (Table 1). *L. peruvianum* var. *dentatum* (lines 3767 and 3772, Peru) was moderately affected; mild disease symptoms were observed on most inoculated plants, and leaves developed yellowing of the tips and curling (Table 2). In contrast, *L. peruvianum* var. *glandulosum* LA 1292 was tolerant or resistant to virus infection, showing only mild or no symptoms. In back-inoculation experiments with *N. benthamiana,* only two inoculated plants developed ToYMV symptoms, and they were mild, indicating that some *L. peruvianum* var. *glandulosum* plants were infected with ToYMV but that the disease symptoms were attenuated.

Lycopersicon pimpinellifolium. Disease symptoms were observed after mechanical and insect transmission of all plants of the of *L. pimpinellifolium* accession LA 2187 (Peru), with a disease rating from 0 to 4 (Table 1). *B. tabaci* transmitted ToYMV to all plants tested. However, symptoms of disease were different from those observed for other *Lycopersicon* species, in that small yellow spots, yellowish vein etching, and reduced leaf size were observed, indicating that this species is susceptible to ToYMV.

ToYMV DNA analysis. Infected and noninfected plants of *N. benthamiana, L. esculentum* cv. Rio Grande, *L. hirsutum* LA 1353, *L. chilense* LA 1969, and symptomless *L. chilense* LA1963 and *L. peruvianum* var. *glandulosum* LA1292 were assayed by PCR. After PCR amplification and agarose gel electrophoresis (Fig. 4), we found a band with about 1.1 kb, which corresponds to an amplification of the ToYMV DNA in infected plants of *N. benthamiana, L. esculentum, L. hirsutum* LA 1353, and *L. chilense* LA 1969. This band was absent in the noninfected plants. In *L. chilense* LA 1963 and *L. peruvianum* var. *glandulosum* LA 1292, PCR did not amplify any ToYMV band (Fig. 4).

DISCUSSION

Wild relatives of the tomato are potential sources of natural resistance to plant viruses. The ToYMV disease was first reported in Venezuela in 1963 as a virus transmitted by *B. tabaci* (6), and more detailed studies were subsequently carried out (11,12,13,25,26). Geminiviruses of tomato with symptoms similar to those of ToYMV that are also transmitted by *B. tabaci* include tomato golden mosaic virus (TGMV) (5,15), TYLCV (3,4,8,27), CdTV (2), TMoV (18), and potato yellow mosaic virus (PYMG) (7,21). The ToYMV is distinct from other whitefly-transmitted (WFT) geminiviruses based on symptomatology, host range, apparently limited geographical distribution (1,2,3,8,10,26,28), and DNA sequence (D. Infante, *unpublished*). Tomato lines and accessions inoculated with ToYMV under greenhouse and field plot conditions exhibited diverse symptoms. Although most plants were susceptible, some plants of accessions LA 1963 and LA 1969 of *L. chilense* were highly resistant. Accession LA 1969 of *L. chilense* has also previously been identified as a source of genetic resistance to TYLCV in Israel (28) and to ToYMV from Venezuela. These results suggest that LA1969 may be a source of a broad spectrum resistance to WFT geminiviruses.

To better characterize resistance–tolerance germ plasm, PCR with degenerate primers was used to detect ToMYV. ToYMV was not detected in *L. peruvianum* var. *glandulosum* LA 1292 and in symptomless *L. chilense* LA 1963 or LA 1969, indicating they are resistant to ToYMV. Nevertheless, the response was not the same in both accessions of *L. chilense* and *L. hirsutum* LA 1353. Both *L. chilense* LA 1969 and *L. hirsutum* LA 1353 could be mechanically inoculated but not with viruliferous *B. tabaci. L. chilense* LA 1963 was not infected either by mechanical inoculation or by viruliferous *B. tabaci.* The difference in response to infection based on the method of inoculation suggests a different mechanism for resistance. In LA 1963, there could be blocking of genes at the molecular level; and in LA 1969 and *L. hirsutum* LA 1353, there may be avoidance of transmission by the insect vector or inhibition of the initial entry of the virus into the plant cells.

Thus, the resistance to ToYMV in *L. chilense* and *L. peruvianum* var. *glandulosum* accessions was demonstrated using transmissions tests, back-inoculation experiments, and the PCR. Further studies are underway to transfer this resistance to cultivated tomato, to protect tomato from this disease.

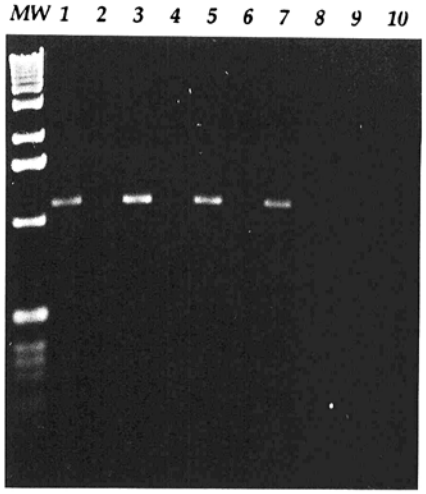

Fig. 4. Agarose gel electrophoresis of polymerase chain reaction (PCR) amplified tomato yellow mosaic virus (ToYMV) DNA. Lanes 1 and 2, *Nicotiana benthamiana* infected and noninfected; lanes 3 and 4, *Lycopersicon esculentum* cv. Rio Grande infected and noninfected; lanes 5 and 6, *L. hirsutum* LA 1353 infected and noninfected; lanes 7 and 8, *L. chilense* LA 1969 infected and noninfected; lane 9, *L. chilense* LA 1963; lane 10, *L. peruvianum* LA 1292. ToYMV DNA is absent in the *L. chilense* LA 1963 and LA 1969, *L. hirsutum* LA 1353, and *L. peruvianum* LA 1292 symptomless after the field test.

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