Host Plant Reactions, Some Properties, and Serology of Peru Tomato Virus

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ABSTRACT

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Peru tomato virus (PTV) is common in tomato crops in the coastal valleys of central Peru. Symptoms in diseased plants are mottle, epinasty, leaf crinkling, and systemic necrotic spotting. The weeds *Nicandra physaloides, Physalis peruviana,* and *Solanum nigrum* are natural hosts. The host range is restricted to species of the Solanaceae and Chenopodiaceae. *Lycopersicon pimpinellifolium, Nicotiana occidentalis, N. glutinosa,* and *Chenopodium amaranticolor* were useful indicator species. Peru tomato virus infected 11 tomato cultivars and the wild tomato species *L. pimpinellifolium, L. chilense,* and *L. peruvianum.* The virus was transmitted following acquisition periods of 30 sec by the aphid *Myzus persicae,* but was not transmitted through seed of tomato or *N. physaloides. Nicotiana occidentalis* sap remained infective when diluted to 10^{-4} but not 10^{-5}, when heated for 10 min at 50 C but not at 55 C, and when stored for 4 but not 5 days. Electron microscopy of infective sap showed long flexuous particles about 775 nm in length which were typical of the potyvirus group. Seven different potyviruses that infect solanaceous hosts were all serologically related to PTV. Of these, potato virus Y (PVY) and tobacco vein-mottling virus (TVMV) were most closely related. However, differences in its host range and symptomatology clearly distinguished PTV from these two, supporting its designation as a distinct virus.

Additional key words: serology.

RESUMEN

Peru tomato virus (PTV) es común en campos de tomate de los valles de la costa central del Perú. Los síntomas que se observan en plantas enfermas son moteado, epinastia, encarrujamiento de hojas y manchas necróticas sistémicas. Las hierbas silvestres *Nicandra physaloides, Physalis peruviana,* y *Solanum nigrum* son hospedantes naturales. El rango de hospedantes está restringido a Solanáceas y Quenopodiáceas. *Lycopersicon pimpinellifolium, Nicotiana occidentalis, N. glutinosa,* y *Chenopodium amaranticolor* son especies indicadoras útiles para detectar el virus. Peru tomato virus infectó artificialmente 11 cultivares de tomate y las especies silvestres *L. pimpinellifolium, L. chilense* y *L. peruvianum.* El virus fue transmitido después de períodos de adquisición de 30 seg por el áfido *Myzus persicae,* pero no a través de semilla de tomate o *N. physaloides.* Jugo de *N. occidentalis* fue aún infectivo cuando se diluyó 10^{-4} pero no 10^{-5}, se calentó por 10 min at 50 C pero no a 55 C o cuando se almacenó por 4 pero no por 5 días. Microscopía electrónica de jugo infectivo mostró partículas alargadas flexuosas de aproximadamente 775 nm de longitud, típicas del grupo potyvirus. Cuando se comparó serológicamente PTV con siete potyvirus diferentes que infectan solanaceas, todos fueron relacionados a éste, siendo el virus Y de la papa (PVY) y tobacco vein-mottling virus (TVMV) los más cercanos. Sin embargo las diferencias en el rango de hospedantes y sintomatología permitió distinguir claramente PTV de estos dos, reforzando su designación como un nuevo potyvirus.

Palabras claves adicionales: serología.

In 1972, Raymer et al (7) reported that a virus which they named Peru tomato virus (PTV) was common in tomato crops in the irrigated desert valleys of coastal Peru. Preliminary data on the host range, symptomatology, and physical properties of PTV have been described and the virus was shown to be a member of the potyvirus group (1,5,7); however, no detailed study has been published.

Because PTV seems of considerable importance to tomato growing in coastal Peru, an isolate obtained in 1972 from tomatoes growing in the Cieneguilla Valley was selected for detailed study.

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This isolate (PTV-C) reacted strongly with an antiserum to the original isolate of PTV (kindly supplied by R. P. Kahn) and had flexuous particles about 750 nm in length, typical of the potyviruses. This paper describes its detailed host range, symptomatology, properties and serology and confirms that PTV is a distinct member of the potyvirus group.

MATERIALS AND METHODS

Virus cultures. The virus was first isolated from the weed *Physalis peruviana* L. An isolate obtained from this weed was passed through six single lesion transfers in *Chenopodium amaranticolor* Coste & Reyn. and later compared in preliminary experiments with another isolate obtained from tomato; both had the same host range and produced identical symptoms in indicator hosts. The isolate from tomato (PTV-C) was selected for a detailed study.

Peru tomato virus-C was maintained in plants of *Nicotiana debneyi* Domin. or *N. occidentalis* Wheeler and these hosts were employed as sources of inocula for the experiments. The same two hosts also were used to culture the following other potyviruses: Colombian datura virus (CDV), henbane mosaic virus (HMV), potato virus A (PVA) (from R. Koenig), tobacco vein-mottling virus (TVMV) (from G. V. Gooding), tobacco etch virus (TEV) (from D. E. Purcifull), pepper veinal mottle virus (PVMV) (from R. H. Kenten), and potato virus Y (PVY) isolated from a Peruvian potato cultivar.

Plants. Indicator hosts came from seedlings transplanted to pots containing sterilized muck soil. Wild tuber-bearing *Solanum* species came initially from true seed supplied by the Potato Introduction Station, Sturgeon Bay, Wisconsin, USA. Later some were propagated by cuttings rooted in peat blocks. Potato cultivars were grown from cuttings supplied by the International Potato Center's seed program.

All tests were done in the greenhouse at 18–22 C. Mechanical inoculations were made by rubbing crude sap onto 22-μm (600-mesh) Carborundum-dusted leaves. Plants were tested for infection by back-inoculation to *Chenopodium amaranticolor*. For study of properties in sap, inoculations were made to groups of at least five plants of *C. amaranticolor*.

Aphid transmission tests. *Myzus persicae* Sulz. were reared on plants of Chinese cabbage, *Brassica pekinensis* (Lour.) Rupr., and used for all transmission tests. Spraying with 0.1% Tamaron (amido-O-methyl-S-methyl phosphate) was used to kill the aphids.

Purification and serology. Peru tomato virus-C was purified by homogenizing infected *N. occidentalis* leaf tissue with 0.1 M PO_4 buffer pH 8 (1 g tissue/ 2 ml buffer) containing 2-mercaptoethanol made up to 0.02 M. The homogenate was clarified by addition of chloroform (20%, v/v). After a low-speed centrifugation the supernatant was centrifuged at 30,000 rpm in a Beckman 30 rotor in an L2-65B ultracentrifuge for 1.5 hr. Pellets were resuspended in 0.01 M PO_4 buffer pH 7.5 After a second low speed centrifugation the supernatant was centrifuged at 40,000 rpm in a Beckman 40 rotor for 45 min. Final pellets were resuspended in the same buffer. Two intravenous injections of the purified preparation (A_{260nm} = 80–150) were given to a rabbit, 1 wk apart. Seven weeks later 1 ml of the virus emulsified 1:1 with Freund's incomplete adjuvant was injected intramuscularly at 1 wk intervals for 6 wk.

The antiserum was tested serologically against the seven potyviruses mentioned above and antisera (from the same donors) to all except CDV and HMV were used in reciprocal tests. Antigens were prepared by subjecting infected leaf sap to the same procedure employed for purification of PTV except that the second cycle of ultracentrifugation was omitted. For titration of antibodies, a modification of the microprecipitation test described by Ball (2) was used. Drops of the partially purified antigens diluted twofold (1/2 – 1/512) were placed in plastic petri dishes with drops of similar dilutions of the different antisera. These dishes then were placed on a mechanical shaker for 15 min and finally incubated in a humid chamber for 2 hr before they were observed with a stereoscopic microscope.

Electron microscopy. Samples prepared from diluted infective sap were stained with 2% neutral phosphotungstate and examined in a Siemens Elmiskop IA electron microscope.

RESULTS

Field symptoms and incidence. In addition to the isolation of PTV-C from a tomato plant growing in the Cieneguilla Valley with pronounced mottle, leaf epinasty, and necrotic spotting symptoms, the virus also was commonly isolated from diseased plants in fields of tomato cultivars VF-145 and VF-198 at La Molina, Lima. Infected plants of both cultivars showed mild or strong mottle, marked epinasty, systemic necrotic spotting of some but rarely all leaves, and leaf crinkling and folding (Fig. 1A). Presence of the virus was confirmed by back inoculations to the diagnostic host *Lycopersicon pimpinellifolium* (Jusl.) Mill. which reacted with systemic necrosis and death. Tobacco mosaic virus (TMV) which also is common in tomato crops in Peru (4) was distinguished from PTV by the necrotic local lesions produced by TMV in *N. glutinosa* L.

PTV also was isolated by inoculation to *L. pimpinellifolium* from three weed species growing in tomato fields at La Molina and nearby: *Physalis peruviana* plants showing strong mosaic and leaf deformation, *Nicandra physaloides* Gaertn. plants with strong mosaic and leaf crinkling and *Solanum nigrum* L. plants with mild mosaic and rugosity. Typical systemic necrosis and death occurred in *L. pimpinellifolium*.

Symptoms in tomato cultivars. Under greenhouse conditions, inoculations of PTV in tomato cultivars San Marzano and Rossol induced initial stunting, severe mosaic, leaf rugosity, blistering, and mild leaf twisting plus crinkling. Symptoms were similar in cultivars Marglobe, Napoli, Ventura, VF-145, and VF-198 but leaf twisting and crinkling were severe and blistering absent (Fig. 1E). Symptoms in this second group resembled more closely those of infected plants in the field although the systemic necrotic spotting and strong epinasty were not reproduced. A third group of cultivars Casablanca, Huando, VF-42, and VF-65, reacted with mild mosaic and some leaf twisting. However, plants of cultivar VF-42 recovered and were almost normal in appearance when mature. Cultivars Casablanca, Huando, Marglobe, VF-42, VF-65, and VF-145 produced fruits that showed mosaic. This symptom appeared when fruits were green, became more intense as they approached maturity, then faded completely when they reached their normal red color.

Host range and symptomatology. Peru tomato virus-C infected 23 species in addition to tomato, but only in the families Chenopodiaceae and Solanaceae (Table 1). The following species in four different families developed no symptoms when inoculated with PTV and no virus was detected in them by back-testing to indicator hosts: *Amaranthus edulis* L., *Gomphrena globosa* L. (Amaranthaceae); *Cucumis sativus* L., *Cucurbita pepo* L. (Cucurbitaceae); *Phaseolus vulgaris* L., *Vigna sinensis* (Torn.)Savi 'Black', *Vigna cylindrica* Skeels (Leguminosae); and *Capsicum pendulum* Willd., *Datura stramonium* L., *Solanum berthaultii* Hawkes (PI 265857), *S. cardiophyllum* Lindl. (PI 275215), *S. curtilobum* Juz. & Buk. (PI 186181), *S. stenotomum* Juz. & Buk. (PI 230512), *S. stoloniferum* Schlechte (PI 230557), *S. tuberosum* subsp. *andigena* Juz. & Buk. 'Renacimiento'; subsp. *tuberosum* × subsp. *andigena* 'Mariva', 'Huancayo', 'Merpata', and 'Participación' (Solanaceae). Also, no symptoms were obtained and no virus was recovered from inoculations in detached leaves of clone 'A6' (*S. demissum* × *S. tuberosum* L.) which reacts with typical local necrotic lesions to PVA and PVY (6).

The most useful indicator hosts were: *Lycopersicon pimpinellifolium* which reacted with leaf epinasty, systemic necrosis, and death (Fig. 1-B), the latter being the most characteristic symptom of the virus which could be reproduced consistently only under moderate temperatures (18–22 C) and heavy shade; *Nicotiana occidentalis* which reacted initially with vein clearing and later with a mosaic characterized by large irregular chlorotic blotches and leaf deformation (Fig. 1D); *C. amaranticolor* which reacted with local

necrotic spots that were sometimes surrounded by a reddish halo (Fig. 1C); and *Nicotiana glutinosa* which reacted with a mild mosaic. Pepper was the only crop, in addition to tomato, which became infected (Fig. 1F).

Limited host range studies were done with nine other isolates from diseased tomatoes or weeds which did not give typical systemic necrosis and death in *L. pimpinellifolium* but produced only stunting, epinasty and severe mottle. These gave identical

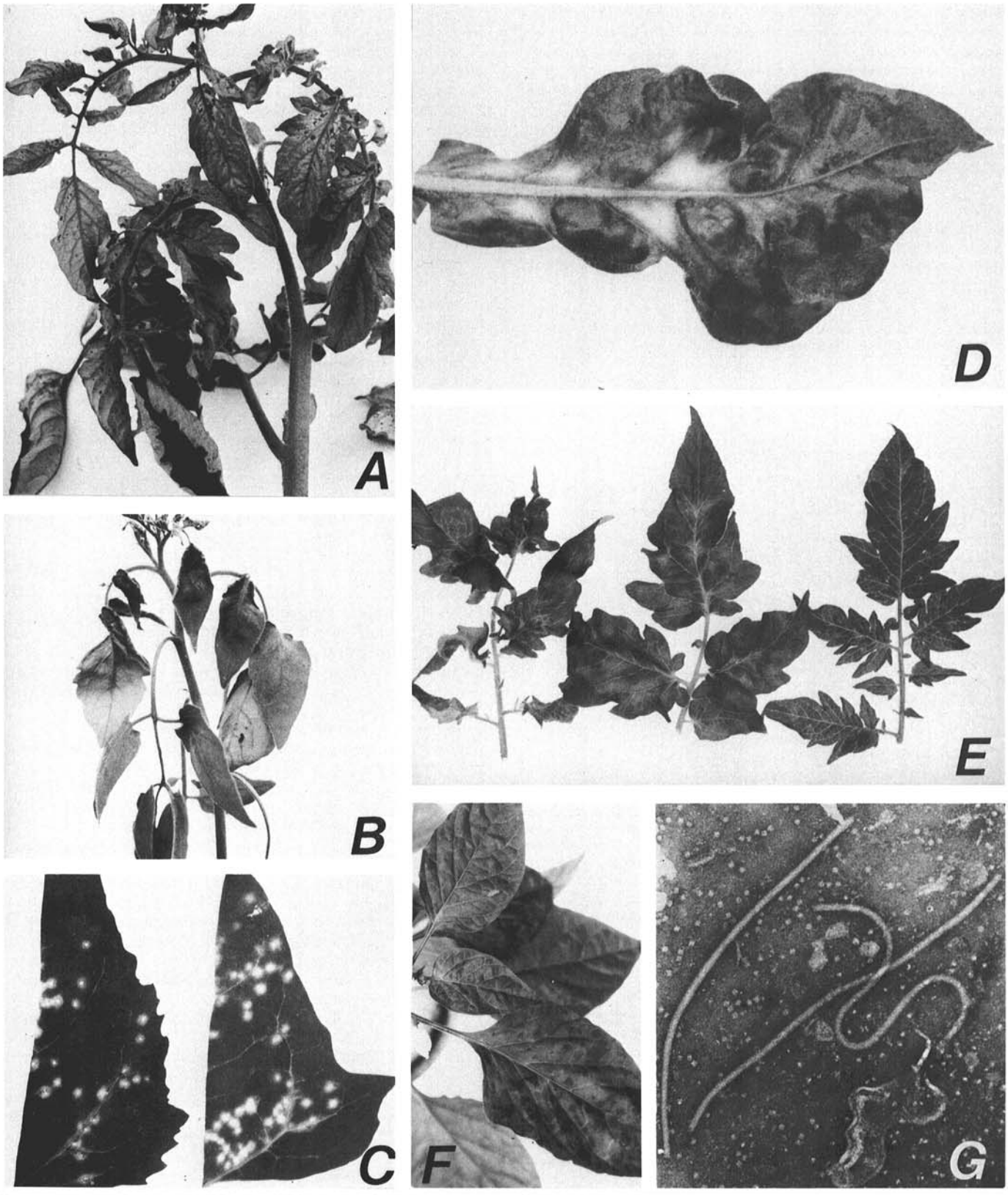

Fig. 1. Symptomatology and electron microscopy of Peru tomato virus (PTV). **A)** naturally infected tomato plant showing symptoms of epinasty, systemic necrotic spotting, and leaf folding. **B)** leaf epinasty and systemic necrosis in *Lycopersicon pimpinellifolium*. **C)** local necrotic lesions in *Chenopodium amaranticolor* (left) and *C. quinoa* (right). **D)** irregular chlorotic blotches and leaf deformation in *Nicotiana occidentalis*. **E)** tomato cultivars VF-198, Ventura, and San Marzano showing symptoms of severe leaf twisting and crinkling, mild crinkling and mosaic, and leaf rugosity, respectively. **F)** mosaic in *Capsicum annuum*. **G)** electron micrograph of particles found in diluted sap of *N. occidentalis* infected with PTV (×80,000).

symptoms to those of PTV-C in *N. occidentalis* and *C. amaranticolor* but caused a severe mosaic, veinclearing, rugosity, and leaf deformation in *N. glutinosa* instead of the mild mosaic typical of PTV-C and similar isolates.

Symptomatological comparisons between PTV and other potyviruses. Peru tomato virus-C and seven potyviruses that infect solanaceae were inoculated to *N. occidentalis, N. debneyi, L. pimpinellifolium,* and *Capsicum frutescens* L. 'Tabasco'.

In *N. occidentalis,* HMV, CDV, and TEV were severe, inducing necrotic spots and death of inoculated leaves. This necrosis later extended to noninoculated leaves, killing the plants (HMV), or was only partial, followed by severe stunting, leaf rugosity and blistering (CDV and TEV). PVA produced mosaic, leaf deformation, blistering and systemic necrotic blotches, but no stunting. PVMV reacted similarly with leaf rugosity, crinkling, mosaic and necrotic streaking. PVY, TVMV, and PTV induced mosaics and leaf deformation of different degrees but no necrosis or stunting. *Nicotiana occidentalis* was very susceptible and useful for differentiating one virus from another by the type of necrosis, mosaic, and leaf deformation produced. None of the viruses induced symptoms similar to those produced by PTV in this host.

In *N. debneyi*, HMV, CDV, and TEV were the most severe, causing mild mosaics and strong leaf deformation with production of filiform leaves (TEV), moderate leaf reduction and crinkling (HMV) and slight deformation with presence of 'green islands' in inoculated leaves (CDV). All other viruses induced mild mosaic and slight deformation, but it was not possible to differentiate one from the other as with *N. occidentalis.*

Lycopersicon pimpinellifolium reacted to CDV, HMV, PVMV, and TEV with similar systemic chlorotic spots, mild mosaic, and epinasty. PVA, PVY, and TVMV induced no symptoms and only PVY was recovered by back-testing of inoculated plants. None produced the systemic necrosis or mottle induced by PTV isolates. In *C. frutescens* 'Tabasco', TEV induced the typical wilting reported for this virus (8). CDV, HMV, and PVMV induced leaf crinkling and systemic chlorotic spots. PVA produced local necrotic spots and leaf drop and PTV induced systemic black irregular spots, stunting, and epinasty. No symptoms were observed with TVMV and PVY.

Aphid transmission. *Myzus persicae* readily transmitted PTV from infected *N. occidentalis* source plants to healthy *N. occidentalis* in short probes. For example, in one trial with single aphids given an acquisition period of 30 sec and an inoculation access time of 15 min, three of 10 plants became infected.

Attempts to transmit by seed. Seeds were harvested from infected *N. physaloides* plants with symptoms of flower breaking and from the tomato cultivars Casablanca, Huando, Marglobe, and VF-65 that showed mosaic of fruits. No symptoms were observed in seedlings grown from these. To check for the presence of PTV, sap of 36 *N. physaloides* seedlings combined in groups of two was inoculated to *C. amaranticolor* plants. Similarly, tissue from 100 seedlings of each tomato cultivar were combined in groups of 10 and inoculated to the same host. No virus was detected in any of the seedlings.

Stability in sap. In infective *N. occidentalis* sap, the thermal inactivation point was 50–55 C, dilution end point 10^{-4}–10^{-5}, and longevity in vitro at room temperature (18–26 C) 4–5 days. Infectivity also was maintained for at least 12 mo in *N. occidentalis* leaves desiccated over silica gel and stored at 2 C.

Electron microscopy. Expressed sap from infected plants contained long flexuous particles. When 40 individual particles from infective *N. occidentalis* sap were measured they ranged from 740 to 800 nm in length with a mean of 775 nm (Fig. 1G).

Serology. Peru tomato virus-C antiserum had a titer of 1/128 in microprecipitation grid titrations using purified antigen and did not react against centrifuged healthy sap of *N. occidentalis* or *N. debneyi.* However some of the antisera to other viruses that were used showed reactions against healthy sap of these indicator hosts. Cross absorption of the antibodies to healthy plant proteins was accomplished with protein prepared by homogenizing healthy *N. debneyi* leaves with 0.5 M citrate buffer pH 6.5 followed by precipitation with ammonium sulfate at 40% saturation, low speed centrifugation, and resuspension in 0.1 M sodium citrate. After this treatment there was no reaction against healthy sap or the prepared protein. Peru tomato virus -C antiserum reacted with partially purified antigens of seven different potyviruses (Table 2) indicating that PTV-C is related to all of them. Reciprocal tests, however, showed that this relationship was only one-sided with PVA, PVMV, and TEV. Taking into consideration the homologous and heterologous titers the results suggest that PTV is more closely related to PVY and TVMV than to any of the others. The difference between these results and those of Raymer et al (7) who found no serological relationship between PTV and PVY may be due to the broader specificity of the PTV antiserum obtained in the present work in which a long series of injections was used for immunization of the rabbit.

TABLE 1. Symptomatology of Peru tomato virus in indicator hosts, wild tomatoes, and potatoes

Indicator species	Symptoms[a]
Capsicum annuum L.	SM
C. frutescens L. 'Tabasco'	E, SNS
C. pubescens R & P.	E, MM
Chenopodium amaranticolor Coste & Reyn.	LNS
C. quinoa Willd.	LNS
Lycopersicon chilense Dun.	Df, R, SM
L. pimpinellifolium (Jusl.) Mill.	E, SN
L. peruvianum (L.) Mill.	Df, SM
L. esculentum Mill.	E, CM, Df, SNS
Nicandra physaloides Gaertn.	R, SM, BK
Nicotiana bigelovii Wats.	Df, SM
N. clevelandii Gray.	Df, SM
N. debneyi Domin.	MM, Cr, SCS
N. glutinosa L.	MM
N. megalosiphon Heurck & Muell.	VC, SM
N. occidentalis Wheeler	VC, Df, SM
N. tabacum L.	R, MM
Physalis floridana Rydb.	Df, SM
Petunia violaceae Lyndl.	MM, SRS, BK
Solanum brachycarpum Corr. (PI 275180)	SS
S. chancayense Ochoa (PI 338615)	CM
S. chacoense Bitt. (PI 275136)	SS
S. mochicense Ochoa (PI 283114)	SCB
S. raphanifolium Card. & Hawkes (PI 210048)	SS

[a] Coded symptom descriptions: BK = flower breaking; CM = chlorotic mottle; Cr = leaf crinkling; Df = leaf deformation; E = leaf epinasty; LNS = local necrotic spots; MM = mild mosaic; R = leaf rugosity; SM = severe mosaic; SN = systemic necrosis and death; SNS = systemic necrotic spots; SCB = systemic chlorotic blotches; SCS = systemic chlorotic spots; SRS = systemic red spots; SS = symptomless systemic infection; VC = vein clearing.

TABLE 2. Homologous and heterologous serological reactions between Peru tomato virus and seven other potyviruses

	Antigen							
Antiserum	PTV	PVA	PVY	TVMV	PVMV	TEV	CDV	HMV[a]
PTV	128[b]	32	16	32	16	16	16	16
PVA	0	256						
PVY	64		128					
TVMV	32			256				
PVMV	0				128			
TEV	0					512		

[a] Abbreviations: PTV, Peru tomato virus; PVA, potato virus A; PVY, potato virus Y; TVMV, tobacco vein mottling virus; PVMV, pepper veinal mottle virus; TEV, tobacco etch virus; CDV, Colombian datura virus; and HMV, henbane mosaic virus.

[b] Reciprocal values of titers in microprecipitation grid tests.

DISCUSSION

These results confirm that PTV-C is a potyvirus as was suggested by Raymer et al (7). It resembles other members of this group in particle size and shape, in its properties in sap, in having a narrow

host range and in being transmitted in short probes by aphids. Moreover, it is serologically related to seven other potyviruses that infect solanaceous hosts, showing closest affinities to PVY and TVMV. It is, however, different from PVY in that it does not infect either potato clone A6 which is the most important diagnostic host for this virus (6) or potato cultivars. Similarly, it differs from TVMV in its reaction in *N. occidentalis* and unlike TVMV it infects *L. pimpinellifolium, Capsicum* spp. and *C. amaranticolor* (9). PTV is therefore sufficiently distinct in host range and symptomatology to support the view of Raymer et al (7) that it be considered a new virus.

Peru tomato virus occurs in the field mainly as two different strains that cause similar symptoms in tomatoes, but differ in severity of symptoms produced in certain indicator hosts. Strain PTV-C induces systemic necrosis and death in *L. pimpinellifolium* but mild mosaic in *N. glutinosa*. The other induces mottle and strong mosaic respectively, more closely resembling the original isolates studied by Raymer et al (7) and Cardich (1).

Peru tomato virus is readily transmitted by *Myzus persicae* which is common in tomato fields in coastal Peru. The epidemiology of the virus in tomato crops probably closely resembles that of PVY in potato, which is characterized by short distance spread within the crop through the activity of both winged and wingless aphids and longer distance spread between fields through viruliferous winged aphids blown by the wind (3). The virus persists in fields in the absence of tomatoes in the alternate hosts *N. physaloides, P. peruviana,* and *S. nigrum* which are common weeds in coastal Peru. Other potential weed hosts which were infected artificially with PTV include *L. pimpinellifolium, L. peruvianum,* and several *Nicotiana* and wild potato species. Peppers also were infected artificially and PTV may be important in this crop. The cultivated potato which is commonly grown in the winter on the coast side by side with tomatoes was not infected by mechanical inoculation with the virus.

Peru tomato virus causes a severe disease in tomato plants. It also affects fruit quality causing a distinct mosaic in unripe fruits. The virus thus seems of considerable economic importance to coastal tomato growers and continuation of the research on control measures initiated by Hikida and Raymer (5) warrants high priority. The virus also may be important in tomato fields in the Andean highland and Amazon regions of Peru, but surveys in these areas have not been made.

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