Viruses Infecting Tomato in Southern Florida

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ABSTRACT

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Viruses occurring in commercial tomato fields in five counties in southern Florida during 1977–1979 were identified on the basis of symptomatology, immunodiffusion tests, indicator host reactions, and aphid transmission. The viruses or diseases and the amount of damage varied with location. Tobacco etch virus (TEV) and potato virus Y (PVY) were the only viruses found in Palm Beach County, where TEV was responsible for extensive losses in 1977–1979. A few samples from Dade County (Homestead) were infected with PVY, which caused little or no commercial loss. TEV, PVY, and tobacco mosaic virus were found in Lee and Collier counties (Naples-Bonita Springs and Immokalee production areas). A newly recognized disease of tomato, referred to here as tomato yellows, was the most widely distributed disease in Lee and Collier counties, involving nearly 100% of the late-spring 1978 tomato acreage in the Naples-Bonita Springs area. The tomato yellows agent was not mechanically transmitted but was transmitted by *Myzus persicae* in a circulative manner. Other studies suggested that the tomato yellows agent is a strain of potato leaf roll virus. The only tomato farm examined in Hendry County in the fall of 1978 showed more than 50% incidence of pseudocurly top. The diseases of most concern are tobacco etch on Florida's east coast and tomato yellows on the west coast.

The virus diseases affecting tomato (*Lycopersicon esculentum* Mill.) have not been intensively surveyed in Florida for many years, and current literature is limited. A disease of tomato resembling curly top was first mentioned as occurring along the lower east coast of Florida in 1950 (18), and Giddings et al (7) reported that a similar disease may have occurred on the west coast of the state since 1944. The disease was thought to resemble a disease caused by beet curly top virus. However, Simons and Cole (15) named the disease pseudocurly top when the causal agent was found to be transmitted by treehoppers rather than leafhoppers.

Conover and Fulton (1) in 1953 isolated potato virus Y (PVY) from naturally infected tomatoes at Homestead, FL, where it occurred alone or in combination with tobacco mosaic virus (TMV). Simons et al (14) correlated the occurrence of PVY in different parts of Florida with older potato production areas and predicted that the introduction of potatoes into the lower east coast and Immokalee areas, where PVY was not then present, would serve to introduce the virus. This prediction was borne out in 1957 (13). Cox in 1965 reported that PVY was involved in significant losses to the east coast tomato crop that occurred during the 1964–1965 season (4).

We report the results of surveys for viruses in tomato fields in southern Florida conducted from December 1977 into the spring of 1979.

MATERIALS AND METHODS

Survey procedures. Three of the four principal tomato-producing areas in southern Florida were surveyed: the lower east coast (Palm Beach County), the Homestead area (Dade County), and the southwestern areas surrounding Naples, Bonita Springs, Immokalee, and Felda (Lee, Collier, and Hendry counties). Only the Palmetto-Ruskin area (Hillsborough and Manatee counties) was excluded. Leaflets were collected from plants (cultivar Walter unless mentioned otherwise) suspected of being infected with a virus and were taken to Belle Glade for virus identification.

Virus identification. Samples were routinely checked for the presence of virus by immunodiffusion tests (11) using antisera for TMV, PVY, tobacco etch virus (TEV), pepper mottle virus (PeMV), and occasionally cucumber mosaic virus. Mechanical inoculations were attempted with all collected tissues. Leaves were triturated in the presence of 0.01 M phosphate buffer, and the juice was rubbed onto Carborundum-dusted leaves of indicator test plants.

Because many viruses may infect both pepper and tomato in southern Florida, three pepper cultivars (*Capsicum annuum* L. 'Early Calwonder', 'Florida VR-2', and 'Delray Bell') (2,3), used previously to identify pepper virus strains (23), were included in the virus host range studies. The principal tomato cultivars used were Walter or Walter PF and Flora-Dade, but other Florida-released and commercial cultivars were tested for susceptibility. A number of tobacco species and other solanaceous species were also included.

Transmission of the tomato yellows agent. Attempts to transmit the tomato yellows agent by mechanical means were unsuccessful, so subsequent transmission tests and host range studies were done with the green peach aphid, *Myzus persicae* (Sulzer). Scions from tomato yellows-affected plants were also grafted to healthy tomato plants.

Early aphid transmission trials were made with several isolates of the tomato yellows agent collected from the Naples-Bonita Springs area. Later, a single isolate originating from a naturally infected tomato plant grown in breeding plots at the Agricultural Research Center at Immokalee was used. It was maintained in Walter tomatoes by periodic transfers with infective aphids.

Two clonal lines of *M. persicae* were used to compare vector efficiency in transmitting the tomato yellows agent. One clone, originally collected in Belle Glade, had been maintained in an insectary for 7 yr; the other, the Fort Lauderdale clone, had been maintained at that facility for 3 yr. The Belle Glade clone was maintained on pepper and was used for all host range tests at Belle Glade. The Fort Lauderdale clone was reared on Chinese cabbage (*Brassica pekinensis* (Lour.) Rupr.) and was used for transmission studies at Fort Lauderdale.

Infected tomato plants with five to six leaves were used as source plants. Test aphids were starved in a petri dish or a stoppered 50-ml flask for 1 hr before the acquisition access period. Aphids were placed on young leaves showing symptoms and were transferred with a camel's-hair brush. For host range determinations, aphids were given a 24-hr acquisition access period and were transferred en

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masse, with at least five aphids on each of five test plants. The plants were held in the laboratory for 48 hr before being moved to the greenhouse. Inoculated plants and healthy controls were sprayed with either oxydemetonmethyl or pirimicarb at that time and regularly thereafter.

Tomato seedlings were used for recovery tests and most transmission studies, although *Physalis floridana* Rydb. seedlings were also used in some of the later tests. Each seedling was covered with a clear butyrate cage capped with a nylon cloth to confine the aphid(s). After a 5–7 day inoculation feeding period at about 25 C, plants were sprayed with malathion and maintained in a separate screenhouse at 28 ± 2 C for periodic observation of symptom development for 8 wk. All inoculated plants and healthy controls were kept free of insects by weekly malathion sprays.

For virus retention tests, the insects were transferred serially to healthy plants every 24 hr until all insects died.

Hemolymph injection. Apterous adult female *M. persicae* reared on tomato yellows-diseased *P. floridana* were used as donors for hemolymph injected into late-instar nymphs. Each donor was first placed on a *P. floridana* seedling for 12 hr to test its inoculativity. Donors were then numbered and the hemolymph was drawn by capillary action of a glass needle. Recipient nymphs were first immobilized in the refrigerator and held by vacuum on the screened end of L-shaped tubing. Inoculum was delivered through the intersegmental membrane of the abdomen. One donor was used for two recipient insects. All aphids that survived injection were transferred singly to *P. floridana* seedlings for infectivity tests.

RESULTS

East coast survey. Epidemics of virus diseases in the east coast tomato crop in 1978 and 1979 began in surrounding fall-seeded bell pepper fields in 1977 and 1978. The predominant virus infecting the fall pepper crop was identified as a common strain of TEV by host range and serologic tests; PeMV occurred to a lesser extent. Virus infection of pepper began as early as mid-October 1977, and numerous pockets of TEV inoculum developed by year's end.

The tomato acreage at Lantana, just north of the main pepper and tomato acreage in Palm Beach County, was surveyed first for virus infection. In mid-December, infected tomato acreage was minimal and limited to PVY and TEV (Table 1). TEV gradually spread into Delray and Boynton Beach tomato farms during January 1978, as aphid populations increased and alate aphids migrated from abandoned and heavily infected pepper fields. The spread of TEV continued unabated for the remainder of the 1978 spring tomato crop. Several farms where tomato seedlings were infected soon after transplanting sustained total losses. The spread of TEV during the 1978–1979 season was essentially the same as in 1977–1978, but losses did not approach those sustained the previous season.

Homestead survey. Only four samples were obtained from the Homestead area because infection was relatively light. Virus appeared to be concentrated on a few farms with a history of virus infection. The only virus isolated and identified by serologic reaction and inoculation to resistant pepper (Florida VR-2) was a common isolate of PVY.

Immokalee area survey. Nine samples were taken in five widely separated tomato-producing areas around Immokalee in the late spring of 1978. The tomato yellows agent was isolated by aphid transmission from plants from one commercial farm and from several breeding lines; TMV was isolated from one line in breeding plots at the Agricultural Research Center near Immokalee.

Naples-Bonita Springs survey. Most of the tomato samples indexed during 1978 came from the western part of the state, a major producing area accounting for more than 8,000 acres annually. Although several farms are isolated, most are grouped in west Naples and Bonita Springs. Walter tomato was the principal cultivar, with Flora-Dade accounting for only five of the 99 samples. TMV, TEV, and PVY were isolated from samples with obvious mosaic symptoms (Table 1). However, most of the samples (84%) did not show mosaic symptoms but rather a mild interveinal chlorosis and a tendency for the leaf margin on the youngest leaves to curl under. It was later observed that tomato fields that had been sprayed with methamidophos also showed some of the same general symptoms, which further confounded early diagnosis. As growing conditions improved and terminal growth resumed, more chlorosis and rugosity became apparent and plants could readily be diagnosed as diseased. The term tomato yellows was coined for referring to these plants. The number of diseased plants increased weekly. By the end of the spring season, most tomato

Table 1. Occurrence and distribution of viruses in tomatoes in southern Florida

Location	No. of farms	No. of samples	Viruses isolated[a]			
			PVY	TEV	TMV	TY
East coast	4[b]	30	2	14	0	NT[c]
Homestead	2[d]	4	2	0	0	NT
Naples-Bonita Springs	8[e]	81	5	1	7	NT
	3[f]	18	0	0	0	18
Immokalee	5[f]	9	0	0	1	4
Total	22	142	9	15	8	22

[a] Potato virus Y (PVY), tobacco etch virus (TEV), tobacco mosaic virus (TMV), and tomato yellows (TY).
[b] Of 52 samples collected from five area pepper farms, 39 yielded TEV, one yielded PVY, and seven yielded pepper mottle virus.
[c] NT = not tested by aphid transmission; mechanical transfers all negative.
[d] Two samples from an adjoining pepper field also yielded PVY.
[e] Sampled before April 1978, when aphid transmission of tomato yellows agent was confirmed.
[f] Sampled late in the season.

Table 2. Response of test plants to mechanical inoculation with two isolates of potato virus Y (PVY-C, PVY-S), tobacco etch virus (TEV), and tobacco mosaic virus (TMV) isolated from field-grown tomatoes[a]

Test plant species Cultivar	Virus			
	PVY-C	PVY-S	TEV	TMV
Capsicum annuum				
Early Calwonder	SM	SM	SM	SM
Florida VR-2	NS	NS	NS	LL
Delray Bell	NS	NS	NS	SM
Datura metel	SM	SM	SM	LL,SN,D
D. stramonium	NS	NS	SM	LL
Lycopersicon esculentum				
Walter	SM	SM	SM	SM
Flora-Dade	SM	SM	SM	SM
Nicotiana benthamiana	SM	SM,SN,D	SM	SM
N. glutinosa	SM	SM,SN	SM	LL,SM,SN
N. hybrid	SM	SM	SM	LL,SM,SN
N. rustica	SM	SM	NT	SM
N. tabacum				
Xanthi	SM	SM,SN,D	SM	LL,SM,SN
White Burley	SM	SM,SN,D	SM	LL,SM
Burley 21	SM	SM	SM	LL,SM
V-20	SM	NS	NS	SM

[a] LL = local lesions; SM = systemic mosaic; SN = systemic necrosis; D = plant death; NS = not susceptible; NT = not tested.

fields in this area showed symptoms, and 100% of plants in some fields were diseased. Yield data were not taken, but growers estimated at least a 25% reduction in yield. The tomato yellows disease was also detected during the spring of 1979, but occurrence and losses were less extensive than in the previous year.

Hendry County survey. A disease diagnosed as pseudocurly top was reported in tomatoes near Felda, north of Immokalee (J. N. Simons, *personal communication*). Nightshade plants (*Solanum nigrum* L.) growing near the borders of the field were also infected, and the treehopper vector (*Micrutalis malleifera* Fowler) was present in the axils of infected nightshade plants. About half the plants in the field were infected. These were the only instances of this disease found.

Virus identification. Plant reactions to the viruses detected during the survey are shown in Table 2 (reactions to the tomato yellows agent are discussed separately). More than one isolate was studied for each virus (PVY, three; TEV, two; TMV, three) but, because most of the isolates gave similar reactions, results were combined. Three isolates of PVY could be distinguished by systemic mosaic patterns on Early Calwonder pepper and several tobacco species, although all reacted similarly in immunodiffusion tests and none infected PVY-resistant peppers. One of the PVY isolates collected at Naples (PVY-S) was consistently more severe on several tobacco species, causing systemic necrosis and eventual death. Homestead, MH-1, Tropic, Bonny Best, Florida 1011, Tropic-Red, Tropic-Gro, Manalucie, Sugar Lump, Manapal, Immokalee, and Indian River tomatoes were susceptible to all isolates of PVY, TEV, and TMV by mechanical inoculation. Two tomato lines with reported virus resistance were provided by J. J. Augustine of the University of Florida at Bradenton. Line 770813 was resistant to TMV, while line 776118 was resistant to at least two isolates of PVY.

Host range of tomato yellows agent. The following solanaceous species were inoculated by mass aphid transfer of the tomato yellows agent: *Datura stramonium* L.; *L. esculentum* 'Walter', 'Walter PF', 'Tropic', 'Tempo', and Flora-Dade'; *Nicotiana benthamiana* Domin; *N. glutinosa* L.; *N. hybrid* (*Nicotiana* × *edwardsonii* Christie and Hall, hybrida nova); *N. rustica* L.; *N. tabacum* L. 'White Burley' and 'Burley 21'; *P. floridana*; *S. nigrum* L.; and *S. tuberosum* L. 'Sebago' and 'Superior'. In one inoculation trial, one of five *D. metel* L. plants showed symptoms, but infection could not be confirmed in subsequent inoculations. The tomato yellows agent was recovered by aphid transmission from the following hosts to tomato; *D. stramonium*, *N. rustica*, *P. floridana*, *S. nigrum*, and *S. tuberosum*. *Gomphrena globosa* L. was the only nonsolanaceous host to become infected. Solanaceous plants that failed to develop symptoms and were negative in recovery tests were *C. annuum* 'Early Calwonder', 'Florida VR-2', and 'Cubanelle' and *S. melongena* L. Other nonsusceptible species were *Beta vulgaris* L. 'US H6' and 'US H7', common ragweed (*Ambrosia artemisiifolia* L.), hairy beggarsticks (*Bidens pilosa* L.), *Lactuca sativa* L. 'Minetto' and 'Valmaine', *Capsella bursa-pastoris* (L.) Medik., and *Hibiscus esculentus* L.

Early symptoms of tomato yellows in tomato seedlings included stunting and interveinal chlorosis. At a later stage, marginal chlorosis and downward leaf rolling on the youngest leaves were quite pronounced and thus diagnostic (Fig. 1). Older infected leaves were leathery in texture and rugose as well as yellowed. Yellowing and leaf roll symptoms were very apparent on *D. stramonium*, *P. floridana*, and *S. tuberosum*. Infected *S. nigrum* plants displayed similar but more subtle symptoms in the greenhouse. Symptoms were readily apparent on this weed growing near tomato fields.

Other nonsolanaceous weeds bordering west coast tomato fields and showing chlorotic symptoms, including *B. pilosa*, *A. artemisiifolia*, and Virginia pepperweed (*Lepidium virginicum* L.), tested negative when indexed by aphids to tomato.

Tomato plants with typical yellows symptoms were dug from three tomato farms near Naples and taken to Belle Glade for graft transmissions. Serologic tests confirmed the absence of PVY, TEV, and TMV. Scions from healthy Walter and Flora-Dade plants were cleft-grafted to the infected stock plants; about a month later, marginal yellowing appeared in the scions. Yellowing and leaf roll symptoms also developed on healthy tomato seedlings when aphids were transferred from the infected scions. D. E. Purcifull at Gainesville confirmed these results with similar field-infected plants. No virus particles were seen with the electron microscope in leaf dip preparations from any yellows-affected tissue (D. E. Purcifull, *personal communication*). This procedure could be expected to reveal particles of the viruses already identified but not a possible phloem-inhabiting pathogen.

Aphid transmission of the tomato yellows agent. In preliminary tests, five apterous adult *M. persicae* were transferred after a 24-hr acquisition access period to Walter and Flora-Dade tomatoes and were given test feedings of 30 sec; 10 and 30 min; and 1, 2, 4, 8, and 24 hr. Transmission occurred only with the 8- and 24-hr feeding times.

The two clones of *M. persicae* showed similar acquisition efficiencies, and transmission efficiency was enhanced as the acquisition access period was lengthened (Table 3). The acquisition threshold of the tomato yellows agent was 1.0 and 1.5 hr for the Fort Lauderdale and Belle Glade clones, respectively.

Tests with multiple insects of the Fort Lauderdale clone resulted in higher transmission than single aphids (Table 4). Latent periods in multiple insects were shorter than those in single insects. The mean retention period, however, did not increase when more insects were used per test plant.

The transmissibility of the tomato yellows agent via hemolymph of *M. persicae* was studied to further characterize the method of transmission. Hemolymph from 40 donors with an inoculativity of 77.5% (31 of 40 *P.*

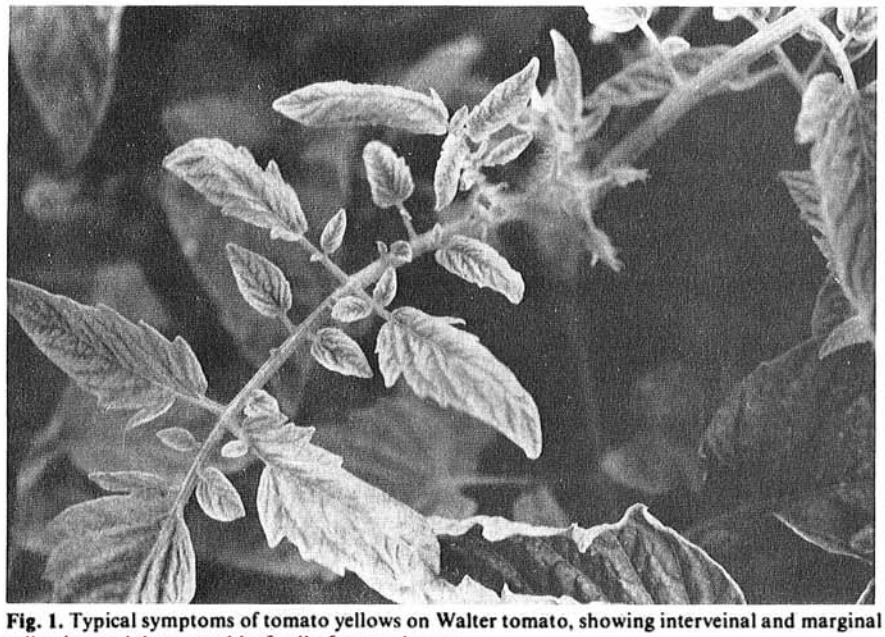

Fig. 1. Typical symptoms of tomato yellows on Walter tomato, showing interveinal and marginal yellowing and downward leaf roll of young leaves.

floridana plants became infected) was used to inject 80 recipient aphids. Of these, 51 (63.8%) survived and resulted in 17.6% transmission (six of 34 *P. floridana* plants became infected).

DISCUSSION

The incidence of virus diseases in tomatoes in southern Florida appears to be correlated with aphid populations and farming practices. In southern Florida, virus diseases of vegetables invariably occur earliest along the east coast, where pepper and cucurbit crops become infected first. The 1977 fall season was somewhat unusual, with aphid populations and virus infection of pepper occurring as early as mid-October (24); TEV was the predominant virus. Although pepper production has probably long had an influence on the particular virus(es) infecting tomato on the east coast (4), this was one of the most severe epidemics in recent years.

Disease incidence was lower in 1979, probably because aphid populations peaked later in the fall of 1978, and a number of pepper farms in the area were experimenting with the commercial use of mineral oil sprays for virus control (16). One pepper farm in the middle of much of the tomato acreage on the lower east coast did not receive the oil spray in either 1977 or 1978, and this contributed to the spread of TEV into the tomato acreage.

Virus spread in winter vegetables in the Homestead area has consistently occurred some time after the reported occurrence along the east coast. Aphid populations (especially *M. persicae*) are known to peak later in this area (22). Pepper acreage around Homestead is limited, and although PVY is associated with pepper, it appears to be a minimal problem for both pepper and tomato at this time.

The most viruses were found in the Naples-Bonita Springs tomato acreage. Aphid-transmitted viruses like PVY and TEV seemed to be associated with fall tomatoes or with winter-transplanted tomatoes adjoining abandoned fall tomato fields. Aphid populations are lowest during midwinter and therefore do not cause appreciable spread of either PVY or TEV. TMV occurred sporadically throughout the fall and spring season and was probably spread by normal field operations.

The widespread occurrence of tomato yellows suggests that it is a potential problem for tomato production in southwestern Florida. In many ways, this disease resembles a leaf roll of tomato attributed to a strain of potato leaf roll virus (PLRV) in New York (9). Tomato yellows is also very similar to potato leaf roll in suscept range and symptomatology (8). Although the tomato yellows agent readily infected tomato, infection of potato was more difficult; however, the agent could be recovered from potato. Natti et al (8) noted that most solanaceous species were susceptible to PLRV and produced similar symptoms, although some hosts, including *C. annuum*, *L. pimpinellifolium*, and *S. nigrum*, were symptomless carriers. In our tests, the tomato yellows agent was readily transmitted to tomato and nightshade, producing diagnostic symptoms that might be expected of a more host-specialized strain of a virus like PLRV. Nightshade has been found naturally infected with the tomato yellows agent in southern Florida and appears to be an important virus source.

The transmission characteristics of the tomato yellows agent also generally agree with those of PLRV. Neither is mechanically transmissible; both are transmitted by grafting and by aphids in a circulative manner. In contrast to the report by Stegwee and Ponsen (17) that PLRV is a propagative virus in *M. persicae*, Eskandari et al (6) recently failed to obtain serial passages beyond one transfer. Other researchers (10,19,20) have also provided evidence in support of a nonpropagative vector-virus relationship. The 1-hr threshold of the tomato yellows agent acquired by *M. persicae* in our study agrees with results for PLRV (5,10,21). The latent period reported for PLRV ranges from 7 to 30–49 hr (5,6,20). Our results indicated variable latent periods for the tomato yellows agent (Table 4); however, latent periods appeared to depend on the length of the acquisition access period and the virus dosage ingested by *M. persicae*, which has also been noted for PLRV (10,19,20).

Several reports indicate that PLRV is not retained by its vector, *M. persicae*, for life (6,20). The retention period of the tomato yellows agent by *M. persicae* was positively related to the length of the acquisition access period and the dose of ingested virus. After a 12-hr acquisition access, none of the test insects retained the tomato yellows agent for life (Table 4). Results of hemolymph injections suggested a circulative nature for the tomato yellows agent in *M. persicae* and indicated that hemolymph injection was much less efficient in making the aphids infective than an acquisition feeding (6). Our data paralleled results reported for PLRV (19,20). Thus, although not conclusive, the evidence strongly suggests that the tomato yellows agent did not multiply in *M. persicae*.

Most evidence suggests a close relationship between PLRV and the tomato yellows agent; however, we did not directly compare our isolate and PLRV. Because other laboratories have reported such wide variations in the transmission properties of PLRV, comparative studies using known PLRV would probably not have yielded a definite answer.

Recently, our tomato yellows isolate has been compared serologically with some similar viruses. In enzyme-linked immunosorbent assay, the tomato isolate reacted negatively with barley yellow

Table 3. Transmission of tomato yellows agent by adult *Myzus persicae* clones

Acquisition access period (hr)	Fort Lauderdale colony		Belle Glade colony	
	Infection[a]	%	Infection[a]	%
0.5	0/32	0.0	0/32	0.0
1.0	1/32	3.2	0/32	0.0
1.5	0/16	0.0	1/16	6.3
2.0	2/16	12.5	3/16	18.8
4.0	2/15	13.3	3/15	20.0
6.0	3/10	33.3	3/14	21.4
8.0	5/14	35.7	5/15	33.3
26.0	7/15	46.6	8/15	53.3
48.0	11/16	68.8	10/16	62.5

[a]Number of plants infected/number tested (one aphid per plant).

Table 4. Transmission characteristics of the tomato yellows agent by third- to fourth-instar nymphs of *Myzus persicae*

Experiment	Nymphs per test plant (no.)	Acquisition access period (hr)	Transmission efficiency[a]	Latent period (hr)			Retention (days)			Longevity (days)		
				Minimum	Maximum	LP_{50}	Minimum	Maximum	Mean	Minimum	Maximum	Mean
1	7	12	9/10 (90%)	<14	60	...[b]	1.5	7.5	5.4	4	13	6.9[b]
2	5	5	12/15 (80%)	<9	29	...	...	...	...	...	...	...
3	1	8	6/16 (37.5%)	16–20	96	40.0	1	5	3.3	3	15	7.6
4	1	12	9/16 (56.3%)	14–16	72	28.5	2	10	6.0	2	17	9.4

[a]Number of *Physalis floridana* plants infected/number of plants tested.
[b] ... = Not tested.

dwarf virus (W. F. Rochow, *personal communication*) and with PLRV when using antiserum of Japanese origin (R. G. Clarke, *personal communication*). However, in tests performed by J. E. Duffus in California, our tomato isolate was found to be serologically related to beet western yellows virus (BWYV), as were a number of isolates of PLRV. The relationship between PLRV and other luteoviruses has recently been shown in immunosorbent electron microscope tests (12). The BWYV-PLRV group appears to be a virus complex set apart by virus-host relationships; the tomato virus in Florida may be another illustration of this phenomenon.

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