Influence of Light Quality on Translocation of Tomato Yellow Top Virus and Potato Leaf Roll Virus in *Lycopersicon peruvianum* and Some of its Tomato Hybrids

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ABSTRACT

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Green peach aphids (*Myzus persicae*) could not recover tomato yellow top virus (TYTV) or potato leaf roll virus (PLRV) from *Lycopersicon peruvianum*, U.S. Department of Agriculture Plant Introduction 128655, and some of its hybrid progenies after they were aphid inoculated as seedlings with the same viruses in a glasshouse. After these plants were graft inoculated, however, aphids routinely recovered TYTV and PLRV from some plants but not others. The infected plants were tolerant (asymptomatic). Their apparent immunity to infection by aphid inoculation was expressed in a glasshouse or in direct sunlight but not in houses covered with a translucent fiberglass material. Virus could be recovered from tolerant plants inoculated by aphids in a glasshouse but only after they were transferred to and incubated in a fiberglass house. The transfer could be delayed at least 8 wk after aphid inoculation without affecting the eventual recovery of virus. Virus could not be recovered from new growth of some tolerant plants infected by graft inoculation after the plants were severed from the infected graft scion. Similarly, virus could not be recovered from new growth of some plants infected by aphid inoculation in the fiberglass house after the plants were transferred to the glasshouse. These results are explicable on the basis that a virus transport function that controls release of virus from initially infected cells was completely or partially inhibited in the glasshouse.

In preliminary studies (7) on resistance to tomato yellow top virus (TYTV) in *Lycopersicon peruvianum* (L.) Mill., U. S. Department of Agriculture Plant Introduction (P. I.) 128655, approximately 40% of the plants in a particular seed lot were infected by aphid inoculation. The remaining 60% were apparently immune. The preliminary studies were performed in a greenhouse covered by a translucent fiberglass material sold commercially under the name Corrulux (Manville Corp., Denver, CO). When these studies were replicated in a glasshouse, no plants of the original seed lot could be infected by aphid inoculation. Apparently, plants that were susceptible to infection by aphid inoculation in the fiberglass house were completely resistant to establishment of infection by aphid inoculation in the glasshouse. The studies reported here were conducted to determine the nature of this resistance to aphid inoculation. In the course of these studies, we learned that some of the *L. peruvianum* plants apparently could not be infected by aphid inoculation under any circumstances. That extreme resistance is examined in a companion paper (5).

Because of the close relationship between potato leaf roll virus (PLRV) and TYTV (6), PLRV isolates were also included in these studies. Although the two viruses are serologically indistinguishable (Thomas et al, *unpublished*), their interactions with *L. peruvianum* were examined separately here because TYTV is biologically distinct from PLRV (4,5). It produces a debilitating and distinct disease of *L. esculentum* Mill. (tomato) which is not produced by PLRV (4), and its epidemiology is not associated with that of PLRV (5).

MATERIALS AND METHODS

Source of germ plasm. *Lycopersicon peruvianum* P. I. 128655 was collected at Charanilla Tampaca, Peru, in 1938 by L. H. Blood (from original record of L. H. Blood), increased by open

pollination at Logan, UT, and later at Prosser, WA. Hybrid progenies were produced from interspecific crosses between a selected P. I. 128655 plant with immunity to beet curly top virus (BCTV) (8,10) and *L. esculentum* Mill. (tomato) 'Bonnie Best.' F_1 and F_2 generations of the hybrids were increased in the field by open pollination. Plants with immunity and complete tolerance to BCTV were selected in the F_3 generation, and plants with resistance to TYTV were selected in the F_4 generation. The F_5 hybrid progenies used in this study were derived from individual, open-pollinated F_4 plants selected for resistance to TYTV in the preliminary studies (7).

Plant culture. Seed of *L. peruvianum* P. I. 128655 and hybrids were germinated in vermiculite, and young seedlings were transplanted into 10-cm plastic pots containing a mixture of sterilized loam, sand, and peat moss. Fertilizer was added to the irrigation water throughout the growing period. Plants were grown in glass and fiberglass houses at a temperature of 25 to 29 C and in growth chambers under conditions designated in the text.

Insect culture. Nonviruliferous green peach aphids (*Myzus persicae* (Sulz.) were reared and maintained on *Raphinus sativus* L. and *Brassica pekinensis* Lour. in an isolated insectory in cages covered with aphid-proof nylon net. They were regularly checked on control plants for virus contamination.

Aphid transmission. Only *M. persicae* was used for aphid transmission. All infection assays were conducted by aphid transmission to *Physalis floridana* Rydb. All aphid acquisitions of virus were conducted on detached leaves of the virus source plants on moist filter paper in a petri plate. Aphids were allowed 48 hr acquisition access and transmission access periods of 72–96 hr. Usually 20 aphids per seedling were used in transmission tests. Aphids were caged on seedlings of test plants under inverted plastic tumblers which had their bottoms removed and covered with nylon net for ventilation. Aphids were killed with nicotine sulfate fumigation at the end of the transmission period.

Graft inoculations. All plants that indexed negative after aphid inoculation were graft inoculated using infected *Datura tatula* L. or tomato as a virus source. Scion and stock union were bound with Parafilm (American Can Company, Greenwich, CT), and the plants were kept in a mist chamber for 8–10 days to enhance development of stock-scion union.

Virus source. TYTV isolates were collected from field-grown tomato in 1980 and 1981 at Prosser, WA (6). PLRV isolates 1 and 2 were collected from infected potatoes at Prosser, and PLRV-4 was obtained from Jim Toomey of the San Luis Valley Research Center, Center, CO.

RESULTS

Discovery of apparent resistance to infection. To pursue previous investigations (7) of the resistance to TYTV in P I. 128655, 144 seedlings were grown and aphid inoculated (approximately 10 aphids/plant) in a glasshouse with the original TYTV isolate (No. 10) used in the preliminary studies, which had been conducted in a fiberglass house (7). None of the plants developed symptoms in the glasshouse. After 6 wk, when plants were approximately 30 cm tall, they were assayed for virus by aphid transmission to *P. floridana*. All assays were negative. The plants were cut back. New shoots that grew from buds at the basal stub were indexed again, and all assays again were negative. A second group of 144 young P. I. 128655 seedlings were inoculated with TYTV isolate 10 using 10 aphids/seedling. Each plant was assayed, cut back, and reassayed as described above. Again, all assays were negative. Susceptible tomato seedlings inoculated at the same time routinely developed symptoms within 3 wk.

Effect of virus isolate on resistance. Because more than a year had elapsed between the preliminary tests conducted in the fiberglass house and those conducted in the glasshouse, it seemed possible that the virus isolate had become attenuated. To test this hypothesis, three seedlings from the same seed lot were inoculated with each of three PLRV and 46 TYTV isolates and incubated in growth chambers at 23 C and a 16-hr day length at 20,000 lx supplied by standard 40-watt cool white fluorescent tubes (90%) and tungsten incandescent bulbs (10%). Again, virus was not recovered from any of the plants. Susceptible control plants were all infected.

In a second test in a glasshouse, seedlings of P. I. 128655 and of each of the two hybrid progenies, derived from crosses with tomato, were aphid inoculated with the original TYTV isolate, three TYTV isolates collected in 1980, 13 TYTV isolates freshly collected from plants with symptoms in the field, and three PLRV isolates. As in the first experiments, no symptoms developed. The plants were cut back, forcing growth of new shoots. Again, all plants indexed negative. Apparently none of the virus isolates could infect plants of the P. I. line or its hybrid progeny in the glasshouse.

Infection by graft inoculation. To determine whether the aphid-inoculated plants in the previous experiment were actually immune to TYTV, each plant was graft inoculated with the same virus isolate previously used for aphid inoculation. Plants were assayed by aphid transmission after 9 wk. Virus was recovered from 33% of *L. peruvianum*, 36% of hybrid 1, and 39% of hybrid 2 plants (Table 1). When cuttings of these plants were grown independently of the infected scion used for inoculation, virus could no longer be recovered from 17 of 41 (41%) cuttings of *L. peruvianum*, 22 of 50 (44%) cuttings of hybrid 1, and 21 of 51 (42%) cuttings of hybrid 2. Although some virus isolates did not infect any of the *L. peruvianum* plants graft inoculated in this experiment, all isolates infected some plants in subsequent experiments (data not given), and there was no difference in response of plants to different isolates. Therefore, data for individual isolates are not given in Table 1. Plants from which virus was never recovered were regarded as immune. All plants from which virus was recovered after graft inoculation were asymptomatic; thus, they were regarded as tolerant. Although virus could be transmitted to the tolerant plants by graft inoculation, aphids apparently could not transmit virus to these plants.

TABLE 1. Susceptibility of *Lycopersicon peruvianum* P. I.[a] 128655 and two of its interspecific hybrid (*L. peruvianum* × *L. esculentum*) progeny populations[b] to tomato yellow top virus (TYTV) and potato leaf roll virus (PLRV) transmitted by graft inoculation

	Responses to graft inoculation[c]								
	P. I. 128655			Hybrid 1			Hybrid 2		
Virus	Persist	Non-persist	No recovery	Persist	Non-persist	No recovery	Persist	Non-persist	No recovery
PLRV	3[d]	0	12	1	0	7	2	0	5
TYTV	21	17	70	27	22	81	28	21	75
Total	24	17	82	28	22	88	30	21	80

[a] P. I. = U.S. Department of Agriculture Plant Introduction.

[b] Fifth-generation open-pollinated progeny of the respective interspecific F_1 hybrids selected in the third generation for resistance to beet curly top virus and in the fourth generation for resistance to TYTV. *L. peruvianum* parent was resistant to beet curly top virus.

[c] Responses of plants 9 wk after graft inoculation: persist = virus persisted in rooted cuttings of inoculated plants; non-persist = virus recovered from inoculated plant containing graft scion but not recovered from rooted cuttings of inoculated plants severed from the graft scion; no recovery = virus not recovered from inoculated plant containing graft scion.

[d] Number of plants. Total number of plants inoculated = sum of plants in each response category.

Infection by aphid inoculation in a fiberglass house. To reconfirm the conclusion of the preliminary studies (7) that P. I. 128655 plants actually could be infected in the fiberglass house environment, plants were inoculated with two TYTV isolates and one PLRV isolate in the original fiberglass house, and comparable plants were inoculated in a glasshouse. All plants remained symptomless. In the fiberglass house, virus was recovered by aphids from 23 of 43 plants inoculated with TYTV-79, 8 of 43 inoculated with TYTV-17, and 20 of 43 inoculated with PLRV-1, 9 wk after inoculation. In contrast, virus was not recovered from any plants in the glasshouse. Clearly, the resistance of tolerant plants to virus infection by aphid inoculation was expressed in the glasshouse but not in the fiberglass house. Twenty-four of the 51 infected plants were placed in the glasshouse and 27 remained in the fiberglass house. After 6 wk, virus was recovered from only 18 of 24 plants switched to the glasshouse (9 of 10, 6 of 10, and 3 of 4 inoculated with PLRV-1, TYTV-79, and TYTV-17, respectively). Virus was recovered from all plants remaining in the fiberglass house.

Efficiency of aphid recovery of virus from infected plants. Fife and Frampton (3) suggested that resistance of sugar beets to infection by BCTV resulted because it was more difficult for the leafhopper vector to probe the phloem of resistant beets than of susceptible beets. Both BCTV and TYTV are phloem limited. To test the efficiency with which aphids could acquire virus from resistant P. I. 128655 plants in the glasshouse, we compared aphid and graft indexing of plants that had been graft inoculated in the glasshouse 9 wk earlier; the two methods detected virus with nearly the same efficiency. Indexing by aphid transmission failed to detect only 2 of 52 infections detected by graft transmission. We conclude that resistance could not be attributable to factors affecting deposition of virus into susceptible tissue by the aphids; rather, it had to be attributable to an effect of the glasshouse environment on the plant and to events occurring in the plant subsequent to deposition of virus.

Virus survival during the infection process. Inactivation of the virus particles deposited in plants by aphids during the initial infection process could account for the apparent resistance of plants to infection in the glasshouse. To test this hypothesis, we determined how long after aphid inoculation virus remained viable in plants in the glasshouse. Five groups of 17 seedlings were inoculated by identical procedures in the glasshouse. One group was transferred to the fiberglass house immediately; additional groups were transferred at 4, 7, and 12 days after inoculation, and one group was retained in the glasshouse. All plants were indexed to *P. floridana* by aphid transmission after 6 wk. Inoculation and subsequent incubation of inoculated seedlings in the glasshouse up to 12 days caused no decrease in the number of plants ultimately infected after transferal to the fiberglass house (Table 2). Virus could not be recovered by aphid transmission from any of the plants retained continuously in the glasshouse. In subsequent experiments, seedlings were incubated for 6 and 8 wk after inoculation in the glasshouse. Still, there was no decrease in numbers of plants that ultimately became infected when the plants were transferred into the fiberglass house. Thus, the virus, deposited by aphids in tolerant plants, was not inactivated in the glasshouse despite the fact that it could never be recovered from such plants as long as they were maintained in the glasshouse.

TABLE 2. Effect of length of incubation after aphid inoculation with tomato yellow top virus (TYTV) and potato leaf roll virus (PLRV) on number of *Lycopersicon peruvianum* P. I.[a] 128655 plants that became infected after transferral to a fiberglass house

Virus isolate	Days of incubation in glasshouse				Glasshouse control
	0	4	7	12	
TYTV 79	5/10[b]	3/10	6/10	5/10	0/10
PLRV 1	2/7	1/7	0/7	1/7	0/7
Total	7/17	4/17	6/17	6/17	0/17

[a] P. I. = U.S. Department of Agriculture Plant Introduction.
[b] Ratio: number of plants with positive index per number inoculated.

Resistance to systemic translocation from inoculation sites. Resistance to systemic translocation of virus from sites of aphid feeding in plants maintained in the glass greenhouse could account for our failure to detect the virus in these plants. To test this hypothesis, 18 seedlings were aphid inoculated in the glasshouse: nine with TYTV-79 and nine with PLRV-1. They were maintained in the glasshouse for 6 wk and indexed by aphid transmission. No virus was detected. The plants were cut back and cuttings were rooted from each plant. This forced new growth from basal buds. The cuttings and the parent plants then were moved to the fiberglass house and indexed 6 wk later. Four of the nine parent plants inoculated with TYTV-79 and two inoculated with PLRV-1 contained virus. Two plants inoculated with TYTV-79 and grown from basal cuttings contained virus. Clearly virus remained viable in tolerant plants following inoculation of the seedlings, but very limited, if any, upward movement into the growing shoots occurred in the glasshouse.

Effect of season on resistance. The experiments reported here, and other experiments measuring the effect of the fiberglass house environment on systemic infection, were conducted throughout the year. The results were unaffected by season. Virus was never recovered from plants inoculated and maintained in the glasshouse and was routinely recovered from a uniform percentage of the same plants after transferal to the fiberglass house.

Effect of supplemental light on resistance. Because light intensity was about four times greater in the glasshouse than in the fiberglass house, it seemed possible that supplemental light might prevent the breaking of resistance to translocation in the fiberglass environment. To test this, three flats with 18 plants each were aphid inoculated with TYTV-79. Two flats were held in the fiberglass house, one under a bank of cool white fluorescent lights and the other under natural light. The third flat was located in the glasshouse. Virus was later recovered from 7 of 17 plants in the fiberglass house under supplemental light, 6 of 17 without supplemental light, and 0 of 17 in the glasshouse.

Effect of direct sunlight. Virus could not be recovered from any of 18 P. I. 128655 plants inoculated with TYTV-79 and held for 8 wk in direct sunlight. Virus was recovered from 5 of 17 comparable plants in the fiberglass house.

Effect of preinoculation and postinoculation dark treatment. Eighteen P. I. 128655 seedlings were deprived of two consecutive photoperiods (60-hr dark treatment), inoculated with TYTV-79, and held in a glasshouse. A similar group of seedlings was given the same dark treatment postinoculation. Virus was recovered by aphid transmission to *P. floridana* from three plants given the preinoculation treatment and no plants given the postinoculation treatment. This was the only instance in which virus was recovered from aphid-inoculated plants maintained in the glasshouse.

Effects of darkness on virus transport. Experiments were performed to determine whether photosynthetic sinks created by placing parts of plants in darkness would cause virus movement into the darkened tissue. In the first test, 12 P. I. 128655 plants inoculated with TYTV-79 in a glasshouse were cut back and pruned so that three to four new shoots grew from the base of each plant. These shoots were indexed and found free of virus. A single shoot on each plant was wrapped in black construction paper. The paper was removed from groups of three plants after 3, 6, 8, and 10 days, and the darkened shoot of each plant was assayed. Virus was recovered only from a shoot of one of three plants darkened for 10 days. In a second test, 17 plants were aphid inoculated with TYTV-17 in the glasshouse. No virus was recovered from any plants 6 wk later. A single shoot on each plant was completely covered with a black paper. The darkened shoots on groups of four plants were indexed after 3, 6, 10, and 14 days. All the assays were negative.

Effects of light intensity, quality, and temperature. Five groups each of 18 seedlings of P. I. 128655 were inoculated with TYTV-79 by aphids. One group was incubated in a growth chamber for 8 wk under light of 9,900 lx (growlux light) at a 16-hr day length at 25 C. The remaining four groups, also in growth chambers, were kept under light intensities of 5,600 lx or 23,700 lx (90% cool white fluoresoent plus 10% incandescent) and at 23 or 35 C under a 16-hr day length for 8 wk. No symptoms developed under any condition.

The seedlings were assayed to *P. floridana*. Virus was recovered from 2 of 18 plants at 23 C and 5,600 lx and 2 of 18 plants at 35 C and 23,700 lx. No virus was recovered from plants incubated under growlux light. Neither temperature nor light intensity affected recovery of virus. The fact that virus was recovered from some plants under cool white incandescent lighting provides additional evidence that the transport function in the *L. peruvianum* plants is affected by light quality.

DISCUSSION

The results provide evidence that the apparent inability of aphids to transmit TYTV and PLRV to *L. peruvianum* P. I. 128655 plants reflects resistance to transport of virus into the growing shoots. Although virus could not be recovered from shoots of tolerant plants that were aphid inoculated and maintained in a glasshouse or in direct sunlight, the aphids certainly introduced virus into the plants, and the virus survived there for weeks. Proof for this is the fact that the aphid-inoculated plants became systemically infected after they were transferred to a fiberglass house. Aphids should have recovered virus from foliage of plants inoculated in the glasshouse if it had been present. Proof for this is the fact that the aphids routinely recovered the same virus from the same plants after the plants became systemically infected subsequent to graft inoculation or to incubation of aphid-inoculated plants in a fiberglass house.

There is a growing body of evidence that cell-to-cell movement of virus is not a passive process. Rather, it appears to be a distinct virus-specific transport function (TF) associated with virus-coded proteins (1). Two conceivable mechanisms advanced by Atabekov and Dorokhov in their review of plant virus transport (1) could account for the restriction of virus transport. The first postulates that virus is capable of entering and replicating in normally susceptible cells but is not able to move from infected cells to new cells without the intervention of a transport function to "open the gates" of the infected cell. Thus, inhibition of TF would prevent systemic transport by inhibiting the release of virus from initially infected cells. This mechanism fits our observations on the resistance in tolerant P. I. 128655 plants. The virus injected by aphids into tolerant P. I. 128655 seedlings apparently moved into the roots and remained there as long as plants were maintained in the glasshouse or in direct sunlight. Alternatively, it could have remained at the basal node near the point of seedling inoculation. Physiological changes in the plant, mediated by the change to the fiberglass house environment, overcame the restriction to virus transport (removed the inhibition against TF), allowing the virus to move upward into the growing points of plants to establish systemic infection.

The failure of virus to persist in new growth of many systemically infected plants when they were transferred (as cuttings or as pruned plants) from the fiberglass house to the glasshouse supports the hypothesis that the TF-mediated release of virus from infected cells is operative in the fiberglass house but inhibited in the glasshouse. However, the fact that virus persisted in many other plants when they were transferred from the fiberglass to the glasshouse does not support this hypothesis. This observation may be explicable on the basis that the inhibition of TF in the glasshouse is less than complete in some plants. The inhibition in such plants could be sufficient to prevent systemic infection in the glasshouse when only one or a few cells, at most, were initially infected following aphid inoculation. However, the inhibition could be insufficient to produce some release of virus when massive numbers of cells were infected during incubation in the fiberglass house.

Graft inoculation should provide an abundance of virus from a susceptible tissue source, that is, a source in which the release of virus from infected cells was not inhibited. Consistent with the hypothesis that systemic infection is inhibited, not by resistance of cells to infection but by restriction of virus to infected cells, the tolerant plants became systemically infected following graft inoculation with a susceptible scion, that is, a scion in which virus would not be restricted to infected cells, thus one that could serve as a source of virus for systemic infection of the resistant stock. Again, the failure of virus to persist in many graft-inoculated plants when they were severed from the graft scion supports this hypothesis. The fact that virus persisted in other plants may be explicable again on the basis of incomplete inhibition of TF in the glasshouse.

The alternate hypothesis (1) is that virus actually moves from initially infected cells without restriction but is unable to establish secondary infections without the intervention of TF. Based on the evidence, however, the hypothesis that virus moved systemically in inoculated, tolerant P. I. 128655 plants but could not initiate new infections in direct sunlight or in the glasshouse is untenable. Growing shoots were shown to be susceptible to infection in the glasshouse. They were infected by virus from infected scions grafted into the shoot tips, and many supported continued replication in the glasshouse once infection was established by graft inoculation or by incubation of aphid-inoculated plants in the fiberglass house. Therefore, if virus had moved into growing shoots from initially infected cells in the glasshouse, it should have infected them systemically.

Bennett (2) demonstrated that BCTV, another phloem-limited virus, moves passively in the phloem with mass food translocation. Thomas and Martin (9) demonstrated that the same virus may move some distance through the phloem from the points of virus injection to sites of initial infection. Our evidence indicates that virus translocation at the time of inoculation was predominantly downward, and initial infection sites were at the base or in the roots of plants. If initial infections had occurred in the shoots of plants inoculated in the glasshouse, cuttings taken from such plants and transferred to the fiberglass house should have developed systemic infection as did the root stock sources of the cuttings. However, only an occasional cutting among those taken at the extreme base of the plant developed systemic infection in the fiberglass house. Such cuttings probably contained initially infected cells.

Because phloem-limited viruses move passively with mass food translocation in the phloem, the failure of virus to infect systemically in the glasshouse in these studies could be explicable on the basis that there was no upward flow of food reserves in the phloem of the tolerant plants. For example, Bennett (2) demonstrated that BCTV remained in the roots of tobacco or sugar beet plants until a food deficit induced in the crown routinely caused the virus to rapidly move from roots to the growing points of shoots. In contrast, food deficits induced in the shoots of inoculated P. I. 128655 plants in these studies resulted in only one systemic infection among 29 plants tested. This exception involved complete darkening of the plant for an extended period of time, a treatment that could have canceled the inhibition of TF induced in direct sunlight or in the glasshouse.

Resistance to virus transport and resistance to tolerance both prevented damage to the plants. If incorporated into either tomato or potato, they would provide superior protection against the devastation of the tomato yellow top and potato leaf roll diseases. The full expression of these types of resistance in the hybrid progenies suggests that incorporation into tomato may be achievable by traditional breeding methods.

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