Evaluation of *Lycopersicon* Germ Plasm for Tomato Spotted Wilt Tospovirus Resistance by Mechanical and Thrips Transmission

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ABSTRACT

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Selected tomato germ plasm representing eight *Lycopersicon* species and five cultivars of *L. esculentum* was evaluated for resistance to a Hawaiian isolate of tomato spotted wilt tospovirus (formerly designated TSWV-L). A comparison of mechanical and thrips inoculation of TSWV across these accessions demonstrated that the two inoculation methods provide different evaluations of tomato germ plasm. Mechanical inoculation was useful in identifying direct TSWV resistance, such as virus replication and translocation. In contrast, thrips inoculation was most useful in identifying insect-mediated components of TSWV resistance, such as those associated with changes in feeding behavior. Although both inoculation methods resulted in systemic TSWV infection in all accessions except *Lycopersicon peruvianum,* the percentage of infection varied significantly among germ plasm screened within and between inoculation methods. While *L. parviflorum,* a wild species, was the most susceptible accession, *L. pennellii, L. chilense,* and *L. peruvianum* were least susceptible to TSWV with both mechanical and thrips inoculations. Thrips inoculation resulted in significantly fewer infected plants compared to mechanical inoculation on *L. esculentum* cultivars Manzana, Brazil, and Anahu, and on *L. hirsutum* f. *glabratum,* indicating resistance to thrips transmission of TSWV. The differences observed between mechanical and thrips inoculation suggest that one should consider results obtained by both methods when evaluating accessions for resistance to TSWV.

Additional keywords: *Frankliniella occidentalis,* western flower thrips

Tomato spotted wilt tospovirus (TSWV) (formerly TSWV-Lettuce serotype or TSWV-L; isolate used herein is designated Maui tomato isolate 2 or TSWV-MT2) causes serious economic losses in many food and ornamental crops worldwide (24,28) and is the type member of the *Tospovirus* genus in the family Bunyaviridae (10). In the Hawaiian islands, the loss of marketable tomato (*Lycopersicon esculentum* Mill.) yield due to TSWV epidemics costs growers millions of dollars and reduces tomato production by 50–90% (4). TSWV is naturally spread by thrips (Thysanoptera: Thripidae) and can also be transmitted mechanically by using sap from infected plants. Although at least seven species of thrips transmit one or more of the tospoviruses, the western flower thrips (WFT), *Frankliniella occidentalis* (Pergande) is thought to be the most important vector species in the Hawaiian islands and in other locations where this species is prevalent (11,32). For thrips to become viruliferous they must acquire TSWV as larvae (26,27,32). Because larvae do not generally disperse, viruliferous adult thrips are most important in the spread of the virus and represent the most likely source of primary inoculum initiating epidemics in crops (11,22,32).

In light of the wide host range of the virus and the large, widely dispersing vector populations that characterize TSWV epidemics, host plant resistance offers the best long-term strategy for TSWV management (2). Consequently, much effort has been invested in screening tomato accessions for resistance to TSWV (8,12,23,29). Screening procedures to identify genetic sources of plant resistance have relied upon natural field infection (29) or mechanical inoculation (9,23). When natural field infection and mass screening with mechanical inoculation have been used, certain germ plasm have shown resistance to TSWV infection under field conditions while being susceptible to mechanical inoculation with infected sap (1). This phenomenon, known as field resistance, has been observed in the evaluation of many crop plants for resistance to a variety of insect-transmitted plant viruses (18). With TSWV, these differences could be attributed to plant factors that alter thrips' response to plants, thus limiting TSWV transmission under field conditions. Plants with field resistance are usually lost, because mechanical inoculation is a preferred method used by plant breeders to screen for TSWV resistance. Yet, these plants may have desirable characters that could be used to limit the spread of TSWV under field conditions. Field resistance to TSWV is observed among many wild species of *Lycopersicon* (6, 30); however, the potential for direct resistance to TSWV or resistance to thrips transmission of TSWV has not been well documented. Resistance to numerous insect pests and some viruses has been documented in several wild *Lycopersicon* species, in particular *L. hirsutum* Humb. & Bonpl. f. *glabratum* Muller, *L. chmielewskii* Rick et al, *L. parviflorum* Rick et al, *L. chilense* Dunal, and *L. pennellii* (Corr.) D'Arcy (7). These wild species have not been screened previously for resistance to TSWV and warrant further investigation.

Another concern about the use of mechanical inoculation for TSWV resistance evaluation is that TSWV main-

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tained by mechanical inoculation may form defective particles (34). These isolates are unable to form complete virus particles and may lose vector transmissibility (17). Thus, screening germ plasm for TSWV resistance exclusively by mechanical inoculation may not approximate field conditions or isolates that are readily transmitted by thrips. In light of these problems, we compared thrips and mechanical inoculation for evaluation of germ plasm for resistance to TSWV. The objective of this study was to compare the response of tomato cultivars and selected wild *Lycopersicon* species to mechanical and thrips inoculation of TSWV.

MATERIALS AND METHODS

Plants. Five *L. esculentum* cultivars and representative lines from eight wild *Lycopersicon* species were chosen for evaluation (Table 1). The *L. esculentum* cultivars evaluated were previously reported as TSWV resistant (8,12,14, 20,33), but several wild *Lycopersicon* species, such as *L. h. glabratum, L. chmielewskii, L. parviflorum, L. chilense,* and *L. pennellii,* have not been previously evaluated. Accessions were selected from the above species based on availability, except that *L. h. glabratum* PI 134417 was included because of reported high levels of resistance to a number of insect pests (19). The cultivar Anahu was included as a positive control for all inoculations, because preliminary data demonstrated that this cultivar was highly susceptible to mechanical inoculation with TSWV. *Lycopersicon peruvianum* (L.) Mill. (PI 128657), previously demonstrated to be highly resistant to TSWV (23), served as a negative control for all inoculations.

Seeds of all tomato accessions were soaked in 2.7% sodium hypochlorite for 30 min and thoroughly rinsed in tap water to facilitate germination. Because of poor germination in many wild *Lycopersicon* species, the number of plants tested in each transmission experiment varied.

Virus isolate. A TSWV isolate designated TSWV-MT2 was collected from infected tomato on the Hawaiian island of Maui and used in all experiments. To avoid the use of a defective isolate, TSWV-MT2 was maintained in *Emilia sonchifolia* (L.) DC. using thrips transmission. The virus source for thrips acquisition in our experiments was *Datura stramonium* L. mechanically inoculated from thrips-inoculated *E. sonchifolia.*

Mechanical inoculation. For mechanical inoculations, leaf tissue from *E. sonchifolia* was triturated with a mortar and pestle in 0.1 M potassium phosphate buffer, pH 7.0, containing 0.01 M sodium sulfite, and maintained on ice. The inoculum was replaced with freshly ground leaf tissue every 15 min. All fully expanded leaves previously dusted with 320-mesh Carborundum were inoculated three times at weekly intervals starting 15 days after germination. After inoculation, the plants were rinsed with distilled water and maintained in a greenhouse for further observation.

The plants were observed 15 and 25 days after the last inoculation for characteristic symptoms such as necrotic or chlorotic lesions, tip necrosis, bronzing, leaf distortions, and formation of ring spots on leaves and fruit. Infection was verified 30 days after the last inoculation by enzyme-linked immunosorbent assay (ELISA) as described below.

Thrips inoculation. The WFT, maintained on virus-free green bean pods (*Phaseolus vulgaris* L. cv. Green Crop) as previously described (31), was utilized for thrips transmissions. For acquisition, 200 to 300 1-day-old WFT larvae were placed on three-to-five TSWV-infected *D. stramonium* leaves excised from three or four different plants. Fresh TSWV-infected leaves were provided every 3 days until pupation. A subsample of 20, 5–6 day old adult thrips from these cohorts were tested by ELISA as previously described (3) to verify acquisition and transtadial passage. Adults emerging from these cohorts were maintained on noninfected bean pods and used to inoculate plants 7–8 days after eclosion.

Test plants were exposed for 4 days to 25 potentially viruliferous adult thrips in cylindrical plastic cages (15 cm in diameter and 32 cm high) in the greenhouse. The cages were covered at both ends with plastic lids and sealed with parafilm to prevent the escape of adult thrips. Provision was made for adequate ventilation to avoid accumulation of moisture. After inoculation access, the plants were sprayed twice at 3-day intervals with diazinon or avermectin to kill adults and newly hatched WFT larvae.

Enzyme-linked immunosorbent assay (ELISA). TSWV infections were verified by direct double antibody sandwich ELISA (3,13) using a polyclonal antibody provided by Dennis Gonsalves. Infected *L. esculentum* cv. Anahu leaves were used as a positive control, with a pooled sample of healthy leaves from each accession on each plate as a healthy control. Samples were taken 30 days after inoculation. Leaves sampled (two to three) from each plant in an accession were pooled for each transmission experiment. The results of ELISA were measured photometrically at 405 nm with an EL 307 EIA reader. Samples were considered positive if absorbance at 405 nm was more than twice the average buffer or healthy tomato control reading, whichever was higher.

Data analysis. The differential response of tomato accessions to mechanical and thrips transmission of TSWV was analyzed by chi-square (21). Accessions were arranged in a descending order based on the percentage of plants infected, and the difference among accessions within a transmission type was analyzed by chi-square.

RESULTS AND DISCUSSION

All *Lycopersicon* species tested (Table 1) except *L. peruvianum* became systemically infected with TSWV by both mechanical and thrips transmission (Table 2). Symptom expression varied greatly among the accessions (Table 3). TSWV infection was confirmed by ELISA by sampling plants exhibiting typical TSWV symptoms (Table 3). Although *L. chilense* was symptomless under our conditions, TSWV could be detected by ELISA in inoculated plants and not in uninoculated controls.

All germ plasm except *L. peruvianum* were TSWV susceptible; however, susceptibility varied significantly among accessions, as well as between mechanical and thrips transmission within accessions (Table 2). When mechanical inoculation was used, cultivars of *L. esculentum,* including Manzana, Brazil, and Anahu, and a wild species, *L. parviflorum,* were highly susceptible to TSWV-MT2, with 72–84% infection. These data contrast with previous reports suggesting that Manzana, Brazil, and Anahu are resis-

Table 1. *Lycopersicon* germ plasm evaluated for resistance to an isolate of tomato spotted wilt tospovirus from Maui

Species	Cultivar/accession no.	Reported resistance to TSWV[z]
L. esculentum	Anahu	12
	Brazil	33
	Manzana	14
	Pearl Harbor	20
	Rey de los Tempranos	14
L. peruvianum	PI 128657	23
L. pimpinellifolium	PI 79532	29
L. hirsutum	LA 1353	6
L. hirsutum f. *glabratum*	PI 134417	N
L. parviflorum	LA 326	N
L. chmielewskii	LA 1306	N
L. pennellii	LA 716	N
L. chilense	LA 2931	N

[z] Reference number. N = no report.

tant to TSWV (12,14,33) and support observations showing the cultivar Manzana to be susceptible under field conditions in the Hawaiian islands (15). In these tests, the SW-1 gene in Anahu apparently did not impart TSWV resistance as previously suggested (12). Three independently inherited recessive genes and two dominant alleles were shown to control resistance to the different isolates of TSWV in resistant tomatoes (9). Thus, the lack of polygenic resistance may be a factor for the susceptibility to TSWV observed in Anahu. Among all the wild *Lycopersicon* species tested, *L. parviflorum* was the only one highly susceptible to TSWV. To the best of our knowledge, this is the first report of a wild *Lycopersicon* species being highly susceptible to TSWV. Thus, caution should be used when considering *L. parviflorum* as a donor parent.

The *L. esculentum* cultivar Rey de los Tempranos and several wild species, *L. h. glabratum, L. chmielewskii, L. pimpinellifolium* (L.) Mill., and *L. hirsutum,* were significantly less susceptible than Manzana, Brazil, Anahu, and *L. parviflorum,* with 16–36% infection. *L. pennellii* was the least susceptible species with only 4% of the plants infected. Our results support previous observations that *L. hirsutum* LA 1353 was susceptible to TSWV under field conditions (29). To our knowledge this is the first report of TSWV infection in the wild *Lycopersicon* species *L. chmielewskii* and *L. pennellii.* The highest level of resistance we observed was in *L. peruvianum,* which had slight local lesions on inoculated leaves but no systemic infections. These findings support earlier observations of *L. peruvianum* resistance under field (9, 16,29) and laboratory (5,23) conditions, and strongly support its use as a donor parent in tomato breeding programs.

When thrips inoculation was used, the percentage of infected plants was not significantly different from mechanical inoculation on seven of the 11 accessions tested (Table 2). Notably, *L. pennellii* and *L. peruvianum* were the most resistant accessions. These results suggest that resistance in these accessions may be due to the virus and not to the vector, and that *L. pennellii* and *L. chilense* may be used as an additional source of TSWV resistance in tomato breeding programs.

In contrast, significantly fewer plants of *L. esculentum* cultivars Manzana, Brazil, and Anahu and the wild germ plasm *L. h. glabratum* were infected by thrips inoculations versus mechanical inoculation. These results suggest that these accessions may be resistant to thrips transmission of TSWV. Further, the findings indicate that previous reports of field resistance in Manzana (14), Anahu (23), and Brazil (33) could be attributed to vector-mediated components for TSWV resistance.

Resistance to arthropods in *L. h. glabratum* (19,25) has largely been attributed to trichomes on its leaves. TSWV infection was lower when thrips versus mechanical inoculation was used on this species. Transmission by thrips to only a few plants indicates that resistance to insect pests may not translate to resistance to the transmission of a virus by an insect vector species. Yet, thrips resistance may explain the poor TSWV transmission to *L. h. glabratum,* and a closer evaluation is needed. Resistance to thrips transmission has been reported to decrease the incidence of TSWV infection in peanuts in India (1).

Comparative analyses show that susceptibility to TSWV was most efficiently evaluated by mechanical transmission (Table 2). Yet sole use of mechanical inoculation may result in the loss of valuable germ plasm, because species with vector resistance may not be identified. In our experiments, mechanical transmission by sap from plants infected through thrips transmission limited the possibility that our screening relied upon a defective isolate. Many screening programs rely on isolates maintained by continuous mechanical passage, a process known to generate defective isolates (17). Differences between previous reports and the susceptibility we observed in some accessions may be due to natural isolate variation or to the use of defective isolates in past screening programs. Although the use of thrips transmission adds an element of uncertainty in conducting a timely evaluation process, our results indicate that screening of selected germ plasm with thrips transmission is well warranted and may result in the identification of valuable accessions.

Table 2. Response of *Lycopersicon* germ plasm to sap and thrips inoculation with a Hawaiian isolate of tomato spotted wilt tospovirus collected from tomato on Maui (TSWV-MT2)

Germ plasm	Plants infected (%)		Mechanical vs. thrips (chi-square)
	Mechanical	Thrips	
Manzana (25/32)[w]	84.0 a[x]	6.25 b	32.94**[y]
L. parviflorum (12/12)	83.33 a	75.00 a	0.25 NS[z]
Brazil (32/32)	75.00 a	25.00 b	14.06**
Anahu (32/32)	72.50 ab	18.75 b	10.94**
L. hirsutum f. *glabratum* (22/32)	36.36 bc	3.13 b	8.11*
Rey de los Tempranos (43/32)	34.88 c	18.75 b	1.63 NS
L. chmielewskii (12/9)	33.33 c	22.22 b	0.04 NS
L. pimpinellifolium (21/24)	28.57 c	41.66 a	1.51 NS
L. hirsutum (12/12)	16.66 c	8.33 b	0.38 NS
L. pennellii (21/21)	4.76 d	9.52 b	0.36 NS
L. chilense (21/21)	0.00 d	0.00 b	0.00 NS
L. peruvianum (15/12)	0.00 d	0.00 b	0.00 NS

[w] No. of plants inoculated with mechanical and thrips inoculations, respectively.
[x] Figures followed by different letters indicate a significant difference at the 0.05% probability level between accessions within a transmission type.
[y] Figures followed by ** and * indicate a significant difference at the 0.01% and 0.05% probability levels, respectively, between mechanical and thrips transmission within accessions.
[z] NS = Not significant at 0.05% probability level.

Table 3. Characteristic symptoms[x] and mean ELISA values from *Lycopersicon* germ plasm infected by a Hawaiian isolate of tomato spotted wilt tospovirus (TSWV-MT2)

Germ plasm	Transmission (ELISA values)		Symptoms[y]
	Mechanical	Thrips	
Manzana	0.879	0.832	B, RS, TB, W
L. parviflorum[z]	0.876	0.858	NL, TB, W
Brazil	0.460	0.521	B, RS, TB, W
Anahu	0.879	0.832	B, RS, TB, W
L. hirsutum f. *glabratum*	1.042	0.849	LD, ST, Y
Rey de los Tempranos	0.710	0.277	B, RS, TB, W
L. chmielewskii	0.901	0.885	LD, RS, Y
L. pimpinellifolium	1.137	1.140	CL, ST
L. hirsutum	0.952	0.827	LD, RS, Y
L. pennellii	0.931	0.720	LD, W, Y
L. peruvianum	0.091	0.110	NSI
L. chilense	0.263	0.426	NVS
Buffer/healthy control	0.065	0.090	

[x] Symptoms identical regardless of the method of inoculation.
[y] B = bronzing, CL = chlorotic lesions, LD = leaf distortion, NL = necrotic lesions, NSI = no systemic infection, NVS = no visible symptoms, RS = ring spot, ST = stunting, TB = tip blight, Y = yellowing, and W = wilting.
[z] Wilting in *L. parviflorum* rapid compared to others.

Thus, one should consider the results obtained by both methods in evaluating germ plasm for resistance to TSWV.

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LITERATURE CITED

1. Amin, P. W. 1985. Apparent resistance of groundnut cultivar Robut 33-1 to bud necrosis disease. Plant Dis. 69:718-719.
2. Cho, J. J., Mau, R. F. L., German, T. L., Hartmann, R. W., Yudin, L. S., Gonsalves, D., and Provvidenti, R. 1989. A multidisciplinary approach to management of tomato spotted wilt virus in Hawaii. Plant Dis. 73:375-383.
3. Cho, J. J., Mau, R. F. L., Hamasaki, R. T., and Gonsalves, D. 1988. Detection of tomato spotted wilt virus in individual thrips by enzyme-linked immunosorbent assay. Phytopathology 78:1348-1352.
4. Cho, J. J., Mau, R. F. L., Mitchell, W. C., Gonsalves, D., and Yudin, L. S. 1987. Host list of tomato spotted wilt virus (TSWV) susceptible plants. Univ. Hawaii Coll. Trop. Agric. Hum. Resour. Res. Ext. Ser. 078.
5. Cho, J. J., Watterson, J. C., Wyatt, C., and Custer, D. M. 1990. Inheritance of tomato spotted wilt virus (TSWV) resistance in tomato. (Abstr.) Phytopathology 80:1027.
6. Costa, A. S. 1944. Observacoes sobre vira-cabeca en tomateiros. Bragantia 4:589-608.
7. Farrer, R. R., and Kennedy, G. G. 1991. Insect and mite resistance in tomato. Pages 121-142 in: Genetic Improvement of Tomato. G. Kalloo, ed. Springer-Verlag, New York.
8. Finlay, K. W. 1952. Inheritance of spotted wilt resistance in the tomato. 1. Identification of strains of the virus by the resistance or susceptibility of tomato species. Aust. J. Sci. Res. 5:303-314.
9. Finlay, K. W. 1953. Inheritance of spotted wilt resistance in tomatoes; Five genes controlling spotted wilt resistance in four tomatoes. Aust. J. Biol. Sci. 6:153-163.
10. Francki, R. I. B., Fauquet, C. M., Knudson, D. L., and Brown, F. 1991. Classification and nomenclature of viruses. Rep. ICTV Arch. Virol., 5th. Suppl. 2. Springer-Verlag, New York.
11. German, T. L., Ullman, D. E., and Moyer, J. W. 1992. Tospoviruses: diagnosis, molecular biology, phylogeny, and vector relationships. Annu. Rev. Phytopathol. 30:315-348.
12. Gilbert, J. C., and Tanaka, J. S. 1971. 'Anahu' an outstanding hybrid maker. Hawaii Farm Sci. 20(3):6-7.
13. Gonsalves, D., and Trujillo, E. E. 1986. Tomato spotted wilt virus in papaya and detection of the virus by ELISA. Plant Dis. 70:501-506.
14. Holmes, F. O. 1948. Resistance to spotted wilt in tomato. Phytopathology 38:467-473.
15. Holmes, F. O. 1954. Inheritance of resistance to plant viruses. Adv. Virus Res. 2:1-29.
16. Hutton, E. M., and Peak, A. R. 1953. Spotted wilt development in resistant and susceptible *Lycopersicon* species. Aust. J. Agric. Res. 4:160-167.
17. Ie, T. S. 1982. A sap transmissible, defective form of tomato spotted wilt virus. J. Gen. Virol. 59:387-391.
18. Jones., A. T. 1987. Control of virus infection in crop plants through vector resistance: a review of achievements, prospects and problems. Ann. Appl. Biol. 111:745-772.
19. Kennedy, G. G. 1984. 2-Tridecanone, tomatoes and *Heliothis zea*: Potential incompatibility of plant antibiosis with insecticidal control. Entomol. Exp. Appl. 35:305-311.
20. Kikuta, K., Hendrix, J. W., and Frazier, W. A. 1945. Pearl Harbor, a tomato variety resistant to spotted wilt in Hawaii. Univ. Hawaii Agric. Exp. Stn. Circ. 24.
21. Little, T. M., and Hill, F. J. 1978. Agricultural Experimentation: Design and Analysis. John Wiley and Sons, New York.
22. Mau, R. F. L., Bautista, R., Cho, J. J., Ullman, D. E., Gusukuma, M., and Custer, D. 1991. Factors affecting epidemiology of TSWV in field crops: Comparative virus acquisition efficiency of vectors and suitability of alternate hosts to *Frankliniella occidentalis* (Pergande). Pages 21-27 in: Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus. H. Hsu and R. H. Lawson, eds. Proc. Workshop U.S. Dep. Agric. Agric. Res. Serv. ARS-87.
23. Paterson, R. G., Scott, S. J., and Gergerich, R. C. 1989. Resistance in two *Lycopersicon* species to an Arkansas isolate of tomato spotted wilt virus. Euphytica 43:173-178.
24. Rice, D. J., German, T. L., Mau, R. F. L., and Fujimoto, F. M. 1990. Dot blot detection of tomato spotted wilt virus RNA in plant and thrips tissues by cDNA clones. Plant Dis. 74:274-276.
25. Rick, C. M. 1982. The potential of exotic germplasm for tomato improvement. Pages 1-28 in: Plant Improvement and Somatic Cell Genetics. I. K. Vasil, W. R. Snowcroft, and K. J. Frey, eds. Academic Press, New York.
26. Sakimura, K. 1962. The present status of thrips-borne viruses. Pages 33-40 in: Biological Transmission of Disease Agents. K. Maramorosch, ed. Academic Press, New York.
27. Sakimura, K. 1963. *Frankliniella fusca,* an additional vector for the tomato spotted wilt virus, with notes on *Thrips tabaci,* another vector. Phytopathology 53:412-415.
28. Sether, D. M., and DeAngelis, J. D. 1992. Tomato spotted wilt virus host list and bibliography. Oreg. State Univ. Agric. Exp. Stn. Spec. Rep. 888.
29. Smith, P. G. 1944. Reaction of *Lycopersicon* spp. to spotted wilt. Phytopathology 34:504-505.
30. Smith, P. G., and Gardner, M. W. 1951. Resistance in tomato to the spotted-wilt virus. Phytopathology 41:257-260.
31. Ullman, D. E., Cho, J. J., Mau, R. F. L., Westcot, D. M., and Custer, D. M. 1992. A midgut barrier to tomato spotted wilt virus acquisition by adult western flower thrips. Phytopathology 82:1333-1342.
32. Ullman, D. E., Cho, J. J., Mau, R. F. L., Westcot, D. M., and Custer, D. M. 1992. Thrips-tomato spotted wilt virus interactions: Morphological, behavioral and cellular components influencing thrips transmission. Pages 195-240 in: Advances in Disease Vector Research. K. F. Harris, ed. Springer-Verlag, New York.
33. Upreti, G. 1983. Inheritance of resistance to tomato spotted wilt virus in tomatoes (*Lycopersicon esculentum* Mill.) M.S. thesis. College of Tropical Agriculture and Human Resources, University of Hawaii, Manoa, Honolulu.
34. Verkleij, F. N., and Peters, D. 1983. Characterization of a defective form of tomato spotted wilt virus. J. Gen. Virol. 64:677-686.