Screening Two *Lycopersicon peruvianum* Collections for Resistance to *Tomato spotted wilt virus*

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ABSTRACT

Gordillo, L. F., Stevens, M. R., Millard, M. A., and Geary, B. 2008. Screening two *Lycopersicon peruvianum* collections for resistance to *Tomato spotted wilt virus*. Plant Dis. 92:694-704.

The United States Department of Agriculture (USDA) Research Service and the Tomato Genetics Resource Center (TGRC) *Lycopersicon peruvianum* germplasm collections (16,335 plants from 285 accessions) were screened with the *Tomato spotted wilt virus* (TSWV) isolates TSWV6 from Hawaii, and An_{wa}-1 from Western Australia. Using TSWV6 to screen for resistance, 10,634 *L. peruvianum* plants from 280 accessions were screened for resistance, resulting in 168 (60%) accessions with 1,437 (14%) plants indicating resistance, with all 1,404 89S (Sw-5+/Sw-5+) and 1,456 89R (Sw-5/Sw-5) controls infected. When using An_{wa}-1 for screening, 864 (15%) of 5,701 *L. peruvianum* plants were uninfected from 106 of the 181 accessions tested, and 472 (95%) of the 495 89S and 421 (73%) of the 574 89R controls were infected. Of the 172 accessions tested with both isolates, 54 were resistant to one isolate but not the other. Additionally, more accessions from the USDA than from the TGRC collection indicated resistance. TSWV-resistant accessions were somewhat equally distributed throughout the *L. peruvianum* geographic range, with an observation that northern Chile and southern Peru seemed to have an unusually high portion of accession indicating resistance. The value of Sw-5 is discussed in relationship to potential additional sources of TSWV resistance.

Additional keywords: *Lycopersicon esculentum*, thrips, *Tospovirus*

Tomato spotted wilt virus (TSWV), classified as a *Tospovirus*, infects cultivated tomato (*Lycopersicon esculentum* Mill.), causing plant stunting, necrotic leaf spotting, mottling, epinasty, plant and fruit deformity, and, in severe cases, death (3,7). Thrips are the natural vectors of tospoviruses, with species of the genus *Frankliniella* and *Thrips* being the most common (8,9,32,43). Because of the globalization of trade these insects have spread worldwide along with their vectored disease (4,28,44,57,60–62). Tospoviruses infect at least 15 monocotyledonous and 69 dicotyledonous families, of which Asteraceae, Solanaceae, and Fabaceae are most com-

monly affected. More than 1,090 plant species have been reported to be infected by this virus, including many crops of economic importance, with vegetable yield losses worldwide estimated at one billion dollars annually (32). In the 2000 growing season, TSWV epidemics in tomato were estimated to cause \$8.8 million in losses in Georgia (43). Cho et al. (7) reported that yield losses in Hawaii have been high enough to cease tomato production in some areas due to TSWV. In Brazil, Argentina, Spain, Portugal, and Italy, it is becoming the most limiting factor for tomato production (1,2,4,30,38,51,65).

Growers have tried to manage TSWV by controlling thrips through different approaches such as crop rotation, leaving the land fallowed, eliminating crop residue, insecticides, weed control, and reflective plastic mulch (29,42). However thrips are minute winged insects that easily migrate into fields, regardless of grower deterrents, then infect plants before insecticides have time to control them effectively (8). Of all the cultural practices tried, weed control and reflective mulches have had the most positive effect on increased marketable tomato yields (29,42,43).

A viable method to control TSWV is through natural resistance found in wild relatives of domesticated tomato plants, which provide a possible control to TSWV and subsequent reduction in fruit damage

(8,43). Stevens et al. (58) screened 188 accessions of seven different *Lycopersicon* spp. for resistance to isolates of TSWV, finding that *L. peruvianum* (L.) Mill. and *L. chilense* Dun. provided the highest level of resistance to TSWV. All available *L. chilense* accessions and 12 *L. peruvianum* accessions were screened for resistance from the United States germplasm collections (54,58). Additionally, a number of other reports (4,10–12,15,18,20,23,24,27, 31,33,47,49,50,52,53,62,63) have identified a high level of TSWV resistance in *L. peruvianum* beginning as early as 1939 (64). In 1946, Norris reported in relationship to TSWV, that “*L. peruvianum* possesses true resistance amounting almost to immunity” (31). Despite this observation, no comprehensive study of the *L. peruvianum* U.S. germplasm collections has been conducted, even though the TSWV resistance gene “Sw-5” was introgressed into the cultivated tomato from this species (7,57,61). Additionally, new TSWV isolates overcoming Sw-5 have been identified in several parts of the world (1,7,46,61). Latham et al. (25) deliberately developed two TSWV isolates, under controlled conditions, which completely infected plants homozygous for Sw-5. Some of these TSWV isolates that infect Sw-5/Sw-5 genotypes have been collected and used in this study.

In recognition of the paucity of comprehensive information on TSWV resistance in *L. peruvianum* and the identification of isolates that infect Sw-5/Sw-5 plants, we initiated a screening of the *L. peruvianum* germplasm. In this study, 285 *L. peruvianum* accessions at the United States Department of Agriculture (USDA) Research Service, Cornell University Geneva, NY and the Tomato Genetics Resource Center (TGRC) at the University of California, Davis were screened for TSWV resistance to isolates completely overwhelming and partially overcoming Sw-5.

MATERIALS AND METHODS

Management of *Lycopersicon* germplasm. In all, 169 TGRC accessions were screened, 38 of which belong to the core collection (henceforth identified as “TGRC Core”) and 116 from the USDA collection, totaling 285 *L. peruvianum* accessions (Tables 1 and 2). Seed of *L. peruvianum* and controls (near-isogenic tomato lines [NIL] 89R [Sw-5/Sw-5] and 89S [Sw-

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Accepted for publication 3 January 2008.

doi:10.1094/PDIS-92-5-0694

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5⁺/Sw-5⁺) were scarified to increase germination with household bleach (2.7% sodium hypochlorite) and distilled water at a 1:1 ratio for 30 min., as recommended by Rick and Hunt (41). They then were washed three to four times with tap water and spread on moist germination paper (Anchor Paper Company, St. Paul, MN) in petri dishes. Germinated seedlings were transplanted to approximately 74 cm³/plant cells filled with peat-based media in commercially available plastic flats. The objective was to test 50 plants per accession; however, actual numbers depended on germination and availability of seed. Eight cells of each flat were dedicated to 89R and 89S (four cells each) as a TSWV inoculation check. The 40 remaining cells were filled with one or more accessions depending on available seedlings.

Maintenance and use of TSWV isolates. Isolate TSWV6 was identified in Hawaii infecting (Sw-5/Sw-5) tomato plants (7). The anemone isolate (An_{wa}-1), to which Sw-5 provides some resistance, was identified on an *Anemone* sp. in Banjup, Western Australia in August 1998, and maintained in cv. Grosse Lisse (Sw-5⁺/Sw-5⁺) (25). These isolates were selected based on three criteria. First, the isolates infected controls differently; TSWV6 infected both Sw-5 and Sw-5⁺ genotypes (7). However, Sw-5 genotypes generally resisted An_{wa}-1 (25) but not Sw-5⁺ genotypes. General symptoms of both TSWV6 and An_{wa}-1 were "tip blight" to whole-plant chlorosis and stunting in the controls, with An_{wa}-1 being the less aggressive of the two. Second, our experience suggested that both isolates produced reliable disease expression with our inoculation method. Finally, these two isolates were from different areas of the world.

Isolate maintenance and resistance screening trials were conducted in controlled access greenhouses at Brigham Young University, Provo, UT. Night temperatures ranged between approximately 18 and 25°C and day temperatures be-

tween approximately 21 and 32°C throughout 10 months of screening.

Both isolates were maintained in *Nicotiana rustica* L. and were transferred by rub inoculating Carborundum-dusted (600-mesh) leaves with sterile cheesecloth pads dipped in 1 to 2°C buffer (0.1 M phosphate buffer, pH 7.4, 0.01 M sodium sulfite), with homogenized infected tissue from both previously inoculated and systemically infected leaves. Isolates were transferred to young, healthy *N. rustica* every 10 days to maintain optimum virulence (57). Transfer of an isolate within 1 to 4 days after the appearance of visual symptoms on the inoculated *N. rustica* second to fourth true leaves produced the most reliable infection for mass inoculations (6,54–58; unpublished data).

Mass inoculation of accessions and controls were accomplished using techniques previously described (54,57,58). Between 20 and 60 flats were inoculated in one setting. TSWV rapidly deactivates once inoculum is prepared; as a result, a set of up to 10 flats was inoculated within 12 to 15 min, after which fresh inoculum was prepared for the next flat set. 89R and 89S TSWV checks were arranged such that two check plants were inoculated before and after every 10 *L. peruvianum* plants. All plants were inoculated between their second and fourth true leaves and reinoculated with the same isolate 6 to 8 days later.

To monitor uncontrolled TSWV spread, 10 to 20 uninoculated 89R and 89S plants were omnipresent in the greenhouse throughout the study. Utilizing mechanically transferred TSWV greatly reduces the possibility of unintended thrips transmission of this virus (19,21). Additionally, a rotation of a regular set of insecticides (Maveric [Wellmark, Schaumburg, IL], Azatin XL [Olympic Horticultural Products, Mainland, PA], Conserve SC [Dow Agro Sciences, Indianapolis, IN], and Orthene 75 [Ortho, Marysville, OH]) were used at labeled rates, approximately once a week, to minimize thrips and other arthro-

pods. No instance of uncontrolled TSWV was identified throughout the study.

Evaluation of TSWV infection. Visual symptoms were used initially for eliminating obviously infected plants. Plants not showing characteristic TSWV symptoms were evaluated by peroxidase double-antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA), supplied by Agdia Inc. (Elkhart, IN), to detect the presence or absence of the virus (57). Plants not responding in ELISA were maintained and visually reevaluated once a week for two additional months. We have observed (unpublished data) that plant stress often encourages phenotypic expression of symptomless TSWV carriers. Plants showing visual virus symptoms were eliminated and counted as infected. Consistently, those plants identified with optical density (OD) values near the threshold used by Stevens et al. (57) were found to become visually infected during the subsequent monitoring period.

Statistical analysis and ArcGIS program. SAS was used to develop the analysis of variance tables for statistical comparisons. The ArcGIS program (Environmental Systems Research Institute, Redlands, CA) was used to position the accessions to their geographical location according to accession passport information.

RESULTS

Summary of accessions response to TSWV isolates. Either the TSWV6 or An_{wa}-1 isolates were screened on a total of 16,335 *L. peruvianum* plants from 285 accessions, and 3,929 (1,899 89S and 2,030 89R) controls (Table 1). Of the 285 accessions screened for TSWV resistance, 172 (about 60%) were tested with both isolates (6,683 and 5,516 *L. peruvianum* plants with TSWV6 and An_{wa}-1, respectively; Table 2). No resistance was detected in 39 (about 23%) of the 172 accessions to either TSWV isolate. Of the 172 accessions tested with both isolates, 23 (about 13%) indicated resistance to An_{wa}-1 but

Table 1. Summary of *Lycopersicon peruvianum* Tomato spotted wilt virus (TSWV) resistance response to the Hawaiian (TSWV6) and Australian anemone (An_{wa}-1) isolates across all accessions, individual plants, and *L. esculentum* (89S and 89R) controls^a

Accessions	TSWV isolates ^b											
	Number of				With resistant reaction							
	Accessions tested		Plants tested		Plants (no.)		Plants (%)		Accessions (no.)		Accessions (%)	
	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1
TGRC Core	35	24	767	962	24	51	3	5	12	10	34	42
TGRC	129	111	5,559	3,575	497	426	9	12	81	66	63	57
USDA	116	42	4,308	1,164	916	387	21	33	75	30	65	71
Totals	280	177	10,634	5,701	1,437	864	14	15	168	106	60	59
Controls ^c												
89S	...	...	1,404	495	0	23	0	5	...	...	...	...
89R	...	...	1,456	574	0	153	0	27	...	...	...	...
Totals	...	...	2,860	1,069	0	176	0	16	...	...	...	...

^a In total, 285 *L. peruvianum* accessions were screened. Of those, 169 were from the Tomato Genetics Resource Center (TGRC), University of California, Davis, 38 of which belong to the core collection (TGRC Core), and 116 from the United States Department of Agriculture (USDA) Research Service collection located at the Cornell University Geneva, NY campus.

^b TSWV isolate TSWV6 infects tomato with a Sw-5/Sw-5 genotype and An_{wa}-1 partially infects the same genotype.

^c Near-isogenic lines 89S (Sw-5⁺/Sw-5⁺) and 89R (Sw-5/Sw-5) were used as controls.

Table 2. All *Lycopersicon peruvianum* accessions tested and ranked according to average percentage of apparent resistant plants to *Tomato spotted wilt virus* (TSWV) isolates TSWV6 and anemone (An_{wa}-1)^a

Plants tested with TSWV isolates ^b								
Accession no.	Avg. (%)	Resistant (%)		Resistant (no.)		Tested (no.)		Origin of the accession ^c
		TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	
PI 126946 ^{de}	68	72	64	33	23	46	36	Culebras, Peru*
PI 128648 ^f	63	80	45	24	10	30	22	Azapa Valley, Chile*
LA 3636	63	63	63	19	27	30	43	Coayllo, Lima, Peru**
PI 128646 ^f	57	42	71	16	17	38	24	Lluta/Arica, Chile*
PI 128649 ^f	57	43	70	17	19	40	27	Arica, Chile*
LA 2742 ^f	56	67	45	31	13	46	29	Camarones-Guancarané, Tarapacá, Chile**
PI 126930 ^{de}	56	56	55	24	12	43	22	Chancay, Peru*
PI 127832	55	52	57	25	25	48	44	Sacabaya, Peru*
PI 128650 ^f	54	39	68	15	27	38	40	Arica, Chile*
PI 128652 ^{fg}	54	48	60	23	25	48	42	Arica, Chile*
PI 128643	53	80	26	28	10	35	39	Lima, Peru*
LA 3900	52	67	36	32	16	48	45	Canta, Lima, Peru**
PI 126441 ^h	52	61	42	22	10	36	24	Canta, Lima, Peru*
PI 127831	51	55	46	21	19	38	41	Sacabandía, Peru*
PI 128645 ^{fi}	49	55	43	26	16	47	37	Lluta/Arica, Chile*
PI 128647 ^f	49	48	50	10	9	21	18	Arica, Chile*
PI 126945	49	36	62	12	23	33	37	Culebras, Peru*
LA 1677	48	23	73	5	30	22	41	Fundo Huaquina to Topara, Lima, Peru**
PI 126944 ^{deg hij}	48	39	57	11	21	28	37	Culebras, Peru*
PI 126928 ^{dei}	47	54	39	26	19	48	49	Pacasmayo, Peru*
PI 126935 ^h	47	51	43	19	13	37	30	Saña, Peru*
LA 3640	41	54	28	26	10	48	36	Mexico City, Mexico**
LA 2745 ^f	40	42	38	20	9	48	24	Pan de Azúcar (Azapa), Tarapacá, Chile**
LA 3858	39	40	38	19	15	48	40	Canta, Lima, Peru**
PI 127830	39	20	58	9	23	44	40	Mollendo, Arequipa, Peru*
LA 2770 ^f	36	38	33	15	7	39	21	Lluta, Tarapacá, Chile**
G 30046	35	46	23	22	9	48	40	Peru*
LA 1975	33	28	37	13	10	47	27	Desvío Santo Domingo, Lima, Peru**
LA 2717	33	44	21	16	6	36	28	Chilca, Lima, Peru**
PI 128651 ^f	33	35	30	17	14	48	47	Arica, Chile*
LA 98	31	23	38	13	18	56	48	Chilca, Lima, Peru**
LA 2959 ^f	31	31	31	13	12	42	39	Chaca-Vitor, Tarapacá, Chile**
PI 126926	31	44	18	21	5	48	28	Pacasmayo, Peru*
LA 2808	26	0	52	0	15	48	29	Huaylas, Ancash, Peru**
LA 3639	25	21	29	7	7	34	24	Catac, Lima, Peru**
LA 3799	25	38	11	18	4	47	37	Rio Pativilca, Ancash, Peru**
G 30027	25	48	2	23	1	48	43	Peru*
LA 2581 ^f	24	22	26	9	5	41	19	Chacarilla (4x), Tarapacá, Chile**
LA 3637	24	19	28	9	8	48	29	Coayllo, Lima, Peru**
PI 326173	23	0	45	0	10	24	22	South America*
LA 1675	22	2	42	1	16	41	38	Toparilla Cañón, Lima, Peru**
PI 126929 ⁱ	22	0	44	0	11	13	25	Pacasmayo, Peru*
LA 1513	21	34	7	11	1	32	14	Atiquipa, Arequipa, Peru**
LA 1647	21	16	25	6	10	37	40	Huaquina, Topara, Ica, Peru**
LA 153	20	8	31	1	15	12	48	Culebras, Ancash, Peru***
LA 464 ^f	20	0	40	0	19	52	48	Hacienda Rosario, Tarapacá, Chile**

(continued on next page)

^a The TSWV6 isolate overcomes *Sw-5/Sw-5* genotypes where An_{wa}-1 partially overcomes the same genotype. In total, 285 *L. peruvianum* accessions were screened. Of those, 169 were from the Tomato Genetics Resource Center (TGRC), University of California, Davis, 38 of which belong to the core collection (TGRC Core), and 116 from the United States Department of Agriculture (USDA) Research Service collection located at the Cornell University Geneva, NY campus.

^b TSWV isolate TSWV6 infects *Sw-5/Sw-5* and *Sw-5⁺/Sw-5* genotypes and An_{wa}-1 genotypes partially infects these genotypes. Avg. (%) = percent average resistant.

^c Asterisks *, **, and *** indicate collections from the USDA, TGRC, and TGRC Core, respectively.

^d Eight *L. peruvianum* accessions that Smith and Paterson et al. reported on TSWV resistance in 1944 and 1989, respectively (34,52).

^e Nine accessions reported as being resistant to TSWV by Segeren et al. in 1993 (49,50).

^f Twenty-six accessions from the southern tip of Peru and northern Chile, with the majority of the accessions associated with a high percentage of TSWV resistance (Fig. 1).

^g Five *L. peruvianum* accessions identified by Cho et al. in 1996 (7) as being resistant to TSWV6.

^h Five of the *L. peruvianum* accessions reported with TSWV resistance by Roselló et al. in 1999 (47).

ⁱ Five of the *L. peruvianum* accessions mentioned in the development of cv. Stevens as a possible source of *Sw-5* (57).

^j *L. peruvianum* accession studied for TSWV resistance by Jordá et al. in 1993 (22).

^k *L. peruvianum* accession studied for TSWV resistance by Stevens et al. in 1994 (58).

^l *L. peruvianum* accession studied and reported on for possible TSWV resistance by Boiteux et al. 1992 (4).

^m *L. peruvianum* accessions originating from Huallanca, Ancash, Peru, where PE-18 originated; PE-18 is the source of *Sw-6* (45-47).

ⁿ Three *L. peruvianum* accessions studied and reported as having a resistance response by Iizuka et al. in 1993 (20).

^o *L. peruvianum* accession used by Gilbert and Tanaka in 1971 (15) for the development of 'Anahu' and also studied for TSWV resistance and reported on by Kumar et al. 1993 (24).

^p *L. peruvianum* accession studied for TSWV resistance by Maluf et al. in 1991 (27).

Table 2. (continued from preceding page)

Plants tested with TSWV isolates ^b								
Accession no.	Avg. (%)	Resistant (%)		Resistant (no.)		Tested (no.)		Origin of the accession ^c
		TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	
LA 2962	20	19	21	9	6	47	29	Chancay, Arequipa, Peru**
LA 2744 ^f	18	9	26	3	12	32	47	Sobraya (Azapa), Tarapacá, Chile***
LA 1373	17	10	24	4	9	40	37	Asia, Lima, Peru**
LA 1475	16	15	17	6	7	40	42	Fundo "Los Anitos", Lima, Peru**
LA 1692	16	12	19	3	5	25	27	Putinza, Lima, Peru**
PI 126444 ^k	16	23	9	11	4	48	43	Canta, Peru*
PI 306811	16	0	32	0	7	24	22	United States*
LA 444 ^{egl}	15	14	15	3	7	22	47	Chincha #1, Ica, Peru***
LA 1300	15	0	29	0	14	53	48	Santa Rosa de Quives, Lima, Peru**
LA 2721	15	29	0	13	0	45	17	Putinza, Lima, Peru**
LA 2724	15	30	0	12	0	40	13	Huaynilla, Lima, Peru**
LA 1270	14	2	26	1	12	42	46	Pisiquillo, Lima, Peru**
LA 2068	14	27	0	10	0	37	27	Chasquitambo, Ancash, Peru**
LA 2732 ^f	14	8	19	1	9	13	48	Moquella, Tarapaca, Chile***
LA 3795	14	28	0	13	0	46	53	Alta Fortaleza, Ancash, Peru**
LA 1473	12	19	5	9	2	48	39	Callahuanca, Santa Eulalia, Lima, Peru**
LA 1552	12	21	3	8	1	39	34	San Mateo, Lima, Peru**
LA 2562 ^m	12	5	19	2	4	42	21	Huallanca, Ancash, Peru**
LA 3797	12	18	6	7	2	39	34	Anca Marca, Ancash, Peru**
LA 111 ⁿ	11	1	21	1	10	122	48	Zupe, Lima, Peru**
LA 1616	11	0	21	0	3	13	14	La Molina, La Rinconada, Lima, Peru**
LA 1694	11	3	18	1	16	33	91	Cacachuhuasín, Lima, Peru**
PI 126439	11	22	0	10	0	46	17	Canta, Peru*
LA 1305	10	17	2	5	1	30	48	Ticrapo, Huancavelica, Peru***
LA 1537	10	14	5	6	1	42	19	Probably Peru**
LA 1646	10	19	0	6	0	32	23	Canta, Lima, Peru**
LA 1358	9	13	5	4	2	31	41	Yautan, Ancash, Peru**
LA 1368	9	13	5	3	2	24	37	San Jose de Palla, Lima, Peru**
LA 1935	9	0	18	0	5	33	28	Lomas de Atiquipa, Arequipa, Peru**
LA 1133	9	0	17	0	8	58	48	Huachipa, Lima, Peru**
LA 2563	9	7	10	3	3	43	31	Canon del Pato, Ancash, Peru**
LA 2575	9	0	17	0	6	47	36	Valle de Casma, Ancash, Peru**
LA 2566	8	15	0	6	0	40	29	Pomacocha-Llameyin, Rio Pocha, Ancash, Peru**
LA 2573	8	2	14	1	5	48	36	Valle de Casma, Ancash, Peru**
G 30036	8	4	11	2	2	48	19	Peru*
LA 1292	7	8	5	1	1	13	22	San Mateo, Lima, Peru***
LA 2561 ^m	7	3	10	1	2	39	20	Huallanca, Ancash, Peru**
LA 2331	7	13	0	6	0	47	43	Agayapampa, La Libertad, Peru**
LA 3664	7	14	0	1	0	7	13	Nazca Grande, Ica, Peru**
G 30040	7	13	0	6	0	48	20	Peru*
G 30044	7	0	13	0	1	42	8	Peru*
LA 1369	6	10	2	4	1	39	45	San Gerónimo, Lima, Peru**
LA 1377	6	5	6	1	2	20	36	Navan, Lima, Peru**
LA 1517	6	8	3	2	1	26	36	Irrigación Santa Rosa, Lima, Peru**
LA 1556	6	5	6	2	2	39	34	Hacienda Higuereta, Lima, Peru**
LA 2164	6	2	10	1	4	47	40	Cuyca, Cajamarca, Peru**
PI 127829	6	11	0	5	0	46	28	San Juan/ Magdalena, Peru*
G 30043	6	6	5	2	1	32	21	Peru*
LA 366	5	0	10	0	5	79	48	Canta, Lima, Peru**
LA 446	5	0	10	0	5	23	48	Atiquipa, Arequipa, Peru**
LA 1161	5	2	8	1	4	42	48	Huachipa, Lima, Peru**
LA 1626	5	10	0	2	0	21	27	Mouth of Rio Rupac, Ancash, Peru***
LA 1977	5	9	0	4	0	47	23	Orcocoto, Lima, Peru**
LA 1981	5	6	3	3	1	48	40	Vocatoma, Ancash, Peru**
LA 2326	5	9	0	4	0	47	25	Above Balsas, Amazonas, Peru**
LA 2333	5	10	0	5	0	48	32	Casmiche, La Libertad, Peru**
LA 2388	5	2	8	1	3	48	39	Cochabamba to Huambos, Cajamarca, Peru**
LA 2555	5	9	0	3	0	34	41	Mariscal Castilla, La Libertad, Peru**
LA 3218	5	4	6	1	2	24	31	Quebrada Guerrero, Arequipa, Peru**
LA 3219	5	9	0	1	0	11	12	Catarindo, Arequipa, Peru**
LA 1554	4	8	0	3	0	36	24	Hualar to Cerro de Pasco, Lima, Peru**
LA 1913	4	3	5	1	1	39	22	Tinguiyo, Ica, Peru**
LA 2809	4	0	7	0	2	26	30	Huaylas, Ancash, Peru**
LA 2834	4	0	7	0	1	6	15	Hacienda Asiento, Ica, Peru**
LA 3154	4	2	6	1	2	48	34	Otoro-Puente Jahuay, Moquegua, Peru**
LA 448	3	0	6	0	3	72	48	Chala, Arequipa, Peru**
LA 1294	3	5	0	1	0	19	47	Surco, Lima, Peru**
LA 1304	3	5	0	3	0	62	47	Pámpano, Huancavelica, Peru**
LA 1983	3	5	0	2	0	42	22	Rio Manta, Ancash, Peru**
LA 2327	3	6	0	3	0	48	33	Aguas Calientes, Cajamarca, Peru**

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Table 2. (continued from preceding page)

Plants tested with TSWV isolates ^b								
Accession no.	Avg. (%)	Resistant (%)		Resistant (no.)		Tested (no.)		Origin of the accession ^c
		TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	
LA 2565	3	0	5	0	1	48	22	Potrero de Pomacocha, Ancash, Peru**
LA 3156	3	5	0	1	0	21	15	Omate Valley, Moquegua, Peru**
PI 127828	3	5	0	1	0	22	25	San Juan, Cajamarca, Peru*
G 30034	3	0	6	0	1	46	18	Peru*
LA 1337	2	1	2	1	1	81	48	Atiquipa, Arequipa, Peru**
LA 1379	2	0	4	0	2	36	47	Cavajo, Lima, Peru***
LA 1653	2	0	3	0	1	36	37	Uchumayo, Arequipa, Peru**
LA 1937	2	4	0	1	0	27	8	Quebrada Torrecillas, Arequipa, Peru***
LA 1949	2	3	0	1	0	34	12	Las Calaveritas, Arequipa, Peru**
LA 1951	2	3	0	1	0	32	39	Ocoña, Arequipa, Peru***
LA 455	1	1	0	1	0	132	44	Tambo, Arequipa, Peru**
LA 752	1	0	2	0	1	48	48	Sisacaya, Lima, Peru**
LA 1280	1	1	0	1	0	102	48	Chaciacyo, Lima, Peru**
LA 1364	1	0	2	0	1	9	48	Alta Fortaleza, Ancash, Peru***
LA 1551	1	2	0	1	0	42	19	Surco, Lima, Peru**
LA 1984	1	0	2	0	1	11	41	Otuzco, La Libertad, Peru***
G 30039	1	2	0	1	0	41	12	Peru*
LA 378	0	0	0	0	0	110	47	Cascas, Cajamarca, Peru**
LA 451	0	0	0	0	0	36	47	Arequipa, Arequipa, Peru**
LA 453	0	0	0	0	0	57	46	Yura, Arequipa, Peru**
LA 462 ^{ef}	0	0	0	0	0	60	35	Sobraya, Tarapaca, Chile**
LA 1032	0	0	0	0	0	27	47	Aricampa, La Libertad, Peru**
LA 1278	0	0	0	0	0	55	8	Trapiche, Lima, Peru**
LA 1331	0	0	0	0	0	21	40	Nazca, Ica, Peru***
LA 1394	0	0	0	0	0	43	38	Balsas, Amazonas, Peru**
LA 1396	0	0	0	0	0	46	30	Balsas (Chachapoyas), Amazonas, Peru**
LA 1474	0	0	0	0	0	8	48	Lomas, de Camaná, Arequipa, Peru***
LA 1708	0	0	0	0	0	39	9	Chamaya to Jaen, Cajamarca, Peru**
LA 1722	0	0	0	0	0	18	22	Ticrapo Viejo, Huancavelica, Peru**
LA 1723	0	0	0	0	0	3	3	La Quinga, Ica, Peru**
LA 1744	0	0	0	0	0	42	20	Putinza, Lima, Peru**
LA 1910	0	0	0	0	0	36	3	Tambillo, Huancavelica, Peru***
LA 1929	0	0	0	0	0	13	48	La Yapana, Ica, Peru***
LA 1944	0	0	0	0	0	41	19	Rio Atico, Arequipa, Peru**
LA 1945	0	0	0	0	0	7	36	Caravelí, Arequipa, Peru***
LA 1947	0	0	0	0	0	21	21	Puerto Atico, Arequipa, Peru**
LA 1955	0	0	0	0	0	46	24	Matarani, Arequipa, Peru**
LA 1985	0	0	0	0	0	47	35	Casmiche, La Libertad, Peru**
LA 2163	0	0	0	0	0	45	45	Cochabamba to Yamaluc, Cajamarca, Peru***
LA 2185	0	0	0	0	0	37	44	Pongo de Rentema, Amazonas, Peru***
LA 2330	0	0	0	0	0	45	20	Chagual, La Libertad, Peru**
LA 2964	0	0	0	0	0	49	48	Quebrada de Burros, Tacna, Peru***
LA 2981-B	0	0	0	0	0	47	47	Torata to Chilligua, Moquegua, Peru***
LA 3220	0	0	0	0	0	5	15	Cocachacra-Quebrada Cachendo, Arequipa, Peru**
LA 3666	0	0	0	0	0	1	24	La Yapa, Ica, Peru**
LA 3781	0	0	0	0	0	7	27	Quebrada Oscollo, Arequipa, Peru**
LA 3783	0	0	0	0	0	11	16	Chapana, Arequipa, Peru**
LA 3787	0	0	0	0	0	26	21	Alta Chaparra, Arequipa, Peru**
LA 3790	0	0	0	0	0	16	33	Caravelí, Arequipa, Peru**
G 30028	0	0	0	0	0	47	25	Peru*
G 30029	0	0	0	0	0	34	19	Peru*
G 30032	0	0	0	0	0	45	22	Peru*
G 30033	0	0	0	0	0	46	23	Peru*
G 30035	0	0	0	0	0	44	8	Peru*
G 30037	0	0	0	0	0	30	13	Peru*
G 30045	0	0	0	0	0	48	7	Peru*
PI 251307	...	74	...	25	...	34	0	Cascas/La Libertad, Peru*
PI 128660 ^{dfig}	...	60	...	28	...	47	0	Tacna, Peru*
PI 251306	...	59	...	23	...	39	0	Culebras/Ancash, Peru*
PI 143679 ^h	...	54	...	25	...	46	0	Manabi, Ecuador*
PI 128653 ^f	...	53	...	24	...	45	0	Arica, Chile*
PI 129147	...	48	...	23	...	48	0	Guayaquil/Salinas, Ecuador*
PI 129152	...	46	...	22	...	48	0	Guayaquil, Ecuador*
PI 129145	...	45	...	20	...	44	0	Tambo, Peru*
PI 128654 ^{fi}	...	44	...	14	...	32	0	Arica, Chile*
PI 128656 ^f	...	41	...	12	...	29	0	Characarilla/Tarapaca, Chile*
PI 128657 ^{defo}	...	40	...	19	...	47	0	Tacna, Peru*
PI 246586 97GI	...	39	...	16	...	41	0	Atico/Arequipa, Peru*
PI 128655 ^f	...	38	...	10	...	26	0	Chacarilla/Tarapaca, Chile*

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Table 2. (continued from preceding page)

Plants tested with TSWV isolates ^b								
Accession no.	Avg. (%)	Resistant (%)		Resistant (no.)		Tested (no.)		Origin of the accession ^c
		TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	
PI 128663	...	35	...	17	...	48	0	Moquegua, Peru*
PI 129149	...	33	...	10	...	30	0	Guayaquil, Ecuador*
PI 390671	...	32	...	9	...	28	0	Lima, Peru*
PI 270435	...	30	...	14	...	47	0	Mexico City, Mexico*
PI 251311 ^h	...	25	...	10	...	40	0	Arequipa, Peru*
PI 251308	...	24	...	7	...	29	0	Atiquipa/Arequipa, Peru*
PI 128661 ^f	...	23	...	10	...	43	0	Tacna, Peru*
PI 390682	...	23	...	11	...	48	0	Lima, Peru*
PI 390681	...	21	...	6	...	28	0	Lima, Peru*
LA 1609	...	20	...	2	...	10	0	Asia-El Pinon, Lima, Peru***
PI 251309	...	19	...	8	...	42	0	Chala/Arequipa, Peru*
PI 251310	...	19	...	4	...	21	0	Atico, Peru*
PI 266375	...	19	...	5	...	26	0	Lima, Peru*
PI 390672	...	18	...	8	...	44	0	Lima, Peru*
PI 390670	...	17	...	7	...	42	0	Lima, Peru*
PI 246586 60OI	...	16	...	5	...	31	0	Atico/Arequipa, Peru*
PI 128659 ^{dfg}	...	13	...	6	...	45	0	Tacna, Peru*
LA 1365	...	12	...	3	...	25	0	Caranquillo, Ancash, Peru***
PI 129146 ^{de}	...	12	...	2	...	17	0	Tambo, Peru*
PI 365956	...	12	...	3	...	25	0	Lima, Peru*
PI 128658 ^f	...	11	...	5	...	45	0	Tacna, Peru*
PI 365942	...	11	...	2	...	18	0	Lima, Peru*
PI 246585	...	9	...	3	...	32	0	Ayacucho, Peru*
PI 390684	...	8	...	3	...	36	0	Lima, Peru*
LA 1350	...	8	...	1	...	12	0	Chauna, Cajamarca, Peru**
LA 110	...	7	...	9	...	123	0	Cajacay, Ancash, Peru**
PI 379029	...	7	...	3	...	44	0	Tambo, Peru*
PI 390680	...	7	...	3	...	43	0	Lima, Peru*
LA 445	...	6	...	3	...	51	0	Chincha #2, Ica, Peru**
PI 390664	...	6	...	2	...	32	0	Paramonga, Peru*
LA 364	...	5	...	1	...	22	0	Canta, Lima, Peru**
LA 1293	...	5	...	2	...	43	0	Matucana, Lima, Peru**
PI 303814	...	5	...	2	...	43	0	Idaho, United States*
PI 365946	...	5	...	1	...	20	0	Puquino, Peru*
LA 370	...	4	...	3	...	79	0	Hacienda Huampaní, Lima, Peru**
PI 365943	...	4	...	2	...	48	0	Lima, Peru*
PI 390669	...	4	...	2	...	48	0	Lima, Peru*
LA 372 ⁿ	...	3	...	3	...	91	0	Culebras #1, Ancash, Peru**
LA 1271	...	3	...	1	...	37	0	Horcón, Lima, Peru**
PI 379015	...	3	...	1	...	40	0	Ticrapo, Peru*
LA 392	...	2	...	1	...	45	0	Llallan, Cajamarca, Peru**
LA 1982 ^m	...	2	...	1	...	42	0	Huallanca, Ancash, Peru***
LA 1283	...	2	...	1	...	41	0	Sta. Cruz de Laya, Lima, Peru**
PI 365947	...	2	...	1	...	47	0	Arequipa, Peru*
PI 365950	...	2	...	1	...	48	0	Caciche, Peru*
LA 371 ^e	...	0	...	0	...	79	0	Zupe, Lima, Peru**
LA 374	...	0	...	0	...	107	0	Culebras #2, Ancash, Peru**
LA 441 ^p	...	0	...	0	...	3	0	Cerro Campana, La Libertad, Peru***
LA 454	...	0	...	0	...	15	0	Tambo, Arequipa, Peru***
LA 1027	...	0	...	0	...	13	0	Cajamarca, Peru**
LA 1031	...	0	...	0	...	92	0	Balsas, Amazonas, Peru**
LA 1274	...	0	...	0	...	2	0	Pocabamba, Lima, Peru***
LA 1284	...	0	...	0	...	30	0	Espiritu Santo, Lima, Peru**
LA 1296	...	0	...	0	...	8	0	Tornamesa, Lima, Peru**
LA 1333	...	0	...	0	...	76	0	Loma Camana, Arequipa, Peru**
LA 1336	...	0	...	0	...	39	0	Atico, Arequipa, Peru**
LA 1339	...	0	...	0	...	35	0	Capillucas, Lima, Peru***
LA 1346	...	0	...	0	...	51	0	Caciche, La Libertad, Peru**
LA 1351	...	0	...	0	...	6	0	Rupe, Cajamarca, Peru***
LA 1360	...	0	...	0	...	29	0	Pariacoto, Ancash, Peru***
LA 1395	...	0	...	0	...	26	0	Chachapoyas, Amazonas, Peru***
LA 1973	...	0	...	0	...	15	0	Yura, Arequipa, Peru***
LA 2152	...	0	...	0	...	2	0	Cospán, Cajamarca, Peru***
LA 2172	...	0	...	0	...	35	0	Cuyca, Cajamarca, Peru***
LA 2328	...	0	...	0	...	1	0	Aricapampa, La Libertad, Peru***
LA 3853	...	0	...	0	...	22	0	Moyopampa, La Libertad, Peru**
PI 251314	...	0	...	0	...	24	0	The Rio Jequetepeque, Peru*
PI 266376	...	0	...	0	...	14	0	Magdalena/Cajamarca, Peru*
PI 365938	...	0	...	0	...	15	0	Pocabamba/Lima, Peru*
PI 365939	...	0	...	0	...	31	0	Pocabamba, Peru*

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Table 2. (continued from preceding page)

Plants tested with TSWV isolates ^b								
Accession no.	Avg. (%)	Resistant (%)		Resistant (no.)		Tested (no.)		Origin of the accession ^c
		TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	TSWV6	An _{wa} -1	
PI 365940	...	0	...	0	...	23	0	Pocabamba, Peru*
PI 365941	...	0	...	0	...	4	0	Quilca/Lima, Peru*
PI 365948	...	0	...	0	...	45	0	Carretera, Peru*
PI 365951	...	0	...	0	...	17	0	Contumazá, Peru*
PI 365952	...	0	...	0	...	13	0	Huaras, Peru*
PI 365953	...	0	...	0	...	24	0	Caranquillo, Peru*
PI 365955	...	0	...	0	...	17	0	Lima, Peru*
PI 365968	...	0	...	0	...	30	0	Cuzco, Peru*
PI 365969	...	0	...	0	...	33	0	Yaca, Peru*
PI 379016	...	0	...	0	...	30	0	Chauna, Peru*
PI 379017	...	0	...	0	...	15	0	Lima, Peru*
PI 379018	...	0	...	0	...	48	0	Lima, Peru*
PI 390665	...	0	...	0	...	48	0	Camaná, Peru*
PI 390666	...	0	...	0	...	44	0	Lima, Peru*
PI 390667	...	0	...	0	...	47	0	Lima, Peru*
PI 390668	...	0	...	0	...	24	0	Lima, Peru*
PI 390673	...	0	...	0	...	42	0	Lima, Peru*
PI 390674	...	0	...	0	...	42	0	Lima, Peru*
PI 390675	...	0	...	0	...	48	0	Lima, Peru*
PI 390676	...	0	...	0	...	48	0	Lima, Peru*
PI 390678	...	0	...	0	...	48	0	Lima, Peru*
PI 390679	...	0	...	0	...	48	0	Lima, Peru*
PI 390683	...	0	...	0	...	48	0	La Libertad, Peru*
PI 390685	...	0	...	0	...	48	0	Cerro de Pasco, Peru*
PI 390687	...	0	...	0	...	22	0	Canchaque, Peru*
LA 107	...	...	4	...	2	0	47	Hacienda San Isidro, Lima, Peru***
LA 385 ⁿ	...	...	0	...	0	0	48	San Juan, Cajamarca, Peru**
LA 1989	...	...	0	...	0	0	4	**
LA 2157	...	...	0	...	0	0	38	Tunel Chotano, Cajamarca, Peru***
LA 2553	...	...	0	...	0	0	48	Balconcillo de San Marcos, Cajamarca, Peru***

not to TSWV6 and 31 (about 18%) had plants with a resistance response to TSWV6 and not to An_{wa}-1. In all, 79 accessions had plants indicating resistance to both isolates (Table 2).

A distinct difference in the TSWV resistance response was identified between germplasm collections. The USDA and TGRC collections had a significantly ($P < 0.0001$) higher level of resistance than the TGRC Core collection. Of the 172 accessions tested with both isolates, 35 of 42 (approximately 83%) USDA, 86 of 109 (approximately 79%) TGRC, and 12 of 21 (approximately 57%) TGRC Core indicated resistance to at least one of the two isolates (Table 2).

Germplasm responses to TSWV6 and An_{wa}-1. When inoculated with TSWV6, all 1,404 89S and 1,456 89R controls were infected (Table 1). Of the 10,634 *L. peruvianum* plants tested from 280 accessions, 14% of the plants were found to be virus free, which was significantly higher than the controls. The 116 USDA, 129 TGRC, and 35 TGRC Core accessions tested with TSWV6 were significantly different from each other (P value < 0.0001) with 21, 9, and 3% of the plants, respectively, virus free (Table 1; Fig. 1A). This pattern was similar when comparing accessions with plants free of the virus (Table 1; Fig. 1B).

An_{wa}-1 was less virulent than TSWV6; 95% of the 495 89S and 73% of the 574 89R controls were infected (Table 1). Of the 5,705 *L. peruvianum* tested with An_{wa}-1,

15% indicated resistance, and these plants were found within 106 of the 177 (59%) accessions tested (Table 1). Using An_{wa}-1, the 42 USDA, 111 TGRC, and 24 TGRC Core accessions were found to be significantly different from each other (P value < 0.0001) with 33, 12, and 5% of the plants, respectively, virus free (Table 1; Fig. 1B).

Geographic distribution of *L. peruvianum* TSWV resistance. We were able to examine the geographical distribution of 260 *L. peruvianum* accessions with area-specific passport data. Of those 260 accessions, 154 were tested with both TSWV isolates, 256 were tested with TSWV6 (Fig. 2A; Table 2) and 158 with An_{wa}-1 (Fig. 2B; Table 2). Resistance to both TSWV isolates was somewhat equally distributed throughout Peru, with perhaps more emphasis along the Peruvian Pacific coastal plane (Fig. 2). However, the Arica, Chile and southern Peru region indicated an unusually high ratio of accessions with resistant plants (Fig. 2, insert 2). Specifically, 23 of 26 (approximately 88%) and 16 of 17 (approximately 94%) of the accessions had $>8\%$ of their plants resistant to TSWV6 and An_{wa}-1, respectively (Fig. 2). This region can be compared with the insert 1 area of Figure 2A and 2B (surrounding Lima, Peru) in which 45 of 102 (about 44%) and 29 of 58 (about 50%) accessions had $>8\%$ of the plants, indicating a resistance response to TSWV6 and An_{wa}-1, respectively.

There is an even greater difference in the accessions from the Arica region (Fig. 2, insert 2), which had $\geq 33\%$ of their plants indicate a resistant response. In all, 19 of 26 (about 73%) and 12 of 17 (about 71%) accessions had a resistance response to TSWV6 and An_{wa}-1, respectively (Fig. 2, insert 2) compared with the region around Lima (Fig. 2, insert 1), where 12 accessions tested with either TSWV6 (about 12%) or An_{wa}-1 (about 21%) had $\geq 33\%$ of their plants free of TSWV.

DISCUSSION

Mechanical inoculation. Several reports have utilized thrips for screening smaller germplasm populations for TSWV resistance (24,44,47). However, due to the impracticalities of managing or controlling thrips, we utilized mechanical inoculation to screen our large plant numbers with two TSWV isolates. Especially when some plants or accessions could be considered TSWV resistant when, in reality, thrips could be either deterred (preference) or possibly resisted by some *L. peruvianum* accessions (24).

A noted drawback to serial mechanical inoculation has been the generation of defective interfering RNAs (DI RNAs) causing attenuation of the TSWV isolate. Generation of these defective isolates can be aggravated during some environmental regimes (19,21,39,40). Nonetheless, there are usable stable TSWV isolates with DI RNAs. Ie (19) described TSWV isolates

Fig. 1. Tomato spotted wilt virus (TSWV) resistance response of the accessions from the United States Department of Agriculture (USDA) Research Service located at the Cornell University Geneva, NY campus, Tomato Genetics Resource Center (TGRC), University of California, Davis, and TGRC-Core collections to the Hawaiian isolate (TSWV 6) and to the anemone isolate (An_{wa}-1) expressed as a percentage of plants free of infection.

Fig. 2. Maps of Peru and Chile created with the Arc/GIS program showing the spatial distribution of the accessions collected according to the global positioning coordinates. There is sufficient passport data to map 256 accessions tested with the **A**, *Tomato spotted wilt virus* (TSWV) Hawaiian isolate (TSWV 6) and **B**, 158 tested with anemone isolate (An_{wa}-1) for a total of 260 between the two isolates. These accessions are maintained at the United States Department of Agriculture Research Service (USDA) located at the Cornell University Geneva, NY campus, Tomato Genetics Resource Center (TGRC), University of California, Davis, and TGRC Core accessions. Accessions are presented with their percent resistance (dot size and color coded). Specific accessions indicated on this map are those with city or region as well as country included in its source information in Table 2.

with DI RNAs which still produced disease after almost 20 years of mechanically transferring the isolates. Norris (31) first identified resistance in *L. peruvianum*, and Finlay (11,12) differentiated Sw₁^a, Sw₁^b, sw₂, sw₃, and sw₄ utilizing mechanical inoculations. Additionally, Sw-5 was named (54,57), mapped (55,56), and subsequently cloned (13) based on TSWV mechanical inoculation methods. We have been working with a new source of TSWV resistance derived from *L. chilense* (6,48) using mechanical inoculation. This resistance source has demonstrated its utility

under naturally high TSWV pressure in repeated field trials (6,48; *unpublished data*). These studies demonstrate that mechanical serial inoculation methods have provided reliable data. In the study reported here, we were unable to identify discernable phenotypic differences in the TSWV symptoms of the controls over the duration of the screening with either TSWV6 or An_{wa}-1, which is in accordance with our previous studies (6,54-58).

TSWV evaluations using both ELISA and visual techniques. Both isolates (TSWV6 and An_{wa}-1) produced a range of

systemic symptoms throughout the study and within a given inoculation, such as tip blight, necrotic and chlorotic lesions, epinasty, and stunting in both the controls and *L. peruvianum* plants. However, both TSWV6 and An_{wa}-1 required more time before the typical symptoms appeared in either the controls or the tested accessions than in our past experiments with either 85-9 or HR-1 (6,54,56-58; *unpublished data*). Using these isolates, we found that many of the inoculated plants indicated TSWV infection according to ELISA and did not always indicate visual symptoms

for several weeks post inoculation. Utilizing ELISA as a selection technique has been used for a number of TSWV resistance experiments (6,34,54–58). The conservative ELISA threshold suggested by Sutula et al. (59) has demonstrated a reasonable method of selecting infected plant material (6,34,54–58).

Differences in controls between the TSWV6 and An_{wa}-1 TSWV isolates. The reaction of 89R and 89S controls demonstrated that TSWV6 was significantly (P value < 0.0001) more virulent than An_{wa}-1. It was unexpected to have 73% of the 89R plants infected using An_{wa}-1 because *Sw*-5 genotypes reportedly were resistant to An_{wa}-1 (25). Using typical TSWV isolates from various areas within the United States, we have found that the degree of resistance provided by *Sw*-5 (*Sw*-5/*Sw*-5 or *Sw*-5/*Sw*-5⁺) results in 80 to 100% of plants being free of TSWV infection (6,57,58; unpublished data). This study shows that An_{wa}-1 overcomes 89R significantly (P value < 0.0001) less often than it infects 89S plants but at a much greater frequency than isolates we have used for past studies (6,57), suggesting that the TSWV isolates used in the Latham and Jones study (25) had a propensity to overcome *Sw*-5 in their study.

Accession resistance responses to TSWV6 and An_{wa}-1. Several studies (20,22,31) have found, when testing two unique isolates, that a given accession may demonstrate resistance to one and not another. Fifty-four accessions tested with both isolates showed resistance to one isolate (Table 2). It is reasonable to attribute some of the purported resistance response in the *L. peruvianum* accessions when working with An_{wa}-1 to individual plants escaping infection because 5% of the 89S controls were not infected by this isolate (Table 1). However, 11 of the 23 accessions with a resistance response to An_{wa}-1 had more than 10% of the plants not infected. Conversely, more than 10% of the plants (13 of the 31 accessions), showed resistance to TSWV6 but not to An_{wa}-1 (Table 2).

The unilateral resistance response (either TSWV6 or An_{wa}-1) of 54 accessions suggests multiple alleles or genes for resistance to TSWV within the *L. peruvianum* germplasm collections. This theory is further supported by studies of smaller populations showing unique *L. peruvianum* resistance responses to varying TSWV isolates (20,22,31).

Geographical distribution of resistant to TSWV. The unusually high percentage (≥81%) of the accessions with >8% plants free of infection to either isolate found in northern Chile and southern Peru is intriguing (Table 2; Fig. 2, inserts 2 and south to map edge, about 325 km). When examining the passport data of the accessions from this area, we found that they were not all collected in the same year or

by the same collection parties. Without additional in-depth studies, it is not possible to determine why apparently higher levels of TSWV resistance have been identified in this area. Curiously, our data suggest that, immediately north of this region, a general paucity of TSWV resistance occurs. However, in the northern part of Peru (near Lima and to the north), there are “pockets” of multiple accessions with higher levels of resistance to both isolates. For instance, the Culebras, Peru region (Fig. 2, northwest corner of inset 1) has a set of four accessions (PI 126944, PI 126945, PI 126946, and PI 127839) with relatively higher levels of resistance to both isolates used in this study. Additionally, the Ecuadorian accessions from three locations in two adjacent provinces (not found in Fig. 2), PI 128663, PI 129152, PI 129147, and PI 143679, tested only with TSWV6, indicated high percentages of virus-free plants ranging from 33 to 54%.

TSWV resistance distribution within the germplasm collections. The USDA and TGRC are collaborative centers and each collection is somewhat representative of the wider indigenous geographical range of the species (Table 2). Hence, it is natural to expect that TSWV resistance would be somewhat equally distributed between these two germplasm collections. The TGRC Core collection was carefully selected using multiple criteria to represent as much *L. peruvianum* diversity as possible. Therefore, it would be expected to have approximately the same percentages of TSWV resistance as found in the greater collections. However, we found the USDA and “noncore” TGRC collections had a similar percentage of accessions with plants that had a resistant response to either TSWV6 or An_{wa}-1 (Fig. 1B), whereas the TGRC Core has significantly less (P < 0.0001). Furthermore, the USDA collection had significantly more (P < 0.0001) resistant plants per individual accession (Fig. 1A).

Previous studies of TSWV resistance within *L. peruvianum* accessions. Of the 285 accessions used in our study, 23 (Table 2) had been screened for TSWV resistance in other studies (4,7,15,20,22–24,34,47,49, 50,52–54,57,58). Of those 23 accessions, 13 were tested with both isolates, 9 with TSWV6, and 1 with An_{wa}-1 (Table 2).

Of the 13 accessions previously reported (4,7,20,22,34,47,49,50,52,58) and tested with both isolates, 12 (PI 126929, PI 126930, PI 126441, PI 126444, PI 126928, PI 126935, PI 126944, PI 126945, PI 126946, PI 128652, LA 111, and LA 444) had no less than 15% of the plants, within an accession, resistant to at least one of the two isolates (Table 2). Of the 13 accessions tested with both isolates, 3 indicated dramatic differences in the resistance responses between the isolates. Two of these three accessions (LA 111 and PI 126929) had little to no resistance to TSWV6 (1

and 0%, respectively) and one (PI 126444) indicated 23% of the plants resistant to TSWV6 and 9% resistant to An_{wa}-1 (Table 2). PI 126444 and LA 111 had been tested previously with multiple isolates. Stevens et al. (58) tested PI 126444 with three isolates and found a similar level of resistance response between the isolates. In contrast to our results, Iizuka et al. (20) found that 100% of the LA 111 plants were resistant to two isolates of TSWV whereas 16% of the plants were susceptible to two other isolates.

Of the 23 accessions examined in previous TSWV resistance studies (7,15,20,24, 27,34,47,49,50,52,57), 10 were tested with either TSWV6 or An_{wa}-1 (Table 2). Only three plants of accession LA 441 (tested with TSWV6) germinated; however, the remaining nine accessions (PI 128654, PI 128657, PI 128659, PI 128660, PI 129146, PI 143679, PI 251311, LA 372, and LA 385) had sufficient plants per accession to provide clear evidence of possible resistance (Table 2). Finding TSWV resistance in these accessions is in agreement with the previous reports (7,15,24,27,34,47,49, 50,52,57). However, little or no resistance was found in LA 372 and LA 385 to TSWV6 and An_{wa}-1, respectively. Both of these accessions demonstrated resistance to three of four isolates used by Iizuka et al. (20).

Tomato lines purported to derive their resistance from *L. peruvianum*. Four tomato cultivars or lines (Anahu, UPV 1, UPV 32, and Stevens) attribute their purported TSWV resistance to *L. peruvianum*. Cv. Anahu (15) was reported to have the TSWV resistance gene *Sw*-1 from PI 128657 (14). Previous research has found Anahu to be easily infected with various TSWV isolates; this study had 40% of the plants free of infection using TSWV6 on PI 128657 (24,33,34). Finding that 40% of the plants resisted TSWV6 suggests the existence of alleles differing from *Sw*-1, or it is quantitatively inherited. Our results, in combination with the past studies of *Sw*-1, do suggest that a given accession may harbor multiple genes for resistance to TSWV.

The tomato lines UPV 1 and UPV 32 were derived from *L. peruvianum* accession PE-18 (46). UPV 1 is purported to have a single dominant unnamed TSWV resistance gene suggesting allelism to *Sw*-5 (46). UPV 32 was identified as having a single resistance gene not allelic to *Sw*-5 named *Sw*-6 (45). We did not have PE-18 to screen; however, this *L. peruvianum* accession was reported to be from Hualanca, Ancash, Peru, where three accessions used in our study originated (LA 1982, LA 2561, and LA 2562; Table 2). Two of these accessions (LA 2561 and LA 2562) were tested with our isolates, resulting in three to four times the number of plants with resistance to An_{wa}-1 than to TSWV6. LA 1982 was tested only with

TSWV6 and it had little resistance (2%), similar to the 3 and 5% found in LA 2561 and LA 2562, respectively. Thus, all three of the accessions from Huallanca, Ancash, Peru indicate little resistance to TSWV6, the isolate which completely overcomes *Sw-5*. These data suggest agreement with the results of PE-18 (45-47) with an *Sw-5*-like response. We have tested UPV 32 with TSWV5 from Hawaii and found it fully susceptible (*unpublished data*). UPV 1 has not been tested in our program.

The last reported cultivar with purported *L. peruvianum*-derived TSWV resistance is Stevens (53,57). This cultivar is one of two separately derived sources of *Sw-5* (5). There is evidence that *Sw-5* (from Stevens) originated from one of the *L. peruvianum* accessions PI 126928, PI 126929, PI 126944, PI 128645, PI 128654, or PI 129109 (57). We were able to include all except PI 129109 in our study. PI 126928, PI 126929, PI 126944, and PI 128645 were tested with both isolates while PI 128654 was tested only with TSWV6. Interestingly, all of these accessions were among the most resistant accessions tested (Table 2). PI 128654 is considered a strong candidate as the source of *Sw-5* (57). However, our data provide an alternative candidate accession, PI 126929, which did not indicate resistance to TSWV6, although it had 44% of the plants indicate *An_{wa}-1* resistance. Even with two lines of evidence for the possible origin of *Sw-5*, it is possible that all six accessions have *Sw-5*. Interestingly, at least five of the six accessions have differing resistance relative to *Sw-5*, in that a substantial number of plants were resistant to TSWV6 in those five accessions.

The value of the *Sw-5* gene. There is clear evidence that variant isolates of TSWV can overcome *Sw-5* (1,7,47,61). Furthermore, studies have demonstrated that tospoviruses can readily overcome both pathogen-derived resistance and natural resistance through reassortment of the TSWV genome (17,36,37). With these two lines of evidence in mind, the question arises as to why *Sw-5* has still been used worldwide, providing a high level of resistance in most areas where utilized. In regions where a TSWV isolate has overcome *Sw-5*, two related conditions have been noted. First, TSWV6 came from a situation where virtually 100% of the *Sw-5*⁺/*Sw-5*⁺ genotypes were naturally infected; thus, the disease pressure was extremely high. Second, where clear case histories can be identified; there often have been year-around cropping of *Sw-5* genotype tomato with consistently "high" *Tospovirus* pressure. Curiously, TSWV6-like isolates have not been found in Hawaii since *Sw-5* was no longer used in the area. In fact, tomato plants with *Sw-5* were planted again several years later in the same region and *Sw-5* provided its normal level of resistance (J. Cho, *personal communication*). This "*Sw-5*

rest" allowed the indigenous tospovirus to revert to an "environmentally fit" tospovirus that did not include the ability to readily overcome *Sw-5*.

These anecdotal observations, coupled with the data we obtained when using *An_{wa}-1*, opens the question to the environmental "fitness" of TSWV isolates that overcome *Sw-5*. *An_{wa}-1* was used in the experiments, demonstrating that TSWV isolates could be selected to overcome TSWV resistance (25). If isolates overcoming *Sw-5* are generally less "environmentally fit," it would explain why growers who seasonally utilize *Sw-5* genotype cultivars where TSWV pressure is high expect as much as 20% of their crop to be infected with the virus. However, regions that have consistently high TSWV pressure and never allow a rest from *Sw-5* are purported to be areas having troubles with TSWV overcoming this resistance. In considering the evidence that tospoviruses can quickly and easily "reshuffle" their genome, developing stable TSWV resistance may be a challenge (17,36,37). However, the slow adaptation of the virus to overcome *Sw-5* coupled with information that this event is documented mostly in areas where TSWV is infecting nearly 100% of known susceptible lines are in complete harmony with Leach et al. (26). Their results suggest that environmental fitness of this pathogen is directly related to the durability of resistance genes. The study we are reporting here was conducted to search for additional genes equal to or of even greater value than *Sw-5* in the *L. peruvianum* germplasm.

Our results demonstrate that there is additional tospovirus resistance to be found in the *L. peruvianum* germplasm. It is unclear as to how much of this resistance is quantitative or qualitative in nature. However, there is evidence that both inheritance patterns for TSWV resistance can be found within *L. peruvianum* germplasm. *Sw-5* was identified from this species (57) and, in an unpublished study, we recently have endeavored to introgress resistance to TSWV6 from PI 128660 into tomato. We found that the high level of tospovirus resistance seems to be quantitative in nature. It becomes clear that mining additional TSWV resistance from *L. peruvianum* is realistic but should be approached with full awareness that both successful introgression of resistance and failure of that objective is a possible outcome.

Making interspecific crosses with *L. peruvianum* is challenging (16,35). Therefore, an optimal strategy that may produce functional, transferable, TSWV resistance would be to focus on accessions that appear to provide resistance to one isolate and not the other. For example, LA 2808 indicated resistance to *An_{wa}-1* and G 30027 to TSWV6, but neither accession suggested resistant to the opposite isolates (Table 2). Even with the obvious hazard of

incorporating isolate-specific resistance, it may be that this resistance is more heritable and different from each other. Attempts have been made to introgress the resistance of PI 128660 and other previously reported accessions into tomato by several breeding programs, resulting in no known long-term usable resistance incorporated into elite cultivars. Identifying more single genes such as *Sw-5* for breeding potentially can provide a suite of resistant genes. Thus, searching for accessions demonstrating clear segregating type resistance may produce genes more readily introgressed with more utility than the resistance introgressions previously attempted.

Although there is clear evidence that tospoviruses can readily overcome various types of resistance (1,17,25,36,37), the environmental fitness of such a tospovirus may prove difficult for an epidemic type of behavior of a new isolate (26). Nevertheless, carefully planned deployment of tospovirus resistance, either natural or pathogen derived, should be part of the overall management of a crop in conditions where this virus is prevalent.

ACKNOWLEDGMENTS

This study was partially supported by funding from the USDA Tomato Germplasm Evaluation Committee. The seed from the germplasm collection used in this study was provided by TGRC at University of California, Davis and the USDA Agricultural Research Service plant genetic resources unit, Cornell University, Geneva, NY. We thank R. D. Horrocks, Plant and Animal Sciences, Brigham Young University, Provo, Utah, for help with the statistics of this article.

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