

Greenhouse and Field Screening of Wild *Lycopersicon* Germplasm for Resistance to the Whitefly *Bemisia argentifolii*

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Thirty-two accessions of wild tomato (*Lycopersicon* spp.) germplasm were evaluated for resistance to the whitefly *Bemisia argentifolii* Bellows & Perring in a greenhouse choice bioassay. Density data were recorded for the adaxial and abaxial leaf surfaces for (i) all life stages of *B. argentifolii* and (ii) types I, IV, V and VI trichomes. Individual plant selections (33 from 22 wild tomato accessions) with high resistance were subsequently tested in the field to verify the resistance found in the greenhouse screening. Resistance was defined by the density of all life stages of the whitefly observed on the eight leaflets sampled at nodes 5 and 7. Only type IV trichomes had a consistent (but low) and significant negative correlation between trichome density and whitefly density for various life stages. The highest whitefly resistance was observed in *Lycopersicon pennellii* accessions LA 716, LA 1340 and LA 2560. The most resistant *L. hirsutum* f. *typicum* accessions were LA 1777 and LA 1353.

KEY WORDS: Silverleaf whitefly; *Bemisia tabaci*; sweetpotato whitefly; tobacco whitefly; host plant resistance; tomato resistance.

INTRODUCTION

The whitefly *Bemisia argentifolii* Bellows & Perring, also known as strain 'B' of the sweetpotato whitefly [*B. tabaci* (Gennadius)], is the key pest of tomato in south Florida (33) and resulted in losses of 500 million dollars to US agriculture in 1992 (28). *Bemisia* whiteflies are difficult to control with insecticides because (a) feeding and oviposition occur mainly on the lower surfaces of leaves (36) and (b) whiteflies develop resistance to insecticides applied for their control (8,39). The use of resistant cultivars would be advantageous because it is compatible with other components of integrated pest management, conserves the environment, and reduces pesticide use, thus slowing the development of insecticide resistance. Little research has been reported on the resistance of commercial tomato cultivars or any germplasm within the cultivated species of tomato (*Lycopersicon esculentum* Mill.). Butler and Henneberry (4) tested a limited number of commercial tomato cultivars and reported small differences in the oviposition preference of strain 'A' of the sweetpotato whitefly. Heinz and Zalom (18) observed a higher oviposition rate by the silverleaf whitefly on tomato cultivars with high trichome density. Limited

Received March 21, 2002; received in final form Aug. 16, 2002; <http://www.phytoparasitica.org> posting Dec. 9, 2002.

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information is available on the resistance of wild *Lycopersicon* to the sweetpotato whitefly and, especially, to the silverleaf whitefly. Some accessions of *Lycopersicon hirsutum* f. *glabratum* C.H. Mull. and *L. hirsutum* f. *typicum* Humb. & Bonpl. have been reported to be resistant to the sweetpotato whitefly, although the whitefly may have been strain B, *i.e.*, *B. argentifolii* (7; E. Shevach-Urkin (1983); M. Yorit (1986), unpub. M.Sc. theses). According to these reports, resistance was achieved by physical interference, *viz.*, the adult whiteflies became entangled in the sticky glandular trichomes, resulting in high mortality. Resistance also has been reported in these wild species to *B. argentifolii* (2,18). Appreciable levels of resistance have been observed in both species of whitefly in some accessions of *Lycopersicon pennellii* (Corr.) D'Arcy (2,18,23; R. Dahan (1985) unpub. M.Sc. thesis); however, the evaluation of the resistance varies when tested by different methods and under different conditions. Clones of accessions of *L. hirsutum* f. *typicum* were found to be less attractive to *B. argentifolii*, and the degree of reduced attractiveness was related to Type IV (single-lobed) glandular trichomes (37).

Currently, no commercial cultivars and no breeding lines are available that possess resistance to this insect. Because the silverleaf whitefly is a species that differs from the earlier known sweetpotato whitefly (28) and because of the possible uncertainty of the species previously evaluated (7; E. Shevach-Urkin (1983); M. Yorit (1986), unpub. M.Sc. theses), we evaluated resistance to silverleaf whitefly in selected wild *Lycopersicon* accessions with artificial infestation under greenhouse conditions and under natural infestation in the field.

MATERIALS AND METHODS

Greenhouse screening Seeds of the wild *Lycopersicon* accessions were acquired from the Genetic Resources unit of the U.S. Department of Agriculture (USDA) Plant Introduction Station at Geneva, New York, and from the Tomato Genetic Stock Center at Davis, California. Thirty-two accessions of wild *Lycopersicon* germplasm first were evaluated in a greenhouse choice bioassay. The criteria for including an accession in this initial evaluation included reported resistance to arthropod pests and/or reported chemical constituents of glandular trichomes (3,6,16,17,22,24,40; M. Yorit (1986), unpub. M.Sc. thesis). There were eight accessions of *L. pennellii* and two of the subspecies *L. pennellii* var. *puberulum* Phil; eight and ten accessions of *L. hirsutum* f. *glabratum* and *L. hirsutum* f. *typicum*, respectively; and four accessions of *Lycopersicon peruvianum* (L.) Mill. For each accession, 25 seedlings were raised in 128-celled (34 cm³ cell size) Speedling[®] flats containing Jiffy[®] soil mix. At the third leaf stage of growth, eight plants were chosen randomly and transplanted into 1,500 cm³ pots containing a sand and peat moss soil mixture. Eight plants of the susceptible tomato cv. 'Solar Set' were grown as a control. The pots were placed on benches in water-cooled, insect-proof fiberglass greenhouses and watered as necessary. There were four replicates in each of two greenhouses arranged in a randomized complete blocks design, with each replicate consisting of one pot of each accession. Supplemental lighting was provided using 40-watt cool white fluorescent and 300-watt incandescent light bulbs to obtain a photoperiod of 16:8 h (L:D). The light intensity was 120–126 $\mu\text{E m}^{-2}\text{s}^{-1}$ (LI-COR Quantum Meter, Model LI-185A, Lambda Instrument Corp., Lincoln, NE, USA) at 1 m below the lamps, although the plants were usually closer than 1 m away. The lights were initially suspended above the plants and were raised as the plants grew. Temperature in the greenhouses ranged from 17–26°C and

the air remained humid, although the relative humidity was not measured. The plants were staked and pruned to one stem.

Approximately 21–28 days after transplanting, the plants were mass-infested with silverleaf whitefly adults from a colony that had been maintained in the laboratory for approx. 5 years on the dwarf tomato cv. 'Florida Lanai' (1). Equal numbers of pots of infested Florida Lanai plants were distributed uniformly in each greenhouse and were left in place without watering for the duration of the trial. Thus, the whitefly adults were forced onto the test plants as the Florida Lanai plants desiccated and died. This method has been used successfully to achieve uniform inoculation of tomato seedlings in a breeding program with whiteflies and with the whitefly-vectored *Tomato yellow leaf curl virus* (J.W.S., unpublished data). The numbers of whitefly adults, eggs, first to fourth instars, and empty pupal cases (emerged adults) were determined on two occasions. The first evaluation was completed 32 days after the mass infestation of the greenhouse began, when the plants had approximately ten true leaves. Four leaflets proximal to the terminal leaflet on the leaves at nodes five and seven (counting from the plant apex, starting with the first unfolded leaflet) were selected. The leaves at these nodes were selected because previous studies had shown that more eggs were located on the leaf at node five and more nymphs were located on the leaf at node seven (31). The leaflets then were harvested, using a pair of steel forceps to sever them from the plant, and transferred directly into a 15-cm-diam plastic petri dish. The samples were taken to the laboratory and trapped whitefly adults, eggs, crawlers, nymphs and empty pupal cases were counted on each leaflet surface for all eight leaflets using a dissecting microscope (Wild-Heerbrugg, Heerbrugg, Switzerland) at a magnification of $\times 12$. The area of the leaflets used for insect counts was measured by use of a portable area meter (LI-COR model LI-3000, Lambda Instrument Corp.).

The density of types IV (glandular, single-lobed), V (non-glandular) and VI (glandular, four-lobed) trichomes (25) was determined from the average of counts made at four binocular microscope fields on each surface of the pair of lateral leaflets proximal to the terminal leaflet of the fifth node that were sampled at 32 days after mass infestation. One of the leaflets was used to determine trichome density on the adaxial leaflet surface, whereas the other was used for the abaxial surface. The dissecting microscope set at $\times 50$ was used for these counts. The fields of view, located in the interior middle section of the leaflet and with equal numbers on each side of the mid-vein, measured approximately 7.1 mm^2 each.

Field resistance verification Based on the evaluation results in the primary greenhouse screening, 33 plants selected from 22 accessions were tested in the field to verify the resistance that was observed in the initial greenhouse screening. These resistant plants, and four susceptible plants representing each of the wild *Lycopersicon* species evaluated, were cut back to a stem height of ~ 30 cm. Two grams of fertilizer (N:P:K; 20:20:20) dissolved in water at 4 g l^{-1} was then added to each pot, and multiple lateral shoots were allowed to grow. These shoots were used to propagate vegetatively the selected plants. The cuttings from the lateral shoots were rooted under intermittent mist.

The rooted cuttings described above were transplanted in the field at the Gulf Coast Research and Education Center, Bradenton, Florida, in March 1995. There were 38 entries: 33 resistant test plants and the four susceptible plants from wild species (obtained by vegetative propagation), and two plants of the susceptible tomato cv. Solar Set (raised from seed). The experiment was laid out in three randomized complete blocks with each entry represented by one plant per block (three cuttings per selected plant with one cutting

in each replicate). The plants were set on 84-cm-wide × 20-cm-high beds of EauGallie fine sand. The beds were spaced on 150-cm centers with seepage irrigation ditches spaced six beds apart. The blocks were arranged parallel to the beds and the irrigation ditches. The plants were spaced at 91 cm, with 2-m separating blocks within the bed. Standard growing practices were followed (19). *Bacillus thuringiensis* was applied to control lepidopteran insect pests, but no other insecticides were applied.

Natural *B. argentifolii* infestation was allowed to occur. Whitefly and trichome density measurements were completed 90 days after the cuttings were transplanted into the field. Leaf samples were taken on the major shoot(s) and brought to the laboratory. The procedures followed for leaf sampling, insect counts, and trichome density determinations were identical to those described for the primary evaluation in the greenhouse.

To compare genotypes, the mean whitefly densities and trichome densities were transformed [square root of (X + 0.5)] prior to analysis of variance (ANOVA) using the PROC GLM statement of SAS and means separation by Duncan's Multiple Range Test (29). Spearman correlations between trichome densities and insect densities were calculated using PROC CORR. Separate analyses were performed for abaxial and adaxial leaflet surfaces.

RESULTS

Greenhouse screening Differences among accessions were significant for the density of eggs, crawlers, second and third instars, and dead adults for adaxial leaf surfaces ($F = 2.3$, $P < 0.001$; $F = 3.02$, $P < 0.001$; $F = 3.29$, $P < 0.001$; and $F = 4.83$, $P < 0.001$; respectively, for eggs, crawlers, second and third instars, and dead adults; $df = 32, 247$) and abaxial leaf surfaces ($F = 4.24$, $P < 0.001$; $F = 3.29$, $P < 0.001$; $F = 3.61$, $P < 0.001$; and $F = 6.46$, $P < 0.001$; respectively, for eggs, crawlers, second and third instars, and dead adults; $df = 32, 247$) (data not shown). Densities were not significantly different among accessions for pupae on the adaxial surface ($F = 1.08$, $P = 0.366$; $df = 32, 247$) and for exuviae and live adults on both leaf surfaces ($F = 1.46$, $P = 0.059$; and $F = 1.09$, $P = 0.346$; respectively, for exuviae on adaxial and abaxial surfaces; $F = 1.40$, $P = 0.084$; and $F = 1.09$, $P = 0.346$; respectively, for live adults on adaxial and abaxial leaf surfaces; $df = 32, 247$) (data not shown). Data were pooled for all immature whitefly life stages for simplicity of presentation and to reduce the tables to acceptable size. Whitefly densities on the adaxial leaf surfaces were much lower than on the abaxial surface (Table 1).

The densities of the combined total of all silverleaf whitefly immature stages differed significantly among accessions ($F = 3.21$, $P < 0.0001$, $df = 32, 7$ for adaxial leaf surface; $F = 5.23$, $P < 0.0001$, $df = 32, 7$ for abaxial leaf surface) (Table 1). Considered separately, the differences in the densities of eggs, crawlers, 2nd and 3rd instar nymphs, and pupae (4th instar) were highly significant ($F = 3.11$, $P < 0.001$, $df = 32, 247$ over both leaf surfaces) (data not shown). A large number of the accessions had lower densities of whiteflies than the susceptible tomato cv. Solar Set, which was used as a standard, but some were equally or more susceptible than the standard (Table 1). Adopting the density of the insect on the host plant as an index of relative resistance, it is apparent that the accessions screened exhibited wide variation for resistance to the silverleaf whitefly.

In general, densities of total whitefly, and immature life stages, were lowest for the accessions of *L. pennellii*, followed by *L. hirsutum* f. *typicum* and *L. hirsutum* f. *glabratum*. The accessions of *L. peruvianum* – and, especially, *L. pennellii* var. *puberulum* – screened

TABLE 1. Mean density^z (cm⁻²) of silverleaf whitefly on leaf surfaces of the 7th leaf node, and of trichomes on leaf surfaces of the 5th leaf node, on plants of *Lycopersicon* germplasm in screening for resistance to *Bemisia argentifolii* in the greenhouse

Taxa and accession no.	Number of plants	Total number of insects ^y on leaf surfaces		Number of type IV trichomes	
		Adaxial	Abaxial	Leaf surface	
				Adaxial	Abaxial
<i>L. pennellii</i>					
LA 1302	8	0.7 b-e	3.1 f-k	464 e-g	1,043 d-h
LA 1340	8	0.2 c-e	<0.1 jk	1,050 a-d	1,692 a-e
LA 1674	5	0.3 c-e	5.5 f-k	851 b-e	1,152 d-h
LA 1809	7	0.4 c-e	1.3 g-k	1,265 a-c	1,650 a-f
PI 246502	8	0.9 b-e	0.8 h-k	1,605 a	3,029 a
LA 2560	8	0.1 de	1.1 h-k	1,312 ab	1,730 a-e
LA 716	6	<0.1 e	0 k	1,081 a-d	1,455 b-g
LA 2963	8	1.0 b-e	11.6 b-i	1,019 a-d	1,464 b-g
<i>L. pennellii</i> var. <i>puberulum</i>					
LA 1911	8	3.2 b	27.9 ab	321 f-h	782 f-h
LA 1912	2	17.4 a	56.2 a	223 g-i	498 g-i
<i>L. hirsutum</i> f. <i>glabratum</i>					
LA 1223	8	1.1 b-e	18.2 b-d	32 ij	2,548 ab
PI 126449	8	0.8 b-e	4.1 d-k	44 ij	1,174 c-h
LA 2144	8	1.3 b-e	26.1 b	33 ij	2,938 a
LA 1265	8	0.5 b-e	4.2 d-k	41 ij	2,368 a-c
PI 134417	8	0.4 c-e	0.6 h-k	99 h-j	2,190 a-c
PI 134418	8	0.6 b-e	0.3 i-k	191 g-j	2,667 a-c
PI 199381	8	1.6 b-e	12.9 b-f	0 j	388 ij
PI 251305	8	1.3 b-e	15.4 b-e	16 ij	2,253 a-e
<i>L. hirsutum</i> f. <i>typicum</i>					
PI 126445	5	1.0 b-e	12.1 b-h	91 h-j	362 hi
PI 127826	7	0.2 c-e	2.1 f-k	693 d-f	1,728 b-g
PI 127827	8	1.0 b-e	10.6 c-j	762 c-f	1,658 a-f
LA 1353	8	0.3 c-e	1.3 g-k	1,475 ab	2,560 a-c
LA 1772	8	0.2 c-e	4.3 d-k	592 c-f	1,023 d-h
LA 1777	8	0.1 e	1.8 g-k	1,311 ab	2,305 a-d
LA 1927	8	1.4 b-e	20.5 b-e	309 f-h	1,004 e-h
LA 2155	8	1.0 b-e	18.3 bc	121 h-j	1,243 c-h
LA 386	8	0.5 b-e	3.0 f-k	600 c-f	1,721 a-e
PI 390513	8	0.8 b-e	16.0 b-d	5 ij	1,661 b-g
<i>L. peruvianum</i>					
PI 127830	8	2.8 bc	14.5 b-g	283 h-j	419 ij
LA 1292	8	2.0 b-d	9.8 b-i	115 ij	307 ij
LA 2151	8	2.6 bc	7.8 c-j	0 j	0 j
LA 364	8	2.0 b-e	14.1 b-e	0 j	0 j
<i>L. esculentum</i>					
Solar Set	8	1.8 bc	12.9 b-e	0 j	0 j

^zWithin columns, means followed by a common letter do not differ significantly ($P=0.05$) by Duncan's Multiple Range Test.

^yTotal number of insects = eggs, crawlers, second and third instars, pupae, and exuviae.

in this experiment, had the highest densities of all whitefly life stages (Table 1). Trichome density differences among accessions were highly significant for both leaf surfaces (for Type IV: $F = 20.88$, $P < 0.001$; $F = 13.69$, $P < 0.001$; for Type V: $F = 26.17$, $P < 0.001$;

TABLE 2. Correlation (r) between the densities of *Bemisia argentifolii* life stages on the 7th leaf node and the density of type IV trichomes on the 5th leaf node observed on plants of wild *Lycopersicon* germplasm selected for resistance to the silverleaf whitefly

Whitefly life stage	Leaf surface			
	Adaxial		Abaxial	
	Greenhouse ^z	Field ^y	Greenhouse ^z	Field ^y
Adaxial surface				
Eggs	-0.35***	-0.19*	-0.20***	-0.03ns
Crawlers	-0.39***	-0.39***	-0.28***	-0.31***
2nd & 3rd instars	-0.31***	-0.28**	-0.28***	-0.28**
Pupae	-0.17***	-0.14ns	-0.12ns	-0.14ns
Exuviae	-0.04ns	—	0.01ns	—
Live adults	0.07ns	—	0.11ns	—
Dead adults	0.59***	-0.12ns	0.26***	-0.15ns
Abaxial surface				
Eggs	-0.52***	-0.31***	-0.28***	-0.12ns
Crawlers	-0.45***	-0.47***	-0.25***	-0.27**
2nd & 3rd instars	-0.40***	-0.40***	-0.21***	-0.28**
Pupae	-0.27***	-0.32***	-0.02ns	-0.12ns
Exuviae	0.06ns	—	0.04ns	—
Live adults	0.06ns	—	0.04ns	—
Dead adults	0.55***	-0.03ns	0.22***	0.01ns

^zMaterial screened and evaluated in the greenhouse; 248 observations were used in computing each correlation coefficient value.

^yMaterial evaluated in the field; 113 observations were used in computing each correlation coefficient value.

ns Nonsignificant.

*, **, *** Significant at $P=0.05$, 0.01 or 0.001 , respectively.

$F = 26.86$, $P < 0.001$; for Type VI: $F = 26.53$, $P < 0.001$; $F = 45.35$, $P < 0.001$; for adaxial and abaxial, respectively; $df = 32, 215$); only type IV data are shown (Table 1). Type I trichome data are not shown because they were not observed in most accessions, except for *L. peruvianum*. Type V and VI trichome data are not shown because these trichome types were either not significantly correlated with densities of whitefly life stages or had small correlations with same. In the case of type V trichomes, correlations with immature life stages were positive, whereas those with dead adults were negative.

Spearman correlation coefficients (r) were calculated between trichome densities and whitefly density measurements, but generally were low (Table 2). The correlation coefficients between the density of type IV and insect density were negative and significant ($P < 0.001$) for eggs, crawlers, and second and third instars combined on both abaxial and adaxial leaf surfaces; however, the correlation coefficients did not explain very much of the variation.

Field resistance verification Differences among the selected plants (representing each accession) for the density of dead adults on the leaf surface were non-significant for either surface ($F = 0.71$, $P = 0.878$; $F = 0.38$, $P = 0.999$; respectively, for adaxial and abaxial leaflet surfaces; $df = 37, 75$) (data not shown). No live adults were found stuck on the leaf surfaces.

None of the plants of *L. pennellii* (except for LA 2963, plant 62) had any whiteflies, either adult or immature stages (Table 3). This degree of consistency among plants was not observed for *L. hirsutum* f. *typicum*, *L. hirsutum* f. *glabratum* or *L. peruvianum*. The plant selected from the accession LA 1265 of *L. hirsutum* f. *glabratum* was the most densely infested by whiteflies of all life stages and even surpassed the susceptible controls.

TABLE 3. Mean density^z (cm⁻²) of silverleaf whitefly on leaves of the 7th leaf node, and of trichomes on leaves of the 5th leaf node, on selected plants of wild *Lycopersicon* germplasm grown in the field to verify resistance to *Bemisia argentifolii*

Taxa and accession no.	Selected plant identity	Total number of insects ^y	Number of type IV trichomes	
			Leaf surface	
			Adaxial	Abaxial
<i>L. pennellii</i>				
LA 1340	p46	0 d	275 kl	359 k
LA 1340	p66	0 d	435 h-l	541 h-k
LA 1340	p76	0 d	419 i-l	954 g-j
LA 1340	p86	0 d	384 j-l	463 i-k
LA 716	p67	0 d	890 d-i	968 g-i
LA 716	p37	0 d	805 e-j	968 g-i
PI 246502	p21	0 d	531 g-k	964 g-i
PI 246502	p51	0 d	664 f-k	1,032 f-h
PI 246502	p71	0 d	786 e-j	1,004 f-h
LA 1302	p15	0 d	309 kl	531 h-k
LA 1674	p210	0 d	386 j-l	533 h-k
LA 1674	p410	0 d	410 j-l	448 jk
LA 1674	p810	0 d	324 kl	463 i-k
LA 2560	p14	0 d	333 kl	469 i-k
LA 2963	p62	8.0 d	82 m-o	108 i
<i>L. hirsutum</i> f. <i>typicum</i>				
LA 386	t121	3.0 d	2,001 a	4,015 a
LA 386	t621	2.0 d	1,487 a-d	3,548 ab
LA 1353	t411	0 d	2,080 ab	2,707 bc
LA 1353	t511	4.0 d	1,353 b-e	2,063 cd
LA 1353	t711	0 d	885 d-h	1,959 c-e
LA 1772	t222	11.3 cd	1,310 c-e	1,703 d-f
LA 1777	t212	4.0 d	1,525 a-e	1,924 c-e
LA 1777	t612	22.3 b-d	1,038 c-g	1,038 g-i
LA 1927	t613	29.3 bc	161 l-n	547 h-k
LA 2155	t617	17.0 b-d	9 o	6 l
PI 127826	t230	4.3 d	1,106 c-f	2,264 cd
PI 127826	t630	0 d	1,043 c-g	2,249 cd
PI 127827	t429	0 d	1,576 a-c	1,872 c-e
PI 127827	t529	5.6 d	224 Im	1,230 e-g
<i>L. hirsutum</i> f. <i>glabratum</i>				
LA 2144	g816	42.7 bc	426 i-l	1,261 e-g
LA 1265	g515	167.3 a	15 no	1,660 d-g
PI 126449	g631	10.0 d	36 m-o	298 k
PI 134417	g227	1.7 d	184 Im	1,849 c-e
<i>L. peruvianum</i>				
LA 2151	r320	12.4 cd	0 o	0 l
LA 2151	r520	3.3 d	0 o	0 l
PI 127830	r128	15.0 cd	0 o	0 l
PI 127830	r328	4.7 d	0 o	0 l
<i>L. esculentum</i>				
Solar Set	esc	47.7 b	0 o	0 l

^zWithin columns, means followed by a common letter do not differ significantly ($P=0.05$) by Duncan's Multiple Range Test.

^yTotal number of insects = eggs, crawlers, second and third instars, and pupae. Insect counts were totaled over adaxial and abaxial leaf surfaces.

Differences among the tested plants were highly significant for the density of all the trichome types evaluated and both leaf surfaces (for Type IV: $F = 24.28$, $P < 0.001$; $F = 36.95$, $P < 0.001$; for Type V: $F = 59.26$, $P < 0.001$; $F = 51.38$, $P < 0.001$; for Type VI: $F = 20.01$, $P < 0.001$; $F = 10.42$, $P < 0.001$; for adaxial and abaxial, respectively; $df = 37$, 76); only type IV trichome data are shown, for the same reasons given for the greenhouse evaluation data presented above. The density of type IV trichomes had a significant negative correlation with the combined density of eggs, crawlers, and second and third instars (Table 2), although the correlations explained only a small portion of the variation.

DISCUSSION

Greenhouse screening Plants within some accessions varied for resistance (data not presented). The wild species under study are largely self-incompatible (20) and outcrossing can occur. Consequently, this intra-accession variation could be due to segregation resulting from earlier cross-pollination between genotypes of different resistance levels. This phenomenon could influence the outcome when screening these wild *Lycopersicon* germplasm as a source of resistance to pests, and the remedy might be that a sizeable number of plants need to be screened for each accession.

The highest level of resistance was observed in *L. pennellii* accessions LA 716, LA 1340 and LA 2560. Other *L. pennellii* accessions that were more resistant than 'Solar Set' were LA 1809 and PI 246502. LA 1302 and LA 1674 had some plants that were slightly susceptible.

In previous work by others, *L. pennelli* LA 716 showed resistance to the potato aphid (11), the greenhouse whitefly, and the two-spotted spider mite (12,13). In our study, LA 716 and the other accessions listed above were resistant to *B. argentifolii*. The resistant plants from the *L. pennellii* taxon were characterized by the absence of immature stages of the whitefly and some dead and/or live adults trapped in trichome exudates. This would suggest similarity of the components of resistance in the accessions. LA 1340 and LA 1674 had significantly higher numbers of dead, stuck whiteflies compared to all the other accessions (data not shown). This might be due to a separate component of resistance present only in these two accessions and not in the other accessions of *L. pennellii*.

Among the accessions of *L. hirsutum* f. *typicum*, LA 1772, LA 386 and PI 127826 had some plants with high resistance. The most resistant *L. hirsutum* f. *typicum* accessions were LA 1777 and LA 1353. Schuster (30) found resistance to the tomato pinworm *Keiferia lycopersicella* (Walsingham) in PI 127826 and PI 134418. Carter *et al.* (5) reported resistance of PI 126445 to the Colorado potato beetle *Leptinotarsa decemlineata* (Say). Eigenbrode and Trumble (9) found LA 1777 to be resistant to the beet armyworm *Spodoptera exigua* (Hubner), whereas Juvik *et al.* (21) reported this accession to be resistant to four lepidopteran pests of tomato in Israel. Fery and Kennedy (10) found PI 127826 to be susceptible to the tobacco hornworm *Manduca sexta* (L.). Channarayappa *et al.* (6) reported a lack of *Tomato leaf curl virus* transmission under field conditions and attributed this to the resistance of LA 386, LA 1777 and PI 390513 to whiteflies.

The *L. hirsutum* f. *glabratum* plants were more homogeneous within each accession than *typicum*, but none showed very high resistance. PI 126449 and LA 1265 were more resistant than the control, whereas PI 134417 and PI 134418 were the most resistant f. *glabratum* accessions evaluated. LA 134417 has been reported resistant to several insect species (38).

The *L. peruvianum* accessions were as susceptible as the cultivated tomato. Chanarayappa *et al.* (6) had observed that accession PI 127830 did not develop symptoms of *Tomato leaf curl virus*, to which it was susceptible. They attributed this to resistance to the whitefly, which vectors the virus.

Of the wild species evaluated, only *L. peruvianum* consistently had type V trichomes (data not shown). This is in agreement with the description of trichomes of *Lycopersicon* by Luckwill (25). However, PI 127830 and LA 1292 had type IV trichomes, which was unexpected for the species *L. peruvianum*. We cannot explain this anomaly other than to speculate on a possible past crossing with a species that possesses type IV trichomes, or the natural presence of type IV trichomes in this species, contrary to Luckwill (25).

The density of type IV trichomes was consistently higher than that of type VI in the wild germplasm (data not shown). The correlation coefficients between trichome density and the density of whiteflies were low but significant in some cases (Table 2). The implication for tomato breeding is that trichome density is not a reliable selection criterion for resistance to *B. argentifolii*.

Field resistance verification The results for the plants evaluated in the field verification were in good agreement with the primary greenhouse screening results; however, a few test plants had a significant difference. The selected resistant plant from LA 1265 was susceptible in the field (Table 3), and plants from LA 1777 appeared more susceptible in the field than in the greenhouse. Interactions can occur between genotypes and the environment and some resistance attributes in *Lycopersicon* (14,15). Trichome density was lower in the field experiment (Table 3) for all the test plants. The negative correlation between trichome and whitefly densities was low but significant in some relationships (Table 2), similar to the results obtained in the greenhouse experiment.

While the density of glandular trichomes may account for a relatively low amount of the resistance observed in these experiments, it is clear that the contents of the trichomes are very important. Muigai *et al.* (27) showed that appressing the leaves of resistant *L. pennellii*, *L. hirsutum* f. *typicum* and *L. hirsutum* f. *glabratum* plants onto the leaves of cultivated tomato resulted in reduced whitefly oviposition on cultivated tomato leaves. Furthermore, 2-undecanone (a methyl ketone constituent of *L. hirsutum* f. *glabratum* glandular trichomes) and ginger oil (which contains, among other things, the sesquiterpene zingiberene, a constituent of *L. hirsutum* f. *typicum* trichomes) were both repellent to *B. argentifolii* adults. Ginger oil also was toxic residually to the adults.

The screening approach used in the research reported here was systematic. Diverse materials were screened by exposing them to high pest pressure and eventually were tested under normal production conditions but with high pest pressure. The identified resistant germplasm has the potential for a broad genetic base for whitefly resistance and could be useful in developing resistant tomato cultivars; however, attempts to transfer the resistance of *L. hirsutum* to germplasm of *L. esculentum* have been unsuccessful to date, due to apparent genetic linkage between resistance and wild characteristics (D.J.S. and J.W.S., unpublished data). Type IV trichomes, which are major reservoirs of the chemicals imparting resistance, do not occur in *L. esculentum* and may be responsible, at least in part, for the difficulty in transferring resistance. Recently, Monforte and Tanksley (26) developed 98 recombinant inbred lines developed from accession LA 1777 that span 85% of the *L. hirsutum* genome. After identifying the lines containing resistance genes, molecular markers may be used to identify crossovers in backcrosses to the same

recurrent parent, thus reducing the size of the *L. hirsutum* chromosome segment and associated linkage drag. Resistant lines with *L. esculentum*-like characteristics could then be developed.

Even though the silverleaf whitefly can cause wilting and death of plants, and irregular ripening of fruit, the major threat to yield losses is through the dissemination of plant viruses such as *Tomato mottle virus* (ToMoV) and *Tomato yellow leaf curl virus* (TYLCV) (34). At least some of the accessions evaluated in the present study are resistant enough to the silverleaf whitefly to reduce the incidence of plants with symptoms of both of the above viruses (D.J.S. and J.W.S., unpublished data). However, once the plants are infected, symptoms are particularly pronounced, suggesting that they are highly susceptible. Recently, germplasm has been developed with broad-based resistance to both ToMoV and TYLCV from the wild tomato species *L. chilense* (35). Even when cultivars with this broad-based resistance are available, germplasm with resistance to the whitefly itself would be desirable to manage the other effects of feeding by the silverleaf whitefly, particularly irregular ripening of fruit. This disorder is characterized by incomplete or inhibited ripening of fruit, particularly in longitudinal sections, and in an increase in internal white tissue. The severity of symptoms of this disorder is directly related to the density of silverleaf whitefly nymphs (32). Therefore, combined virus and whitefly resistance would provide a comprehensive management approach for the silverleaf whitefly and associated viruses and disorders.

ACKNOWLEDGMENTS

This research was supported by the Florida Agricultural Experiment Station, and approved for publication as Journal Series No. R-08995.

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