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PROGRESS IN BREEDING TOMATOES FOR RESISTANCE TO TOMATO SPOTTED WILT

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ABSTRACT

Among 32 *Lycopersicon* spp. accessions field tested for tomato spotted wilt virus (TSWV) resistance in the summer season of 1985/86 in Paulinia county, five were found to be resistant to this viral disease: *L. peruvianum* "LA-444-1", *L. hirsutum* "PI 127826", *L. hirsutum* var. *glabratum* "PI 134417", *L. pimpenellifoium* "PI 732293-2V" and *L. esculentum* "Rey de Los Tempranos". Segregating populations and/or breeding lines created from crosses between susceptible commercial tomato cultivars and TSWV-resistant *Lycopersicon* spp. accessions were evaluated in a series of experiments performed from 1986 through 1989. These populations and breeding lines trace back to crosses with "Rey de Los Tempranos", "PI 732293-2V", "PI 127826" and "PI 134417". Emphasis was placed on populations originated from crosses with "Rey de Los Tempranos", the sole *L. esculentum* accession with TSWV resistance. In 1988, we selected five stable advanced breeding lines with both TSWV resistance and superior horticultural traits (comparable to the standard tomato cultivar Angela Gigante I-5100). In 1989, the superior performance of these resistant lines was confirmed in a replicated trial. Data indicate that resistance to TSWV found in "Rey de Los Tempranos" is controlled by recessive allele(s).

INTRODUCTION

Tomato spotted wilt (TSW) is the single most important viral disease of tomatoes in Brazil. It is a limiting factor for summer production of tomatoes in subtropical areas of Southern Brazil, especially in the State of São Paulo, the country's

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leading tomato producer. Symptoms are a function of the viral strain, of the host genotype, and of developmental stage of the host at the time of infection (Ie, 1970; Cupertino *et al.*, 1981).

Host range of the tomato spotted wilt virus (TSWV) is very wide: the virus has been found in at least 166 plant species in 34 families, including seven monocotyledonous families (Ie, 1970), with prominence in the Solanaceae, in which at least 63 species are hosts (Best, 1968).

The virus is transmitted by the thrips *Thrips tabaci, Frankliniella schultzei, F. occidentalis* and *F. fusca* (Ie, 1970; Francki and Hatta, 1981). It is acquired by the thrips larvae but not by adults, though only adults transmit. Thus transmission is only by adults that fed on infected plants in the larval stage.

Common symptoms in tomatoes (*Lycopersicon esculentum* MIll.) are bronzing and downward curling of top leaves, circular spots and necrosis on the leaves and stems, and dark streaks on stems and petioles. Fruiting is impaired, and fruit are usually small, seedless and malformed.

Attempts to control TSWV by insecticides aimed at the vector have met with little success, although a reduction in incidence has been reported in some cases (Francki and Hatta, 1981; Costa *et al.*, 1977). This is to be expected since much of the infection in tomatoes appears to be from viruliferous thrips migrating from virus reservoirs outside the crops. The destruction of such reservoirs, which would decrease the amount of inoculum entering the crop, poses difficult problems because of the extensive host range of TSWV which includes many diverse ornamental and weedy species (Francki and Hatta, 1981).

Sources of resistance to TSWV have been found in *Lycopersicon* sp. (Kikuta *et al.*, 1945; Finlay, 1952, 1953; Eskes and Nagai, 1981; Araújo *et al.*, 1983; Upreti and Hartmann, 1984; Cupertino *et al.*, 1986; Paterson *et al.*, 1989). The inheritance of TSWV resistance is probably polygenic, individual resistance genes being specific for certain viral strains (Finlay, 1952, 1953; Patterson *et al.*, 1989).

This paper reports on the progress of a breeding programme aimed at developing tomato cultivars with resistance to TSWV, carried out during a five-year period (1985 through 1989) at the Bioplanta Tecnologia de Plantas Research Station in Paulinia County, State of São Paulo, Brazil. Throughout this paper, the term *resistance* will be used to mean all mechanisms that reduce crop losses, and not necessarily as a synomym for immunity.

Because the design of each experiment was dependent on the results obtained in the previous one, we will report the methodology and results together for each experiment, in chronological sequence.

FIELD TRIALS

Summer 1985/86 trial: Screening of Lycopersicon accessions for TSWV resistance

Thirty two *Lycopersicon* accessions were field tested during the summer of 1989 for their level of resistance to TSWV, under natural epithytotic conditions. the majority (28) of the accessions were cultivars of lines of *L. esculentum*, the remainder being representative of wild species (one accession each of *L. peruvianum, L. hirsutum, L. hirsutum* var. *glabratum* and *L. pimpinellifolium*). Thirty plants of each accession comprised each plot. Plants were scored on a scale from 1 to 5, as follows:

1 = no symptoms;
2 = light symptoms, with no apparent impairment of fruit set;
3 = light symptoms, with some impairment of fruit set; necrosis on a few leaflets or branches;
4 = plant necrosis on most branches and leaves; severe impairment of fruit set;
5 = severe necrosis in all plant parts, or plant death.

An overall plot score equivalent to the prevalent plant score was recorded, as was the range of individual plant scores. The experiment was not replicated, therefore a reliable estimate of the environmental variance was not available. Nevertheless, the results (Table I) leave little doubt as to the differences among accessions. All but five of the accessions tested proved to be highly susceptible to the virus, with symptoms on individual plants ranging from 4 to 5; these susceptible accessions were *L. esculentum* types varying in maturity and growth habit (e.g. New Yorker Special - early, determinant; Olho Roxo - late, indeterminant).

Only five of the accessions appeared to be of value to breeding for TSWV tolerance/resistance:

Rey de Los Tempranos: the sole *L. esculentum* accession tested which had a degree of TSWV tolerance; a few plants showed downward curling of top leaves, leaf/branch necrosis, impaired fruit set, abnormally developed fruit (seedless), and were rated 5 on the disease symptoms scale; however, the majority of the plants had mild symptoms of TSW, with good or excellent set of normal, fully seeded fruit. The overall rating for Rey de Los Tempranos was 2, which typically is a plant with a few curled or necrotic leaflets or branches, but with most leaves symptomless and with normal fruit set.

Table I - Tomato spotted wilt ratings in *Lycopersicon* accessions grown under epiphytotic conditions. Paulinia County, State of São Paulo, Brazil. Summer 1985/86 (1 = no symptoms; 5 = plants dead or severely necrosed).

Accession	Plot rating	Range	Species
LA 444-1	1	1 - 2	*L. peruvianum*
PI 127826	1	1 - 2	*L. hirsutum*
PI 134417	2	1 - 3	*L. hirsutum* var. *glabratum*
PI 732293-2V	2	1 - 4	*L. pimpinellifolium*
Rey de Los Tempranos	2	1 - 5	*L. esculentum*
Euromech	5	4 - 5	*L. esculentum*
Florida - 1B	5	4 - 5	*L. esculentum*
Motelle	5	4 - 5	*L. esculentum*
Peto 86	5	5 - 5	*L. esculentum*
Principe Gigante	5	4 - 5	*L. esculentum*
Rio Fuego	5	4 - 5	*L. esculentum*
Angela Gigante I-5100	5	5 - 5	*L. esculentum*
Bull	5	5 - 5	*L. esculentum*
Calypso	5	5 - 5	*L. esculentum*
Europeel	5	5 - 5	*L. esculentum*
Momor	5	5 - 5	*L. esculentum*
New Yorker Special	5	5 - 5	*L. esculentum*
Olho Roxo	5	5 - 5	*L. esculentum*
Petomech	5	5 - 5	*L. esculentum*
Peto 94C	5	4 - 5	*L. esculentum*
Peto 98	5	5 - 5	*L. esculentum*
Peto 102	5	5 - 5	*L. esculentum*
Peto 460	5	5 - 5	*L. esculentum*
Pieraline	5	5 - 5	*L. esculentum*
Raminho	5	5 - 5	*L. esculentum*
Rio Grande	5	5 - 5	*L. esculentum*
Rodade	5	5 - 5	*L. esculentum*
Romor	5	5 - 5	*L. esculentum*
Rotella	5	5 - 5	*L. esculentum*
Tropic	5	5 - 5	*L. esculentum*
XP-5200	5	5 - 5	*L. esculentum*
74T2	5	5 - 5	*L. esculentum*

PI 732293-2V: a selection of *L. pimpinellifolium* PI 732293 obtained from H. Nagai (IAC/Instituto Agronômico de Campinas) had a reaction similar to that of Rey de Los Tempranos, with a few plants with symptoms rated up to 4, but with a plot symptom rating of 2.

PI 127826: an accession of *L. hirsutum* var. *typicum*. Plants were very vigorous, with some necrosis on older leaves, though the majority of leaves appeared symptomless. All plants evaluated were considered tolerant or resistant, flowering was apparently normal and no plant had a disease rating higher than 2. Plot symptom rating was 1.

PI 134417: an accession of *L. hirsutum* var. *glabratum*. Plants were vigorous, with necrosis on a few branches and leaves located in both older or younger plant parts. Flowering was normal and profuse. Overall rating for PI 134417 was 2, but some plants had higher disease ratings (= 3), though never as high as in Rey de Los Tempranos or PI 732293-2V.

LA 444-1: an accession of *L. peruvianum*. Plants were vigorous with profuse flowering. All plants evaluated were considered tolerant or resistant, and no plant had a disease rating higher than 2. Plot symptom rating was 1.

In view of the difficulty in obtaining the cross *L. esculentum* x *L. peruvianum*, accession LA 444-1 was not considered a priority in our breeding programme, in spite of its high level of resistance to TSWV. The other four sources of resistance were used in backcross programmes with commercial tomato cultivars, independently from each other, on the assumption that all four sources of resistance are controlled by different genes.

Summer 1986/87 trial: Evaluation of TSWV resistance in breeding lines issued from crosses with Rey de Los Tempranos or L. pimpinellifolium "PI 732293/2V"

Seventeen tomato breeding lines and cultivars (Table II) were field tested in the summer of 1986/87 in 30-plant plots, under natural epiphytotic conditions. Plants were individually scored for symptoms at the time of flowering or fruit set, and the plot score was calculated as an average of the individual plant scores. Two of the cultivars (Rio Fuego, Angela Gigante I-5100) had been previously found to be susceptible to TSWV, whereas Rey de Los Tempranos had been previously considered resistant (Table I). Tropicana-509 was presumed to be susceptible to TSWV, because it is nearly isogenic to Tropic, found in 1985/86 to be susceptible. Pearl Harbor was not included in the 1985/86 trial, but was included in the 1986/87 trial because of its reported resistance to TSWV in Hawaii (Kikuta *et al.*, 1945). Five of the breeding lines (those with codes starting with BPX-198-) are F_5 progenies issued

from the cross *L. esculentum* "Calypso" x *L. pimpinellifolium* "PI 732293-2V". The remaining seven breeding lines (with codes starting with BPX-199-) are F_3 progenies ussued from the first backcross to cv. Angela Gigante I-5100 of the F_1 (Angela Gigante I-5100 x Rey de Los Tempranos).

Table II - Tomato spotted wilt ratings in *Lycopersicon* cultivars and breeding lines grown under epiphytotic conditions. Paulinia County, State of São Paulo, Brazil. Summer 1986/87 (1 = no symptoms; 5 = plants dead or severely necrosed).

Cultivar/Line	Plot mean
Tropicana - 509	3.8
Rio Fuego	3.7
Pearl Harbor	3.7
BPX-198-13C[(a)]	3.3
BPX-198-06C[(a)]	3.2
Angela Gigante I-5100	3.0
BPX-198-09C[(a)]	2.7
BPX-199-11B[(b)]	2.4
Rey de Los Tempranos	2.2
BPX-199-04B[(b)]	2.2
BPX-199-05B[(b)]	2.2
BPX-199-09B[(b)]	2.2
BPX-198-10C[(a)]	2.0
BPX-199-14B[(b)]	1.9
BPX-199-08B[(b)]	1.9
BPX-199-16B[(b)]	1.8
BPX-198-03C[(a)]	1.3

[(a)] F_5 breeding line issued from the cross *L. esculentum* "Calypso" x *L. pimpinellifolium* "PI 732293-2V".
[(b)] F_3 line issued from the 1st. backcross to cv. Angela Gigante I-5100 of the cross Angela Gigante I-5100 x Rey de Los Tempranos.

The results for the cultivars in this trial (Table II) agree with those reported in this paper for the previous year: Rey de Los Tempranos had a lower disease incidence than Tropicana, Rio Fuego and Angela Gigante. Pearl Harbor was found to be as susceptible as Tropicana and Rio Fuego, and more so than Angela Gigante I-5100. For lack of a reliable estimate of experimental error, the lower susceptibility

of Angela Gigante I-5100 relative to the other susceptible cultivars remains to be confirmed in subsequent trials.

At least six lines derived from crosses with Rey de Los Tempranos and one derived from a cross with *L. pimpinellifolium* "PI 732293-2V" had disease scores equal to or lower than Rey de Los Tempranos, and can therefore be considered resistant to TSWV. This indicates that there has been progress in the introgression of the genes for resistance into susceptible cultivars.

Summer 1987/88 trial: Evaluation of TSWV resistance in breeding lines obtained from crosses with Rey de Los Tempranos, L. pimpinellifolium "PI 732293-2V" or L. hirsutum "PI 127826"

Two susceptible cultivars (Angela Gigante I-5100, Rio Fuego) and one resistant accession (Rey de Los Tempranos) were used as checks in a trial that included 80 other breeding lines with various degrees of TSWV resistance (Table III). An augmented randomized complete block design was used, the check treatments being common to all 12 blocks. Plots comprised 20 plants, which were rated individually at flowering/fruit set according to the scale reported here. To ensure severe epiphytotic conditions in the field, peanuts (which are excellent hosts to the thrips vectors) were grown between tomato rows.

Table III - Tomato spotted wilt ratings in *Lycopersicon* cultivars and breeding lines grown under epiphytotic conditions. Paulinia County, State of São Paulo, Brazil. Summer 1987/88 (1 = no symptoms; 5 = plants dead or severely necrosed).

Cultivar/Line[a]	Plot mean[b]	Cultivar/Line[a]	Plot mean[b]	Cultivar/Line[a]	Plot mean[b]
BPX-276-04D pl#23	5.0	BPX-276-04D pl#40	4.1	BPX-276-16D pl#05	3.8
BPX-276-04D pl#09	5.0	BPX-199-16C	4.1	BPX-276-04D pl# ?	3.7
BPX-276-04D pl#13	5.0	BPX-276-16D pl#37	4.1	BPX-196-11D pl#06	3.7
BPX-276-04D pl#15	5.0	BPX-276-16D pl#25	4.1	BPX-196-11D pl#02	3.7
Angela Gigante I-5100	4.8	BPX-276-16D pl#47	4.0	BPX-276-08D pl#05	3.7
BPX-276-04D pl#25	4.8	BPX-276-16D pl#29	4.0	BPX-276-08D pl#34	3.6
BPX-276-04D pl#08	4.8	BPX-199-04C	4.0	BPX-276-**D pl#12	3.6
BPX-276-16D pl#38	4.8	BPX-276-04D pl#03	4.0	BPX-276-08D pl#30	3.6
BPX-276-16D pl#14	4.8	BPX-276-08D pl#31	4.0	BPX-276-08D pl#07	3.5
Rio Fuego	4.7	BPX-276-16D pl#18	4.0	BPX-199-08C	3.5

Continued

Table III - Continued.

Cultivar/Line[a]	Plot mean[b]	Cultivar/Line[a]	Plot mean[b]	Cultivar/Line[a]	Plot men[b]
BPX-276-04D pl#02	4.7	BPX-276-08D pl#17	4.0	BPX-276-08D pl#26	3.5
BPX-276-04D pl#07	4.7	BPX-276-08D pl#16	4.0	BPX-276-16D pl#31	3.5
BPX-276-16D pl#22	4.6	BPX-276-04D pl#16	3.9	BPX-276-08D pl#15	3.5
BPX-276-16D pl#10	4.6	BPX0276-08D pl#18	3.9	BPX-276-08D pl#02	3.5
BPX-276-04D pl#31	4.6	BPX-276-08D pl#25	3.9	Rey de Los Tempranos	3.4
BPX-276-04D pl#11	4.6	BPX-276-16D pl#20	3.9	BPX-276-16D pl#16	3.4
BPX-196-11D pl#04	4.4	BPX-276-08D pl#37	3.9	BPX-276-16D pl#30	3.4
BPX-276-04D pl#32	4.4	BPX-276-16D pl#21	3.9	BPX-276-08D pl#06	3.4
BPX-196-11D pl#01	4.4	BPX-276-16D pl#48	3.9	BPX-276-08D pl#14	3.4
BPX-276-04D pl#24	4.4	BPX-276-16D pl#32	3.9	BPX-276-16D pl#08	3.4
BPX-196-11D pl#05	4.3	BPX-276-16D pl#19	3.9	BPX-276-08D pl#33	3.2
BPX-276-04D pl#28	4.3	BPX-276-16D pl#49	3.9	BPX-276-08D pl#28	3.2
BPX-276-04D pl#31	4.3	BPX-276-08D pl#01	3.8	BPX-276-04D pl#21	2.9
BPX-276-16D pl#24	4.3	BPX-276-08D pl#29	3.8	BPX-276-16D pl#55	2.9
BPX-276-04D pl#35	4.3	BPX-276-04D pl#05	3.8	BPX-276-16D pl#06	2.8
BPX-276-16D pl#15	4.2	BPX-276-16D pl#17	3.8	BPX-276-08D pl#27	2.7
BPX-276-16D pl#28	4.2	BPX-276-08D pl#38	3.8	BPX-198-03D	2.5
BPX-276-04D pl#01	4.2	BPX-276-08D pl#04	3.8		

[a] Lines starting with BPX-199 and BPX-276- are issued from crosses with Rey de Los Tempranos; those starting with BPX-196-, from crosses with *L. hirsutum* "PI 127826"; those starting with BPX-198-, from crosses with *L. pimpinellifolium* "PI 732293-2V".

[b] Means reported for Angela Gigante I-5100, Rio Fuego and Rey de Los Tempranos are means of 12 plots, with 20 plants per plot; otherwise, means are single-plot means (20 plants), adjusted for block effects.

Of the 80 lines tested, one was derived from crosses with *L. pimpinellifolium* "PI 732293-2V" (the F_6 line BPX-198-03D, whose respective F_5 line was tested in the Summer 1986/87 trial), and five were derived from crosses with *L. hirsutum* "PI 127826" (i.e., lines with codes starting with BPX-196-). The remaining lines were derived from crosses which involved Rey de Los Tempranos as source of TSWV resistance and cv. Angela Gigante I-5100 as the recurrent parent. Lines BPX-199-04C, BPX-199-08C and BPX-199-16C are F_4 lines whose F_3 counterparts were tested in the Summer 1986/87 trial; they represent the 1st backcross generation to the recurrent parent Angela Gigante I-5100. Lines whose codes start with BPX-276-04D,

BPX-276-08D and BPX-276-16D were derived respectively from BPX-199-04B, BPX-199-08D and BPX-199-16B, after one additional backcross to the Angela background.

It is clear from comparison of the check treatment means in this trial (Table III) with the means of the same treatments in previous (Tables I and II) that TSWV incidence may vary from year to year, but the ranks of the susceptible checks Rio Fuego and Angela Gigante relative to the resistant check Rey de Los Tempranos do not vary: the resistance of Rey de Los Tempranos is evident both in years of low (Table II) and high (Tables I and III) spotted wilt incidence.

The F_6 line BPX-198-03D, derived from *L. pimpinellifolium*, confirmed in this trial (Table III) the performance of its F_5 counterpart in the previous year (Table II), with a lower TSWV disease rating than Rey de Los Tempranos. Two lines issued from crosses with *L. hirsutum* "PI 127826" (BPX-196-11D pl#06 and BPX-196-11D pl#02) also showed resistance levels comparable to that of Rey de Los Tempranos. These are indications of progress in the introgression of resistance genes from those two wild accessions into a *L. esculentum* background.

Of the three first backcross lines with resistance issued from Rey de Los Tempranos, only one (BPX-199-08C) had a resistance level comparable to the latter. The other two lines (BPX-199-04C and BPX-199-16C) had reactions intermediate between Rey de Los Tempranos and Angela Gigante I-5100. Second backcross lines (BPX-276-) derived from those three ranged from as susceptible as Angela Gigante I-5100 to as resistant or more so than Rey de Los Tempranos. Eleven of these second backcross lines had lower TSWV infection ratings than the resistant parent.

Winter/Spring 1988 trial: Evaluation of TSWV resistance in breeding lines issued from crosses with Reys de Los Tempranos

Seventeen of the second backcross breeding lines issued from crosses with Reys de Los Tempranos, and previously shown to have a level of TSWV resistance comparable to that of the latter (Table III) were included in a trial in the Winter/Spring season of 1988 (Table IV). Susceptible cultivars Angela Gigante I-5100 and Santa Clara were also included in the trial as checks. Plants were rated individually as in the previous trials. The number of plants evaluated per line ranged from 31 to 55. The transplanting date was July 8, 1988, and evaluations were made 90 days later, i.e., when fruit from the first trusses began to ripen.

The results in Table IV are consistent with those of the previous trial (Table III). All of the 17 BPX-276- lines proved to be resistant to TSWV (ratings between 1.1 and 1.6), whereas Angela Gigante I = 5100 and Santa Clara again proved susceptible (rated 3.9 or higher). All 17 lines are from the second backcross to an Angela

Gigante background, and therefore have a reasonable degree of isogenicity (87.5%) to the recurrent parent. Therefore, the differences in spotted wilt ratings between the lines and the recurrent parent cannot be accounted for by differences in the genotypic background, and demonstrate that the gene or genes for TSWV resistance in Rey de Los Tempranos were successfully introgressed into an Angela Gigante I-5100 background.

Table IV - Tomato spotted wilt ratings in *Lycopersicon* cultivars and breeding lines grown under epiphytotic conditions. Paulinia County, State of São Paulo, Brazil. Winter/Spring 1988 (1 - no symptoms; 5 = plants dead or severely necrosed).

Line/Cultivar[a]	% Plants with scores					
	1	2	3	4	5	Plot mean
BPX-276-04D pl#21	68	20	8	4	0	1.5
BPX-276-08D pl#02	83	13	4	0	0	1.2
BPX-276-08D pl#06	75	17	3	6	0	1.4
BPX-276-08D pl#07	91	9	0	0	0	1.1
BPX-276-08D pl#14	79	18	3	0	0	1.2
BPX-276-08D pl#15	94	0	6	0	0	1.1
BPX-276-08D pl#26	94	0	6	0	0	1.1
BPX-276-08D pl#27	64	21	11	2	2	1.6
BPX-276-08D pl#28	94	4	2	0	0	1.1
BPX-276-08D pl#33	70	11	15	4	0	1.5
BPX-276-08D pl#34	77	21	2	0	0	1.3
BPX-276-16D pl#06	77	13	10	0	0	1.3
BPX-276-16D pl#08	75	20	3	3	0	1.3
BPX-276-16D pl#16	79	8	11	3	0	1.4
BPX-276-16D pl#30	81	19	0	0	0	1.2
BPX-276-16D pl#31	82	16	3	0	0	1.2
BPX-276-16D pl#55	87	7	5	0	0	1.2
Angela Gigante I-5100	0	5	32	30	34	3.9
Santa Clara	(only scores 3, 4 and 5)					> 4.0[b]

[a] BPX-276- designates TSWV-resistant F_3 lines issued from the cross Angela Gigante I-5100 x Rey de Los Tempranos, after two additional backcrosses to Angela.

[b] Precise ratings not available, due to the fact that many plants died much before the evaluation date.

All 17 second backcross lines can be considered homozygous for TSWV resistance. Nevertheless, a few plants in these lines showed symptoms ratings of 4 or 5 (generalized necrosis or plant death), repeating the performance of the resistant parent Rey de los Tempranos in previous years (Tables I, II and III). The resistance gained from Rey de Los Tempranos is therefore not absolute immunity, but rather a tolerance type of resistance, functional in the sense of delaying symptom expression and escaping economic damage. In fact, observations made ca. 20 days after the evaluation date indicated that most plants of the resistant lines showed TSWV symptoms, but by then the harvests were essentially over, and no major loss in yield was evident.

Five of these 17 TSWV resistant lines, that were phenotypically stable for fruit shape and similar to Angela Gigante I-5100, were selected for further testing.

Summer 1988/89 trial: Evaluation of TSWV resistance in cultivars and in breeding lines issued from crosses with Rey de Los Tempranos, L. pimpinellifolium "PI 732293-2V", L. hirsutum "PI 127826" or L. hirsutum var. glabratum "PI 134417"

Three susceptible (Angela Gigante I-5100, Santa Clara, and Nemadoro) and one resistant cultivar (Rey de Los Tempranos) were tested during the Summer of 1988/89 in a randomized complete block design with three replications, along with 14 other populations and breeding lines. These included lines issued from crosses of commercial cultivars with *L. hirsutum* var. *glabratum* "PI 134417", *L. hirsutum* "PI 127826", *L. pimpinellifolium* "PI 732293-2V", and *L. esculentum* "Rey de Los Tempranos", in addition to populations known to be heterozygous for TSWV resistance (Table V). Plots comprised 20 plants each, and peanuts were sown between the tomato rows as before. Plants were rated individually as in the previous trials, at two different evaluation dates: on April 28 (early flowering stage) and on May 5, 1989.

The examination of treatment means (Table V) indicates that cultivars Nemadoro and Santa Clara are clearly susceptible, contrasting with Rey de Los Tempranos. The cultivar Angela Gigante I-5100, however, had a disease incidence rating intermediate between Rey de Los Tempranos and Nemadoro or Santa Clara, and did not differ significantly from either the resistant accession or the susceptible checks (Table VI). The lower susceptibility of Angela Gigante I-5100 relative to other susceptible cultivars displayed in the Summer of 1986/87 appears to be confirmed, but cannot be relied upon to effectively control TSWV, because visible reduction in yield is nonetheless evident.

Table V - Mean separation (Duncan test, prob. = 0.05) for TSWV scores of different tomato cultivars and breeding lines grown under epiphytotic conditions, and measured on two different dates. Paulinia County, State of São Paulo, Brazil. Summer 1988/89 (1 = no symptoms; 5 = plants dead or severely necrosed).

Treatments	Mean squares for	
	Scores on April 28	Scores on May 5
Angela Gigante I-5100	2.6 bcde	2.8 abcde
Santa Clara	3.4 a	3.6 a
Nemadoro	2.7 abc	3.4 ab
Rey de Los Tempranos	1.7 fg	2.0 def
BPX-270A pl#36[a]	2.4 bcdef	2.5 bcdef
BPX-285-02A pl#03[c]	1.6 g	1.8 ef
BPX-285-01A pl#16[c]	2.0 defg	1.7 f
BPX-275-2C[b]	1.5 g	1.7 f
BPX-296[d]	2.1 cdefg	2.2 cdef
BPX-198-3E[e]	1.9 efg	2.3 cdef
BPX-285-02A pl#20[c]	1.6 g	1.9 ef
F_1 (Santa Clara x BPX-276-bu-D)[f]	2.9 ab	3.0 abcd
F_1 (Nemadoro x BPX-276-bu-D)[f]	2.6 bcd	3.2 abc
BPX-276-16E pl#31[f]	1.8 fg	2.1 def
BPX-276-08E pl#34[f]	1.5 g	1.7 f
BPX-276-08E pl#02[f]	1.5 g	1.9 def
BPX-276-16E pl#55[f]	2.1 cdefg	2.2 cdef
BPX-276-08E pl#28[f]	1.8 efg	2.5 bcdef

[a] Population issued from a cross of a Flora-Dade background breeding line with a TSWV-resistant single F_2 plant of (*L. esculentum* x *L. hirsutum* var. *glabratum* "PI 134417"); heterozygous for the resistance issued from PI 134417.

[b] F_5 line issued from the 1st backcross to *L. esculentum* of the F_1 (*L. esculentum* x *L. hirsutum* "PI 127826").

[c] F_3 line issued from the 2nd backcross to *L. esculentum* of the F_1 (*L. esculentum* x *L. hirsutum* "PI 127826").

[d] F_1 of a TSWV-susceptible line (with an Angela Gigante I-5100 background) with a pool of TSWV-resistant lines with the same genotypic background.

[e] F_7 line issued from a cross of *L. esculentum* "Calypso x *L. pimpinellifolium* "PI 732293-2V".

[f] BPX-276- designates TSWV-resistant F_4 lines issued from the cross Angela Gigante I-5100 x Rey de Los Tempranos, after two additional backcrosses to Angela; BPX-276-bu-D designates a pool of plants from several of these lines.

Table VI - Significance of different contrasts for TSWV incidence measured on May 5, 1989. Paulinia County, State of São Paulo, Brazil. Summer 1988/89.

Source	d.f.	Mean squares[(b)]
Contrasts[(a)]		
BPX-276 vs. Angela	1	1.391 *
BPX-276 vs. BPX-296	1	0.046 ns
BPX-276 vs. Rey de Los Tempranos	1	0.0206 ns
Angela vs. Rey de Los Tempranos	1	1.050 ns
Angela vs. (S. Clara # Nemadoro)	1	0.848 ns
Angela vs. BPX-296	1	0.558 ns
S. Clara vs. F_1 (S. Clara x BPX-276-bu-D)	1	0.528 ns
Nemadoro vs. F_1 (Nemadoro x BPX-276-bu-D)	1	0.036 ns
Homoz. susceptible vs. Heterozygotes	1	0.923 ns
Homoz. resistant vs. Heterozygotes	1	3.305 **
BPX-198 vs. Angela	1	0.465 ns
BPX-198 vs. (Angela + S. Clara + Nemadoro)	1	2.210 *
BPX-198 vs. Rey de Los Tempranos	1	0.117 ns
BPX-285 + 275 vs. Angela	1	2.724 **
BPX-285 + 275 vs. (Angela + S. Clara + Nemadoro)	1	11.56 ***
BPX-285 + 275 vs. Rey de Los Tempranos	1	0.125 ns
BPX-270 vs. Angela	1	0.206 ns
BPX-270 vs. (Angela + S. Clara + Nemadoro)	1	1.456*
BPX-270 vs. ReY de Los Tempranos	1	0.326 ns
Error	34	0.306

(a) Codes: Angela = Angela Gigante I-5100; S. Clara = Santa Clara; BPX-276 = designates the set of the five TSWV-resistant F_4 lines issued from the cross Angela Gigante I-5100 x Rey de Los Tempranos, after two additional backcrosses to Angela; BPX-276-bu-D designates a pool of plants from several of these lines; BPX-296 = F_1 of a TSWV = susceptible line (with an Angela Gigante I-5100 background) with a pool of TSWV-resistant lines with the same genotypic background; BPX-198 = designates line BPX-198-3E, an F_7 line issued from a cross of *L. esculentum* "Calypso" x *L. pimpinellifolium* "PI 732293-2V"; BPX-285 + 275 = designates a set of three lines BPX-285- and 1 line BPX-275-, all of them with TSWV resistance issued from *L. hirsutum* "PI 127826"; BPX-270 = designates BPX-270A pl#36, a population issued from the cross of a Flora-Dade background breeding line with a TSWV-resistant single F_2 plant of (*L. esculentum* x *L. hirsutum* var. *glabratum* "PI 134417"); heterozygous for the resistance issued from PI 134417. Homoz. resistant vs. Heterozygotes = designates the contrast between Reys de Los Tempranos and its five TSWV resistant derivative lines (BPX-276-) vs. the correspondent heterozygotes for TSWV resistance [BPX-296, F_1 (S. Clara x BPX-276-bu-D) and F_1 (Nemadoro x BPX-276-bu-D)]. Homoz. susceptible vs. Heterozygotes = designates the contrast between the homogyous susceptible cultivars Angela Gigante I-5100, Santa Clara and Nemadoro vs. their respective heterozygotes for the Rey de Los Tempranos TSWV resistance [BPX-296, F_1 (S. Clara x BPX-276-bu-D) and F_1 (Nemadoro x BPX-276-bu-D)].

(b) ns = non-significant at the 0.05 level; * = significant at the 0.05 level; ** = significant at the 0.01 level; *** = significant at the 0.001 level.

The level of TSWV resistance of the breeding lines BPX-276-16E pl#31, BPX-276-16E pl#55, BPX-276-08E pl#02, BPX-276-08E pl#34 and BPX-276-08E pl#28 was comparable to that of Rey de Los Tempranos, indicating that resistance traits from the former were successfully transferred from the latter to an Angela background. The resistance of these five F_4 lines or their earlier generation counterparts was therefore confirmed in at least three trials (Tables III, IV and V), indicating that the lines are indeed fixed for the Rey de Los Tempranos source of resistance. The gene or genes controlling this resistance appear to be recessive: the F_1 (Santa Clara x BPX-276-bu-D) and the F_1 (Nemadoro x BPX-276-bu-D) are as susceptible to TSWV as their respective susceptible parents Santa Clara and Nemadoro (Tables V and VI). These results for the Santa Clara and Nemadoro backgrounds appear to contrast with those obtained with the Angela background, where the heterozygote (BPX-296) had a disease rating comparable to that of the TSWV resistant lines; however, this apparently contradictory result can be accounted for by the lower susceptibility of Angela Gigante I-5100 relative to Santa Clara and Nemadoro (Tables V), already reported in the Summer of 1986/87 trial (Table II): the heterozygote BPX-296 did not differ statistically from either the resistant lines BPX-276- or the susceptible parent Angela (Table VI). We cannot exclude the hypothesis that the modifier genes responsible for the lower TSWV susceptibility in the Angela background render gene action of the genes issued from Rey de Los Tempranos dominant rather than recessive.

Another line heterozygous for TSWV resistance is BPX-270A pl#36, whose resistance source was *L. hirsutum* var. *glabratum* "PI 134417". Its performance is comparable (Tables V and VI) to that of Rey de Los Tempranos or the BPX-276- lines, indicating a degree of dominance for the resistance genes issued from the wild parent, at least in the background of the recurrent *L. esculentum* lines used in the crosses (Tropic and Flora-Dade).

Lines BPX-275-2C and its derivatives BPX-285-02A pl#03 and BPX-285-02A pl#16, with the *L. hirsutum* "PI 127826" source of resistance, had disease ratings comparable to those of Rey de Los Tempranos or the BPX-276- lines, indicating that we were able to recover acceptable levels of resistance even after two backcrosses to *L. esculentum*.

The resistance of line BPX-198-03E derived from crosses with *L. pimpinellifolium* "PI 732293-2V" was confirmed again in this trial (Tables V and VI), repeating the performance of its earlier generation predecessors in the Summer of 1986/87 (Table II) and in the Summer of 1987/88 (Table III) trials.

DISCUSSION

Five sources of resistance to TSWV were identified in the genus *Lycopersicon*, one in the cultivated species (*L. esculentum* "Rey de Los Tempranos") and four in wild accessions (*L. pimpinellifolium* "PI 732293-2V", *L. hirsutum* var. *glabratum* "PI 134417", *L. hirsutum* "PI 127826" and *L. peruvianum* "LA 444-1"). With the exception of *L. peruvianum*, all resistant accessions were used in crosses and backcrosses to *L. esculentum* cultivars during the period of 1986 through 1989.

The cultivar Angela Gigante I-5100 is doubtless susceptible to TSWV, but in years of low disease incidence (Tables II and V) it tends to show a lower degree of susceptibility to TSWV than cultivars such as Santa Clara and Nemadoro. It is possible that the modifier genes in Angela responsible for the lower TSWV incidence may interact with resistance genes issued from the sources of resistance, e.g., rendering the genes issued from Rey de Los Tempranos dominant in the Angela background, in spite of being recessive in the Santa Clara and Nemadoro backgrounds (Tables V and VI). These modifiers in the Angela background may prove useful to obtain higher levels of TSWV resistance issued from the sources under study, should Angela be chosen as a recurrent parent.

During 1986-89, five advanced breeding lines (BPX-276-16E pl#31, BPX-276-16E pl#55, BPX-276-08E pl#02, BPX-276-08E pl#34 and BPX-276-08E pl#28) were developed that, in addition to a TSWV resistance level comparable to Rey de Los Tempranos, were shown to bear essentially the same horticultural quality as the susceptible recurrent parent Angela Gigante I-5100. The resistance level of these lines was confirmed in at least three field trials over a two year period (Tables III, IV and V). The resistance obtained from Rey de Los Tempranos is apparently controlled by a recessive gene(s), a result consistent with the conclusions of Upreti and Hartmann (1984).

Our results, as far as the resistance issued from Rey de Los Tempranos is concerned, agrees with results by Upreti and Hartman (1984) in Hawaii, but disagree with those of Paterson *et al.* (1989) in Arkansas. The latter suggest that the discrepancy may be due to the different TSWV isolates utilized. However, a careful examination of their paper reveals that the differences can be accounted for by different methodologies in the evaluation of resistance: Paterson *et al.* (1989) considered resistant only those plants that were without symptoms and which tested negative for the enzyme-linked immunosorbent assay (ELISA) test, after two artificial inoculations with TSWV. Their criterion may be too drastic to detect mechanisms of resistance other than immunity, leaving out accessions such as Rey de Los Tempranos, which has a tolerance type resistance, functional in the sense of delaying symptom expression and escaping economic damage. Our results, as well as those or Upreti

and Hartmann (1984), are based on a scale of symptoms, and they agree entirely. In fact, if symptoms alone are considered, the data of Paterson *et al.* (1989) also agree with ours, since the percent plants without symptoms is significantly lower for Rey de Los Tempranos than for any other *L. esculentum* line they tested except Hawaii 8411 (probably another resistant accession that went undetected with their methodology).

All of our trials were conducted in the field under natural infection conditions, sometimes using peanuts as spreader rows for the thrips vectors. Resistance proved to be stable over the years, even considering putative variations in the viral isolates and/or intensity of disease incidence from year to year. Resistant breeding lines derived from crosses with susceptible *L. esculentum* cultivars could be obtained from all sources of resistance, indicating that there has been progress in the introgression of the genes for resistance from these sources.

RESUMO

Dentre 32 acessos de *Lycopersicon* spp. testados para resistência ao virus do vira-cabeça do tomateiro no município de Paulínia em 1985/86, cinco se revelaram úteis como fontes de resistência à doença: *L. peruvianum* "LA-444-1", *L. hirsutum* "PI 127826", *L. hirsutum* var. *glabratum* "PI 134417", *L. pimpinellifolium* "PI 732293-2V" e *L. esculentum* "Reys de Los Tempranos". Populações segregantes e linhagens derivadas de cruzamentos de cultivares comerciais de tomate com os acessos resistentes a TSWV foram avaliadas numa série de experimentos nos anos de 1986 a 1989. Estas populações e linhagens derivam de cruzamentos com "Rey de Los Tempranos", "PI 732293-2V", "PI 127826" and "PI 134417". Ênfase foi colocada nas populações que tinham como fonte de resistência Rey de Los Tempranos, a única fonte de resistência encontrada dentro de *L. esculentum*. Em 1988, foram selecionadas 5 linhagens avançadas que aliavam um nível de resistência comparável ao de Rey de Los Tempranos a caracteres hortícolas comparáveis a Angela Gigante I-5100. Em 1989, a performance superior destas linhagens avançadas foi confirmada em experimento com repetições. Há indicações de que a resistência derivada de Rey de Los Tempranos seja controlada por alelo(s) recessivo(s).

REFERENCES

Araújo, M.T., Avila, A.C., Cupertino, F.P. and Maluf, W.R. (1983). (*L. hirsutum*) nova fonte de resistência ao virus do vira-cabeça (TSWV). In: *Congresso Brasileiro de Olericultura*, 23. *Resumos*. Rio de Janeiro.

Best, R.J. (1968). Tomato spotted wilt virus. *Adv. Virus Res. 13*: 65-146.

Costa, C.L., Costa, A.S. and Nagai, H. (1977). Controle de vira-cabeça do tomateiro pela destruição do vetor. III. Efeito de inseticida sistêmico granulado combinado com pulverizações. *Fitopatol. Brasil. 2*: 23-24.

Cupertino, F.P., Avila, A.C., Araújo, M.T. and Kitajima, E.W. (1981). Caracterização de isolados de vira-cabeça para emprego em programa de melhoramento do tomateiro. *Fitopatol. Brasil. 6*: 525.

Cupertino, F.P., Avila, A.C., Araújo, M.T. and Maluf, W.R. (1986). Fontes de resistência ao virus de vira-cabeça em *Lycopersicon. Fitopatol. Bras. 11*: 330.

Eskes, A.B. and Nagai, H. (1981). Nova fonte de resistência ao vírus de vira-cabeça do tomateiro, derivada de *Lycopersicon pimpinellifolium* (Jusl.) Mill. In: *Congresso Brasileiro de Olericultura*, 21., Campinas, 1981. *Resumos*. Campinas, SOB, 1981. p. 164.

Finlay, K.W. (1952). Inheritance of resistance to spotted wilt virus in tomato. I. Identification of strains of the virus by the resistance or susceptibility of tomato species. *Australian J. Scientific research 5*: 303-314.

Finlay, K.W. (1953). Inheritance of spotted wilt resistance in the tomato. *Austr. J. Biolog. Sci. 6*: 153-163.

Francki, R.I.B. and Hatta, T. (1981). Tomato spotted wilt virus. In: (Kurstak, E., ed.). *Handbook of Plant Virus Infections and Comparative Diagnosis*. Chapter 17. p. 491-512.

Ie, T.S. (1970). Tomato spotted wilt virus. *Commonwealth Mycological Institute/Association of Applied Biologists (C.M.I./A.A.B.). Description of Plant Viruses No. 39*. 4p.

Kikuta, K., Hendrix, J.W. and Frazier, W.A. (1945). Pearl Harbor, a tomato variety resistant to spotted wilt in Hawaii. *Circular 24. University of Hawaii Agricultural Experiment Station*.

Peterson, 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.

Upreti, G. and Hartmann, R.W. (1984). Inheritance of resistance to spotted wilt virus in tomato. *IAAS (Institute of Agriculture and Animal Science) Journal (Nepal) 4*: 19-25.

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