scribed above is presented in graphic form in Fig. 1.

Having *ms-10* bracketed by two selectable markers overcomes the previously outlined problems encountered when trying to use male-sterility for hybrid seed production. Tight linkage with the codominant *Prx-2* marker allows one to make successive backcrosses to lines into which the male-sterility gene is being introduced by selecting on the basis of the *Prx-2* genotypes without having to make progeny tests to score the male-sterile phenotype directly. The procedure reduces the number of generations for such transfer, resulting in a savings of time and resources. With such tight linkage between *Prx-2* and *ms-10* ($\approx$ 1 cM), seven successive backcrosses can be made, with a 90% chance of maintaining the recessive sterility gene in the resulting line. The success of the transfer can be checked by assaying progeny for the linked anthocyaninless character. Since the two marker genes bracket the male-sterile gene, it is extremely unlikely that plants would carry both the peroxidase and the anthocyanin markers, but have lost the male-sterile gene. Such an event would require a double crossover, which would be expected to occur only once in $\approx$5000 plants.

Once the male-sterile gene has been transferred into a prospective parental line, sterile plants can be selected at the seedling stage either from backcross or F_2 seed lots. Assuming a 5-cM map distance between *ms-10* and *aa*, the percentage of escapes (fertile anthocyaninless seedlings) would be 5% in the backcross and 10% in the F_2. Thus, populations that are 95% or 90% sterile, respectively, could be transplanted to the field to use as seed parents for hybrid production. Remaining fertiles (recombinants) would have to be rogued at anthesis. Without use of the *aa* selection, 50% (backcross) and 75% (F_2) of the field plants would otherwise be fertile and have to be rogued.

It is likely that hybrids will continue to play an important role in tomato production. With the rising costs of labor required for hand emasculation, there is increasing incentive to develop an efficient and reliable male-sterility system in this crop. The above described research takes several known components of tomato genetics, namely genic male-sterility (*ms-10*), a morphological marker (*aa*), and an isozyme marker (*Prx-2*), and combines them in a selection scheme that removes many of the obstacles to using genic male-sterility for production of hybrid tomato seed.

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Verticillium Wilt Resistance in Eggplant, Related *Solanum* Species, and Interspecific Hybrids

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Abstract. **No significant resistance to verticillium wilt (*Verticillium dahliae* Kleb) was found in 59 eggplant (*Solanum melongena* L.) accessions, in a sexual hybrid between *S. melongena* and *S. integrifolium*, or in eight somatic hybrid clones between *S. melongena* and *S. sisymbriifolium*. A relatively high degree of resistance was observed in accessions of *S. aculeatissimum*, *S. scabrum*, and *S. sisymbriifolium*. All 58 accessions of *S. gilo* tested were susceptible, as were all accessions of *S. incanum*, *S. integrifolium*, *S. laciniatum*, *S. macrocarpum*, *S. mammosum*, and *S. nodiflorum*.**

Verticillium wilt of eggplant, caused by *Verticillium dahliae* Kleb, often is severe in tropical and temperate areas and is an important limiting factor in production of the crop (3, 9, 10, 18, 19, 22). Resistance to the wilt among eggplant cultivars varies, and some cultivars have been used as sources of resistance in breeding programs (10–12, 23). None, however, has sufficiently high resistance under field conditions to control the disease adequately. The apparently complex inheritance of resistance (13) and the variable virulence of the fungus (12) have made the development of commercial eggplant cultivars with reliable resistance to verticillium wilt a recurring goal in several breeding programs for many years.

Nontuberous species of *Solanum,* including near and distant relatives of eggplant, have been considered as possible sources of wilt resistance. Among them, *S. gilo, S. integrifolium, S. sisymbriifolium,* and *S. torvum* have been identified as valuable (4, 9, 15, 22, 24). Nothmann and Ben-Yephet (19) evaluated 340 eggplant accessions and 14 related species under greenhouse conditions. They found no vertical resistance, but different degrees of disease severity were observed in the hot and in the cool season. Few reports of evaluations of wilt resistance in interspecific hybrids exist between eggplant and its relatives (15, 24). In many cases, sexual crosses have not been possible, and, where they were, sterile hybrids have been produced (17). Where relationships are distant, cell culture offers possibilities of hybridization. Somatic hybrids have been produced with *S. melongena* and *S. sisymbriifolium,* and resistances to nematodes and mites have been transferred (5, 7).

Past evaluations of eggplant germplasm accessions have noted many with varying degrees of resistance (1, 2, 9, 10–12, 19, 20, 25). We have tested again those accessions, tested 33 additional eggplant introductions in the USDA germplasm collection not previously screened for resistance, and extended our observations to include 12 other related species. We also have included in our evaluations eight clones of the somatic hybrid *S. melongena* x *S. sisymbriifolium* produced by Gleddie et al. (8). They were kindly furnished by W. Keller (Agriculture Canada, Ottawa).

Verticillium isolate S202 was kindly furnished by S. Wilhelm (Univ. of California, Berkeley). It was obtained originally form diseased strawberry roots grown from single conidia and, when cultured in potato dextrose agar (PDA), produced microsclerotia. Spores for inoculations were produced by placing a 1-cm-diameter section from a PDA culture of the fungus in flasks containing 500 ml of potato dextrose broth (PDB). The culture was shaken on a rotary shaker for 2 weeks at 26° to 28°C and filtered through several layers of cheesecloth. The spores were sedimented by centrifugation at $\approx 6000 \times g$ for 15 min and resuspended in distilled water at 3×10^6 spores/ml.

Seeds were germinated in an equal mixture of vermiculite, perlite, and peat in

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Table 1. Response of *Solanum* spp. to infection by wilt pathogen *V. dahliae* isolate S202 by the root immersion method.

	Disease severity	
Species[y]	Height[x]	Foliar[w] symptoms
S. aculeatissimum		
PI 183949	95 a	1.2 d
PI 331063	78 b	1.5 c
PI 312108	58 c	1.5 c
PI 308877	56 c	1.5 c
S. gilo		
58 accessions (PIs)	37 de	2.5 b
S. incanum		
PI 381155	27 f	3.4 a
PI 390211	30 ef	3.4 a
S. integrifolium		
PI 374695	31 ef	2.9 ab
S. laciniatum		
PI 337310	24 f	2.0 bc
PI 337284	28 f	2.0 bc
S. macrocarpum		
Acc. 256	49 d	3.3 a
S. melongena		
26 accessions (PIs)	69 c	2.6 b
33 accessions (mostly PIs)	34 e	3.2 a
S. melogena + *S. integrifolium*		
hybrid VF (F1)	59 c	2.8 b
S. nodiflorum		
Acc. 85-16	35 e	2.0 bc
PI 247828	40 d	2.3 b
S. scabrum		
Acc. 2161	58 c	1.1 d
S. sisymbriifolium		
PI 381291	74 b	1.2 d
PI 424861	79 b	1.2 d
PI 331140	73 bc	1.0 d
PI 337597	74 b	1.0 d
PI 358311	75 b	1.1 d
Acc. 2501	100 a	1.3 d
S. mammosum		
PI 245968	41 d	3.0 a
PI 305323	31 e	2.8 b
PI 370045	38 de	3.1 a
S. torvum		
Acc. 3708	67 c	1.7 c
Acc. 4	64 c	1.4 c
Acc. 85-22	62 c	1.5 c

[z]Means separated by Duncan's multiple range test $P = 5\%$.

[y]Species sources = PI; Plant Introduction Station, Experiment, Ga.; Acc. 256 (*S. macrocarpum*), New York State Agricultural Experiment Station, Geneva (NYSAES); 26 accessions of *S. melongena* reported in the literature as resistant or tolerant (1, 2, 11–13, 20); 33 accessions received at the Plant Introduction Station after 1979 and not previously screened and cultivars obtained through private sources; *S. nodiflorum* Acc. 85-16, NYSAES; *S. scabrum* Acc. 2161, Gredina Botanica Cluj, Romania; *S. sisymbriifolium* Acc. 2501, Zentralinstitut für genetik und Kulturpflanzen Forschung, Gatersleben, G.D.R.; *S. torvum* Acc. 3708, Jardin Botanique l'Univ. L. Pasteur de Stratsbourg, France; Acc. 4, Takii seed Company, Kyoto, Japan; hybrid VF = sexual cross F1 between *S. melongena S. integrifolium* (27).

[x]Height = mean percent of controls.

[w]Foliar symptoms = 1, very slight wilt and/or yellowing of cotyledons and lowest two leaves; 2, half of total leaves wilted, yellowing or necrotic; 3, three-fourths of total leaves affected; 4, plants killed or dying.

wooden nursery flats. Seedlings were removed 20 to 40 days later. Their roots were washed in tap water and 1 cm was cut from the root tips and immersed for 1 hr in the spore suspension or in distilled water. The treated seedlings were planted 2 cm apart in rows in nursery flats containing the same soil mixture. In some tests, the fungus was introduced by injection into the lower stem of plants that were individually potted or in rows in nursery flats. Four punctures were made near the soil line, and ≈1 ml was introduced, although some of the liquid inevitably dripped out of the punctures. There were usually no less than 10 inoculated plants per accession in each test, and any accession found having some degree of resistance was tested again during 1-year period. The tests were made under greenhouse conditions with temperatures varying from 26° to 32°C.

Somatic hybrids 3b, 6, 7, 10, 12, 13, 14, and 16, produced from protoplast fusion of *S. melongena* and *S. sisymbriifolium* (8), were maintained axenically as vegetative cuttings on MS (16) or B5 (6) basal agar media at 26° to 28°C under 16 hr of fluorescent light with 1132 μW·cm^{-2} intensity. They were transferred to individual pots with the perlite–vermiculite–peat mixture and maintained in the greenhouse until established, usually 2 to 3 months, before inoculation. They were inoculated by the two methods described previously.

Disease incidence was evaluated in terms of severity of foliar symptoms and reduction of plant height as compared with control plants. Foliar symptoms were rated on a 0 to 4 scale, in which 0 = no disease; 1 = slight wilt and yellowing of the cotyledons and lowest leaves; 2 = at least 50% of the leaves wilted, yellowing, or necrotic; 3 = at least 75% of the leaves wilted, yellowing, or necrotic; and 4 = plants killed or almost dead from the infection. Effects on plant height were determined in terms of percent height compared with checks. Disease severity ratings were made 1 month after inoculation, when seedlings were usually 2 months old, and on somatic hybrid clones usually 3 to 4 months after establishment in the greenhouse.

The following eggplant accessions previously reported to have some degree of resistance were tested with isolate S202 using 1-month-old plants: PIs 169650, 169666, 171851, 176759, 204731 (1); 169640, 169651, 180485, 194166 (2); 286099, 286103, 286106, 286107, (13); 120796, 116677, 164941, 167328, 167381, 169667, 173104, 174362, 176761 (11, 12); 164458, 381160, 381166, 320504 (20). They had a mean disease rating of 2.6, with one-half to three-fourths of their leaves either wilted or with yellowing or necrotic areas (Table 1). In some instances, plants had severe foliar symptoms but were not stunted. Accessions of eggplant not previously screened had a more severe mean foliar disease rating of 3.2 and their height was more affected (Table 1) than those that had been screened. The following accessions were tested: 'Black Magic', 'Rosita', 'Habota', 'Kumamoto', 'Mutsumoto', and 'Sudowara'; and PIs 430568, 430664-72, 436679, 436680, 452122-24, 462370-73, 476415, 478388-94.

Table 2. Response of somatic hybrids of *Solanum melongena* x *S. sisymbriifolium* inoculated by injection with *V. dahliae* isolate S202.

	Characteristics of disease development[z]	
Clone	Height[y]	Foliar symptoms[x]
3b	65.6 d	3.0 a
6	86.5 bc	2.7 b
7	119.6 a	2.0 c
10	71.9 d	2.2 bc
12	81.4 c	2.6 b
13	97.4 b	2.0 c
14	68.7 d	2.7 b
16	101.5 b	2.2 bc

[z]Means separated by Duncan's multiple range test, $P = 5\%$.

[y]Height: mean percent of controls.

[y]Foliar Symptoms: 1, very slight wilt and/or yellowing of cotyledons and the two lowest leaves; 2, half of total leaves wilted, yellowing, or necrotic, 3, three-fourths of total leaves affected; 4, plants killed or dying.

All accessions of *S. gilo* (194166, 420226, 420230, 424859, 424866, 441839, 441841, 441847, 441848, 441853, 441859, 441862, 441872, 441908, 441874 to 441893, 441896 – 441909, and 441912) were susceptible, as was the sexual hybrid VF of *S. melongena* x *S. integrifolium* (Table 1). All accessions of *S. sisymbriifolium* developed very light foliar symptoms, which were limited to a delayed yellowing of a few leaves that occasionally was associated with wilting. Infection in *S. sisymbriifolium* accessions often limited plant height by 25% as compared to the controls, except for accession 2501, in which height was not affected in three trials. Three other species, *S. aculeatissimum, S. scabrum,* and *S. torvum* also showed a relatively high degree of resistance. *Solanum gilo, S. incanum, S. integrifolium, S. laciniatum, S. macrocarpum, S. mammosum,* and *S. nodiflorum* developed moderate to severe symptoms of disease (Table 1).

Roots of the somatic hybrid clones were weak and limited in growth, making the root immersion method less suitable for inoculations than stem injections. When stem injection was used, disease developed in all clones and none had the high resistance shown by accessions of *S. sisymbriifolium* (Table 2).

We found all eggplant accessions tested to be susceptible to verticillium wilt. Some accessions were more affected than others, but none, however, showed the relatively high resistance of *S. sisymbriifolium, S. aculeatissumum,* and *S. torvum.* The accessions of *S. gilo* found resistance by Silveira et al. (22) were susceptible under our greenhouse test conditions.

The resistance to wilt demonstrated by *S. sisymbriifolium* was, unfortunately, not expressed in somatic hybrid clones resulting from protoplast fusion between *S. melongena* and *S. sisymbriifolium.* The sterility of the somatic hybrids, their weak root system (8), and their lack of wilt resistance may make a selective transfer of genetic characters more appealing, perhaps through such vectors as *Agrobacterium tumefaciens* (14) or by direct transfer of hybrids genes (21). We found several related species to have significant degrees of resistance to verticillium wilt when tested under greenhouse conditions. Additional tests, preferably conducted under field conditions, are still needed to determine if the resistant species related to eggplant are suitable donors of verticillium wilt resistance.

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