Sources of resistance to early blight, *Alternaria solani,* and transfer to tomato, *Lycopersicon esculentum*[1]

Franklin W. Martin and Paul Hepperly[2]

ABSTRACT

Tomato entries reported as early blight resistant were collected and evaluated under severe early blight infection in the warm rainy summer months of 1982-1985 in Mayagüez, Puerto Rico to identify sources with useful resistance in Puerto Rico. Of the common tomato lines, 84B 510-4 was the closest in resistance to the best wild tomato species, which are less susceptible to early blight than common tomatoes. Useful field resistance was found in the minority of cases, but one or more entries of *L. esculentum* f. *cerasiforme, L. pimpinellifolium, L. esculentum* X *L. pimpinellifolium,* and *L. hirsutum* var. *typicum* showed useful early blight resistance. Lowest disease ratings were found in varieties of *L. hirsutum,* which also showed the lowest yield. Better fruiting was found in *L. pimpinellifolium* although resistance levels were slightly less. Crosses of *L. pimpinellifolium* and *L. hirsutum* with useful early blight resistance to susceptible *L. esculentum* were followed in F_1, F_2, and F_3 generations. Resistance appeared partially dominant from F_1 disease ratings, and segregation in F_2 suggested that many modifying genes both dominant and recessive were probably involved in conditioning early blight resistance. Generally, common tomatoes appear much more susceptible to early blight than wild species. To enlarge the pool of early blight resistence genes, F_2 selection and progressive back crosses are suggested. Susceptible tomatoes were defoliated by early blight within one month after first flower during the warm rainy months; whereas, entries with useful resistance defoliated from 6 weeks to 2 months after the same stage.

INTRODUCTION

A susceptible host, a well distributed and adapted pathogen, and an environment conducive to disease are the major ingredients for severe epidemics on crop plants. In the warm humid tropics, tomato production is severely limited by diseases. Yang (10) cited 35 fungal and bacterial diseases affecting tropical tomato production. Tomato production has been most difficult in the warm rainy season occurring in summer and fall in Puerto Rico. Not only are warm temperatures harmful to fruit set, but severe early blight consistently causes early defoliation. For successful year-round tomato production a combination of blight resistance and heat tolerance will be essential.

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[2]Tropical Agriculture Research Station, United States Department of Agriculture, Agricultural Research Service, Box 70, Mayagüez, Puerto Rico 00709.

Early blight is a fungal disease caused by *Alternaria solani* (Ell. & Martin). The foliar phase is the most common and destructive one of the diseases. Characteristically, brown necrotic lesions show dark concentric rings associated with periodic development of the fungus. Necrotic patches are surrounded by chlorotic halos caused by fungal toxin production (7). Leaf necrosis and chlorosis lead to premature death of leaves and reduced crop yield and quality. Besides foliar symptoms, collar rot (stem canker) and fruit rots have been attributed to *A. solani*.

Although Reynard and Andrus (8) found resistance to collar rot, no tomatoes currently used in the tropics have adequate early blight resistance. Fungicides are generally used for disease control, greatly increasing production costs and environmental hazards. There are numerous reports of early blight resistance in temperate areas, many of which have never been verified especially under a severe tropical environment. Clark et al. (4) have summarized recent reports of early blight resistance in tomatoes.

Working on foliar resistance to early blight Walter (9) reported that two or more recessive genes control the disease. Barksdale (1) developed techniques for stimulating in vitro conidia formation and inoculating field plants. Lines of processing tomatoes with improved early blight resistance have been developed by Barksdale and Stoner (2) by means of F_2 selection after artificial inoculation of *A. solani*. A wild green fruited tomato, *Lycopersicon hirsutum* (PI 126445), was used as an early blight resistance source in the Piedmont area of North Carolina (5). Resistance to early blight with this source has decreased under progressive backcrossing; thus both minor and major genes seem to condition early blight resistance.

The metabolic processes which condition resistance to early blight are less understood than the nature of gene action involved in the same process. Zhuchenko et al. (11) found tomatine, a common tomato glycoalkaloid, highly associated with *A. solani* resistance. Total tannins and phenols were suggested as possible resistance components by Bhatia et al. (3).

Considering the importance of early blight in Puerto Rico, and the lack of verification of many sources reported for early blight resistance, we initiated evaluation of the usefulness of reported sources of resistance under our warm humid summers.

MATERIALS AND METHODS

All of the *Lycopersicon esculentum*, *L. pimpinellifolium*, and *L. hirsutum* accessions as well as numerous hybrids and doubtful accessions listed in the compendium of Clark et al. (4) and suggested to be resistant to *Alternaria* were requested, and most were obtained from the North Central Plant Introduction Station together with seeds of other species.

Lines segregating for resistance to *Alternaria* were obtained from Gardner, Barksdale, and Stoner. Cultivars believed to be resistant to collar rot (Manalucie, Floradel, Flora-Dade and Walter) brought the number of accessions to 192 (table 1).

Twenty five plants of each accession were grown in the field at Mayagüez, Puerto Rico, in the summers of 1982-1985. During this season, night temperatures are warm (25° C), the days hotter (up to 32° C), with high humidity and frequent afternoon showers. The plants were established in individual peat pots in late May or early June, transplanted to rows in the field about 5 weeks later, fertilized at the rate of 600 kg/ha with 10-10-5 NPK, and irrigated as necessary. Summer rains were highly irregular until August, when they were frequent and intense.

Each year the plants were inspected 3 to 5 times at approximately 2 week intervals and were rated for early blight on the basis of a 0 to 9 scale where, 0 represented no visible symptoms of *Alternaria* and 9 represented complete defoliation. The infection begins in the lower leaves, and in susceptible hosts is rapidly transmitted through all parts of the plant. In 1983 the young plants at flowering were inoculated with spores of locally collected *Alternaria*, and in 1984 and 1985 a selected line, Flora-Dade, was planted at the front of each varietal plot to serve as a disease spreader. Each year selections of the most *Alternaria* free plants were crossed to one or more of three cultivars used as recurrent parents, Flora-Dade, Calypso, or Kewalo. F_1 hybrids were often self pollinated in field or greenhouse to obtain F_2 seed. When crosses failed, as was common during the hot humid summer, open-pollinated fruits were collected to preserve the most resistant lines.

RESULTS

The course of the disease was very much the same during each year, and can be illustrated by the records of 1985: August 1, trace infections noted; August 16, Flora-Dade and other susceptible lines with up to 9 infected leaves, resistant lines with 5 or fewer; September 5, susceptible lines with 50-100% defoliation, resistant lines with less than 50% defoliation; September 16, susceptible lines 100% defoliated, resistant lines 50-100 percent defoliated.

Evaluation was difficult because of great differences in the morphology and maturity of the lines, other defoliating diseases (Buckeye stem canker, *Phytophthora parasitica*, and leaf mold, *Fulvia fulvum* syn. *Cladosporium fulvum*), tangling of the vines of indeterminate types, and regrowth of susceptible indeterminate plants during periodic dry spells. Furthermore, Flora-Dade itself was somewhat resistant and may not be an ideal spreader, except that it still lives and spreads spores when more susceptible lines are already defoliated. The comparison of individual plants in segregating lines was very difficult. Nevertheless, evaluation of lines over three to four different dates, and, to a lesser extent, of individual plants in segregating families helped to clarify the resistance status of lines and individual plants.

Table 1 gives the classification of all lines tested and their relative susceptibilities. The vast majority (144) of the lines, identified by PI number or our local numbers, were susceptible or highly susceptible to *A. solani* and are not identified further here (6). Only one line, cultivar Manalucie, was found partially (lightly) resistant. Six *L. esculentum* f. *cerasiforme* were lightly resistant and one was usefully resistant. Eleven *L. pimpinellifolium* lines were lightly resistant and six were highly resistant. Six lines of suspected hybrids of *L. esculentum* x *L. pimpinellifolium* were lightly resistant. Of only eight *L. hirsutum* f. *typicum* lines, seven were highly resistant. Furthermore, this resistance appeared to be stronger than any other resistance found in this study. Table 2 gives lines classified as partially resistant or highly resistant.

Of the breeding lines of Gardner and Barksdale and Stoner, in 1982 only one appeared lightly resistant and another highly resistant. In 1985

TABLE 1.—*Relative susceptibility of* Lycopersicon *lines to early blight (*Alternaria solani*) in Mayagüez, Puerto Rico*

Lines	Number of lines tested	Number of lines found			
		Highly susceptible[1]	Susceptible	Light resistance	Useful resistance
L. esculentum Cultivars and primitive varieties	69	58	10	1	0
Breeding lines for resistance, Gardner; Barksdale and Stoner	22	14	6	1	1
Derivatives of above lines	4	1	1	2	0
Barksdale's advanced lines (1985 only)	10	2	0	8	1
L. esculentum f. *cerasiforme*	22	6	9	6	1
L. pimpinellifolium	25	6	2	11	6
Suspected hybrids	27	9	12	6	0
L. esculentum x *L. pimpinellifolium*	4	0	3	0	1
L. hirsutum var. *glabratum*	1	0	1	0	0
L. hirsutum var. *typicum*	8	0	0	1	7
Totals	192	96	49	31	16

[1] These 4 categories of susceptibility are based on pragmatic judgement of differences found at the various times each plant was examined. Because each plant was scored several times as disease progressed, the pragmatic score cannot be directly compared to the 0-9 ratings made only for each observation.

TABLE 2.—Lycopersicon *lines classified as light resistance (LR) or useful resistant (UR) to early blight (*Alternaria solani*)*

PI or other number	Disease reaction[1]	Nature of line	Subsequent follow up
TARS-T-1 (Manalucie)	LR	Established cultivar resistant to collar rot	None
TARS-T-148	UR	Stoner's 81B22	Backcrossed to Flora-Dade
TARS-T-153	LR	Stoner's 81B35	Backcrossed to Flora-Dade
TARS-T-47	LR	F_1 with Flora-Dade and Stoner's 81B22	Further backcrossing
TARS-T-48	LR	F_1 With Flora-Dade and Stoner's 81B35	Further backcrossing
100697	LR	*L. cerasiforme*	None
124163	LR	"	"
126942	LR	"	"
127817	LR	"	"
129041	LR	"	"
195779	LR	"	"
406758	UR	"	"
127805	LR	*L. pimpinellifolium*	"
133542	LR	"	"
143527	LR	"	"
212408	UR	"	"
251320	UR	"	"
313943	LR	"	"
344102	LR	"	"
344103	LR	"	"
365912	UR	"	Crossed to Calypso
365917	LR	"	None
365928	UR	"	Crossed to Calypso
379058	LR	"	None
390519	UR	"	Crossed to Calypso
390692	LR	"	None
303662	UR	"	"
313943	LR	"	"
112835	LR	Suspected hybrid, *L. esculentum* x *L. pimpinellifolium*	"
118405	LR	"	"
118407	LR	"	"
118784	LR	"	"
205014	LR	"	"
309815	LR	"	"
390513	UR	*L. hirsutum*	Crossed to *L. esculentum*
390514	UR	"	"
390516	UR	"	"
390658	UR	"	"
390659	LR	"	"
390660	UR	"	"
390662	UR	"	"
390663	UR	"	"

[1] UR = Useful resistance and LR = light resistance (see note, table 1).

only three of the more advanced lines of Barksdale appeared lightly resistant, and one usefully resistant.

A very large number of crosses were made with the standard *L. esculentum* cultivars. The majority of these crosses failed, but later it was possible to repeat some of the crosses and some F_1 hybrids were obtained.

Resistance in hybrids with L. hirsutum

L. hirsutum f. *glabratum* is usually not sufficiently resistant to be used as a source. The F_1's with f. *typicum* were partially or highly resistant to *A. solani*. The plants are large and vigorous, variable in flowering and fruiting, and never carried a normal fruit load, which in itself might give a false indication of resistance. Parent lines differed in resistance carried to the F_1 (table 3).

If resistance is controlled chiefly by dominant genes, it should appear also in the first backcross to the recurrent *L. esculentum* parent. The levels of resistance found in some BC_1 and BC_2 hybrids reached the useful (UR) level in several cases. This was also true in F_2 from BC_1 hybrids (table 4).

Ususally one can select from F_2 generations for the most resistant plants in order to capture recessive as well as dominant genes for resistance. In practice, this proved difficult. F_2 plants segregated widely for traits of both parents and were often infertile (table 5). Sharp judgement is needed to identify the resistant plants among the F_2. They should be selected from among those that have as many fruits as possible, but even so, pollination to the recurrent parents often failed. For this reason, only four F_2 populations were grown.

Resistance in hybrids with L. pimpinellifolium

In general *L. pimpinellifolium* flowers and fruits readily in the hot humid climate of the Mayagüez summers. The fruit loads may be large,

TABLE 3.—*Resistance to* Alternaria solani *in F_1 hybrids of* L. esculentum x L. hirsutum *f.* typicum

L. esculentum parent	*L. hirsutum* parent	Years tested	No. of plants evaluated	Range of resistance noted[1]
Calypso	TA51 (390513)	1984	7	S-LR
Flora-Dade	TA52 (390514)	1983	3	UR
Kewalo	"	1983, 1985	11	UR
Calypso	"	1983, 1984	5	UR
Calypso	TA53 (390516)	1984, 1985	8	LR
Calypso	TP54 (390658)	1984	3	LR
Flora-Dade	"	1985	2	LR
Flora-Dade	TP57 (390662)	1984, 1985	5	UR

[1] S = Susceptible; LR = light resistance; and UR = useful resistance (see note, table 1).

TABLE 4.—*Resistance of BC hybrids of* L. esculentum x L. hirsutum *to* Alternaria solani

L. esculentum recurrent parent	*L. hirsutum* parent	Years tested	No. of plants evaluated	Highest resistance noted[1]
		BC_1		
Flora-Dade	TA52 (390514)	1983, 1984	22	UR
Kewalo	TA52 (390514)	1983, 1985	25	UR
Calypso	TA52 (390514)	1983, 1985	24	UR
Kewalo	TA58 (390663)	1984	5	UR
Calypso	TA51 (390513)	1984	15	S
Kewalo	TA53 (390516)	1985	7	LR
Calypso	TA57 (390662)	1985	54	UR
		BC_2		
Flora-Dade	TA52 (390514)	1984	28	S
Calypso	TA57 (390662)	1984	14	S
		F_2 *of* BC_1		
Flora-Dade	TA52 (390514)	1984	17	UR
Kewalo	TA52 (390514)	1984	12	LR
Calypso	TA52 (390514)	1984	15	LR
Kewalo	TA52 (390514)	1985	10	UR
Calypso	TA52 (390514)	1985	9	UR

[1] S = Susceptible; LR = light resistance; and UR = useful resistance (see note, table 1).

TABLE 5.—*Resistance of* F_2 *hybrids of* L. esculentum x L. hirsutum *to* Alternaria solani

L. esculentum parent	*L. hirsutum* parent	Years tested	No. of plants evaluated	Highest resistance noted[1]
Calypso	TA51 (390513)	1984	14	LR
Flora-Dade	TA51 (390513)	1984	15	LR
Kewalo	TA52 (390514)	1984	11	UR
Calypso	TA57 (390662)	1985	35	UR

[1] LR = Light resistance and UR = useful resistance (see note, table 1).

in spite of small fruit size, and whereas some lines are susceptible (table 1) others are resistant (table 2).

Crosses with *L. pimpinellifolium* are not difficult to make, but during the hot summer the recurrent parents themselves are not very fertile. The hybrids are highly fertile except that some are unfruitful in hot weather. It has been possible to observe early blight resistance in hybrids over several years and several generations.

The resistance of *L. pimpinellifolium* to *A. solani* is usually less than that of *L. hirsutum*. This resistance is seen in the F_1, suggesting dominance, but in the F_2 very few plants are resistant, suggesting that many genes are involved in resistance. Recovery in a single plant of all such genes is difficult (table 6).

TABLE 6.—*Resistance to* Alternaria solani *in hybrids of* L. esculentum x L. pimpinellifolium

Recurrent *L. esculentum* parent	*L. pimpinellifolium* parent	Years tested	No. of plants evaluated	Highest resistance noted[1]
		F₁		
Calypso	TA209 (395912)	1984	10	LR
Calypso	TA201 (395928)	1984	10	LR
Calypso	TA220 (390519)	1984	10	UR
Calypso	TA209 (365912)	1985	5	LR
Calypso	TA211 (365928)	1985	1	S
		F₂		
Calypso	TA209 (365912)	1984	25	LR
Calypso	TA211 (365928)	1984	25	LR
Calypso	TA220 (390519)	1984	23	UR
Calypso	TA209 (365912)	1985	17	UR
Calypso	TA220 (390519)	1985	16	UR

[1] S = Susceptible; LR = light resistance; and UR = useful resistance (see note, table 1).

TABLE 7.—*Resistance in advanced canning tomato lines from the USA under Mayagüez conditions*[1]

Our field number	Barksdale's line designation	No. of plants evaluated	Resistance noted[2]
130	84B 176	14	HS-S
131	84B 196	14	S-LR
132	83B 694	5	S-LR
133	84B 166	8	HS-LR
134	83B 696	5	S-LR
135	84B 465-1	4	S-LR
136	84B 500-1	10	S-LR
137	84B 510-3	14	S-LR
138	84B 510-4	14	LR-UR

[1] 1985, Lines of Barksdale.

[2] S = Susceptible; HS = highly susceptible; LR = light resistance; and UR = useful resistance (see note, table 1).

Resistance of L. esculentum *lines from elsewhere*

Through the goodwill of Barksdale, the most resistant lines in the USA were tested in 1985. These are canning tomatoes (table 7). The resistance developed in the United States to *A. solani* appears to be useful there. In 4 years of testing we have not found that resistance adequate for Puerto Rico.

The Barksdale lines appeared to be still segregating for resistance. In most cases, resistance was light and insufficient for use in Puerto Rico. However, in one line, 84B 510-4, resistance was better and might have been sufficient for Puerto Rican conditions. Resistance in this line was almost as good as any we have extracted so far from *L. hirsutum* or *L. pimpinellifolium*.

DISCUSSION

There can be no doubt that both *Lycopersicon hirsutum* and *L. pimpinellifolium* contain genes affecting susceptibility to early blight, caused by *A. solani*. Apparently both dominant and recessive genes are present. Four years of observation suggest that these genes could give sufficient resistance to this disease to the market tomato, *L. esculentum*, to permit tomato production during the hot humid weather of the tropical summer. The problem is to transfer these genes into suitable cultivars of the market tomato by normal hybridization and selection techniques.

The difficulty lies in the problem of identifying and thus selecting the individual genes. This is also complicated by the interaction of such genes with others that affect the morphology of the plant, other disease susceptibilities, and growth patterns; for example, fruit load, a desirable characteristic, increases disease reaction. Whereas it would be ideal to be able to identify each gene by its major and minor effects, this does not appear to be feasible now in the tropics.

Therefore, we suggest the following procedures in searching for resistance to *A. solani* in the tropics.

1. Make all evaluations in comparison to the best resistant lines now available (probably Manalucie and the breeding lines of Barksdale and Stoner).
2. Observe the resistant parents on several seasons, and then select the best for crossing.
3. Cross to established varieties which have characteristics needed in the tropics, especially with ability to set fruit under hot night temperatures.
4. Make the first backcross, producing as many seeds as possible.
5. Self-pollinate the backcross hybrids, select for resistance to hot night temperature and for early blight resistance.
6. Grow the F_2 of the BC_1 during a time when natural *A. solani* infection is high, or use controlled inoculations under conditions favorable for disease development.
7. Select the best F_2 segregants for a further backcross, and repeat the cycle.
8. Cross resistant selections from *L. hirsutum* and *L. pimpinellifolium* in hopes of enlarging the pool of resistant genes. This procedure is similar to that recommended by Barksdale (1), and although slow, can lead to the successful transfer of several genes affecting early blight resistance.

RESUMEN

Fuentes de resistencia al tizón temprano, *Alternaria solani* y su transferencia al tomate, *Lycopersicon esculentum*

Líneas de tomate informadas como resistentes al tizón temprano se sembraron y evaluaron bajo infestaciones severamente afectades por el tizón temprano durante la estación lluviosa (verano) de 1982-1985 en Mayagüez, Puerto Rico.

El propósito era identificar las líneas con resistencia útil en Puerto Rico. Esto se definió como poco tizón a pesar de condiciones apropiadas para la enfermedad y sin control químico. Resistencia útil en el campo se encontró en la minoría de los casos, pero una o más líneas de *L. esculentum* f. *cerasiforme, L. pimpinellifolium, L. esculentum* x *L. pimpinellifolium*, y *L. hirsutum* var. *typicium* mostraron resistencia útil. Las menos afectadas fueron variedades de *L. hirsutum*, las cuales también arrojaron los rendimientos más bajos. La mejor producción de tomates se obtuvo con *L. pimpinellifolium* aunque acusaba menos resistencia. Cruces de *L. esculentum* con *L. hirsutum* con resistencia útil se estudiaron en las generaciones F_1, F_2 y F_3. La resistencia parecía ser dominante en la F_1, pero la segregación en la F_2 sugirió que muchos genes modificadores, dominantes y recesivos, probablemente estuvieron envueltos en la resistencia al tizón temprano. De las líneas de tomate común, 84B 510-4 obtenida de T. Barksdale, era la que más se acercaba en resistencia a las especies silvestres. Generalmente, tomates comunes parecen ser más susceptibles al tizón temprano que las especies silvestres. Para aumentar la agrupación de genes para resistencia, se sugieren seleccionar en la F_2 y retrocruces progresivos. Las variedades susceptibles se defoliaron un mes después de iniciarse la floración durante el lluvioso verano, mientras que las variedades con resistencia útil se defoliaron 6 u 8 semanas después de dicha etapa.

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