An Analysis of Plant Breeding Procedures for Obtaining Curly Top Resistance in Tomato

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ABSTRACT

Methods of breeding tomato varieties for curly top resistance were evaluated. Some genetic factor or factors had eliminated or modified the expression of genes for curly top resistance in the modified backcross to *Lycopersicon esculentum* Mill. by the hybrid *L. esculentum* X *L. peruvianum* var. *dentatum* Dun. Resistance of the USDA breeding lines, CVF4 and C5, was also less than that of *L. peruvianum* var. *dentatum*, which was included in their ancestry. Failure of breeding methods to retain the high level of curly top resistance of *L. peruvianum* var. *dentatum* was attributed to the consistent loss of resistance in the modified backcross of the original interspecific hybrids, and sharing of genes for resistance by later intercrossed lines.

In additional curly top tests, "F_2" progeny (from seed set in the field on F_1 plants which were either selfpollinated or received pollen from hybrid offspring of *L. peruvianum* var. *dentatum*) expressed considerable resistance. It will be necessary, however, to overcome the factor or factors causing the loss of resistance in order to achieve greater success in future breeding programs. This will require considerable research with original interspecific crosses and less with existing, partially resistant breeding lines.

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Since the discovery of high levels of resistance to the curly top virus in wild species of *Lycopersicon* by Blood (1) and Virgin (16) over 30 years ago, extensive efforts have been made to transfer this resistance to a commercial tomato variety (2, 5). In recent years, the Idaho Experiment Station released two tomato varieties, Owyhee and Payette (13, 14); and the USDA program in Utah released two breeding lines, CVF4 and C5 (4, 8). Widespread tests indicate, however, that the Owyhee, Payette, and CVF4 lines possess but partial resistance to the curly top virus (8). In contrast, Martin & Thomas (8) described the resistance of the C5 breeding line as comparing favorably with that of *L. peruvianum* var. *dentatum* Dun., being able to withstand severe curly top exposure.

Martin & Clark (7) concluded that the difficulty encountered by tomato breeders in transferring the high levels of curly top resistance from the wild species of tomato to a commercially acceptable variety was due to the probable polygenic nature of curly top resistance in tomato, the effect of the environment on expression of resistance, and the loss of resistance in the backcrossing and horticultural selection necessary to reconstitute recurrent commercial parents. Randall (10) proposed that the partial loss of resistance in the development of Owyhee was due to inefficient selection. He suggested that the problem was due to variability of the virus strains from year to year, inadequate methods used to expose the genotypes, and the use of selfing and outcrossing with relatively small populations.

In the past, tomato breeders have used a modified backcross and/or recurrent selection breeding methods (4, 8, 13, 14). The modified backcross design involved alternating between a backcross to *L.*

esculentum and a progeny test of the selected plants (10). The objective of the current study was to evaluate these conventional breeding procedures used by tomato breeders in their efforts to develop tomato varieties with high levels of curly top resistance.

MATERIALS AND METHODS.–Owing to the interspecific barriers which exist in *Lycopersicon* (9), a single hybrid between *L. esculentum* and *L. peruvianum* var. *dentatum* was obtained for this study. This F_1 hybrid was self-incompatible, but fruit set was obtained in the backcross to *L. esculentum*, from which 48 first-backcross plants were obtained. Each of the backcross plants was assigned a D number *(dentatum)* for purposes of identification.

We determined resistance to the curly top virus by infesting healthy tomato seedlings, 10 days after transplanting them, with four viruliferous adult leafhoppers/plant. These leafhoppers were carrying Utah Collection 3 of the curly top virus. In previous curly top tests, this virus collection was shown to be highly virulent on commercial tomato varieties. The resistant and susceptible controls for all tests were, respectively, *L. peruvianum* var. *dentatum* and VF7, a Verticillium-Fusarium wilt-resistant *L. esculentum* breeding line.

RESULTS AND DISCUSSION.–*Backcross F_2 and F_3 tests.*–In curly top tests of 1,536 backcross F_2 plants (Table 1), the over-all proportion of surviving F_2 seedlings was significantly less than the proportion of surviving *L. peruvianum* var. *dentatum* seedlings. In all instances, the number of surviving F_2 seedlings was low. In later curly top tests of the backcross F_3 seedlings, performed as a progeny test of the backcross F_2 plants which had survived the previous curly top tests, the proportion of surviving F_3 seedlings was also significantly less than the proportion of surviving *L. peruvianum* var. *dentatum* seedlings. Furthermore, results of these progeny tests showed that none of the F_2 plants possessed curly top resistance comparable to that of *L. peruvianum* var. *dentatum*. Combined test results, therefore, suggest that the total curly top resistance of *L. peruvianum* var. *dentatum* was not transferred to the backcross F_2 and F_3 plants. In contrast to the hypothesis proposed by Martin & Clark (7) and also to that proposed by Randall (10) to explain the difficulty encountered in obtaining a highly resistant commercial tomato variety, the F_2 and F_3 seedling curly top tests indicate that a partial loss of curly top resistance occurs in the very early stages of the breeding programs (in the first modified backcross).

TABLE 1. Proportions of F_2 and F_3 progeny of 48 different backcross F_1 plants that survived inoculation with curly top virus[a]

Plant tested	No. progeny tested	Proportion of progeny surviving
Backcross F_2		
D lines	1,536	.033[e]
dentatum[b]	320	.597*
VF7[c]	320	.006
Backcross F_3[d]		
D lines	576	.099[f]
dentatum	60	.850**
VF7	60	.017

[a]Observations were made 60 days after inoculation; each plant received four infective leafhoppers.

[b]Curly top-resistant control, *Lycopersicon peruvianum* var. *dentatum*.

[c]Curly top susceptible *L. esculentum* control.

[d]F_3 progeny of backcross F_2 plants surviving the previous curly top tests.

[e]*,[f]** Statistical significance at the .5% level as determined by the X^2 test comparing proportions of surviving progeny with a 2 X 2 contingency table.

TABLE 2. Comparison of curly top development in the CVF4 and C5 breeding lines[a] to that expressed by *Lycopersicon peruvianum* var. *dentatum* 60 days after inoculation with curly top virus[b]

Plant tested	No. plants tested	Proportion of plants surviving
C5	90	.222[e]
dentatum[c]	30	.666*
VF7[d]	20	.000
CVF4	90	.244[f]
dentatum	30	.767**
VF7	20	.000

[a]USDA breeding lines developed by the modified backcross and recurrent selection.

[b]Four infective leafhoppers/plant.

[c]Curly top-resistant control, *L. peruvianum* var. *dentatum*.

[d]Curly top-susceptible *L. esculentum* control.

[e]*,[f]** Statistical significance at the .5% level as determined by the X^2 test comparing proportions of surviving plants with a 2 X 2 contingency table.

In previous interspecific tomato crosses, researchers have observed apparent abnormal segregation of introduced marker genes. Explanations proposed for their observations were: selective elimination of gametes (12); reduction in chiasma frequency (12); zygotic elimination (11); the interaction of a system or systems of modifiers (15); and linkage to genes unfavorably affecting pollen tube growth (3). The results of the F_2 and F_3 curly top tests, however, do not indicate which of these factors or possibly others is responsible for the loss of curly top resistance in the current study.

CVF4 and C5 curly top tests.–The curly top tests of the USDA breeding lines, CVF4 and C5, indicated that these lines possess significantly less resistance than does *L. peruvianum* var. *dentatum* (Table 2), which has been included in their ancestry (6). It is apparent, therefore, that some curly top resistance was lost in their development. Results of the backcross F_2 and F_3 curly top tests suggest that the initial loss of resistance occurred in the modified backcross of the original interspecific hybrids. Additional support for this proposal is provided by results of curly top tests reported by Martin (5) in

TABLE 3. Comparison of curly top development in "F_2", D78-2, and *Lycopersicon peruvianum* var. *dentatum* plants[a] 30 days after inoculation with curly top virus[b]

Plant tested	Proportion of plants that survived
dentatum[c]	.857[g]
"F_2"[d]	.786[h]
D78-2[e]	.229*,**
VF7[f]	.057

[a]Seventy plants of each tested.
[b]Four infective leafhoppers/plant.
[c]Curly top-resistant control, *L. peruvianum* var. *dentatum*.
[d]Progeny of field-pollinated F_1 hybrid.
[e]Curly top-resistant selection developed by a modified backcross.
[f]Curly top-susceptible *L. esculentum* control.
[g*,h**] Statistical significance at the .5% level as determined by the X^2 test comparing proportions of surviving plants with a 2 X 2 contingency table.

which he compared the resistance possessed by the best breeding lines derived from *L. peruvianum* var. *dentatum* and *L. peruvianum* var. *humifusum* Mull. to that possessed by these two wild tomato varieties. Martin reported that all of these derived breeding lines expressed less curly top resistance than the wild variety from which they were obtained. Although the objective of intercrossing the derived breeding lines was to accumulate genes for curly top resistance from the various tomato breeding lines (5), the CVF4 and C5 curly top tests indicate that only limited success was achieved. Apparently in the later developmental stages of CVF4 and C5, genes for curly top resistance were shared by the intercrossed partially resistant breeding lines.

"F_2" seedling tests.—Curly top tests of the "F_2" seedlings (from seed set in the field on F_1 plants which were either selfpollinated or received pollen from other hybrid offspring of *L. peruvianum* var. *dentatum*) were conducted to compare the level of curly top resistance expressed by the "F_2" seedlings to that expressed by a resistant backcross F_2 selection developed by the modified backcross in this study. Test results (Table 3) show that significantly more curly top resistance was expressed by the "F_2" seedlings than was expressed by one of the better backcross F_2 selections (D78-2). It appears that the factor or factors that were responsible for the loss of resistance in the modified backcross were not functioning to the same degree in the cross(es) encountered in obtaining the "F_2" seedlings.

Results of the current study show that the modified backcross and recurrent selection breeding methods have been unsuccessful as methods to obtain commercial tomato varieties with curly top resistance equal to that of the most resistant wild tomatoes. For several years, considerable research has been conducted on existing, partially resistant breeding lines with but limited success. To achieve greater success in the future, it will be necessary to overcome the factor or factors responsible for the loss of resistance. Emphasis must, therefore, be placed on research with the original interspecific tomato crosses.

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