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The Inheritance of Resistance to Tobacco Mosaic Virus in an Interspecific Tomato Cross

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The Inheritance of Resistance to Tobacco Mosaic Virus in an Interspecific Tomato Cross

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THIS paper deals with a study of the inheritance of the resistance to tobacco mosaic through the interspecific tomato cross, the resistant *Lycopersicon hirsutum* Humb. and Bonpl. crossed with the susceptible *L. esculentum* Mill.

Three phases of the study were undertaken:

(1) To determine the nature and degree of resistance of the resistant parent.

(2) To determine whether the resistance was recoverable in good quality tomatoes for use in commercial tomatoes.

(3) To determine if a correlation existed between virus infectivity and symptom expression.

A number of workers have found that *Lycopersicon hirsutum* exhibited a high degree of resistance to tobacco mosaic virus. Porte *et al.* (10) found the virus to be present in the symptomless *L. hirsutum* plants. Work by Doolittle, et al. (3) showed the virus to be present in varying, and sometimes fairly high, concentrations. He reported, however, that a few plants seemed to be immune to the virus.

Doolittle and Porte, (2) in working with progenies of *L. esculentum* X *L. hirsutum* crosses, found tolerant individuals but none with the high resistance of the *L. hirsutum* parent. There was an indication that these progeny plants had a tendency to escape natural infection to a higher degree than the Marglobe control. Kikuta, *et al.* (6) pointed out the possibility that the resistance to tobacco mosaic might be incompletely dominant, since all of the *L. esculentum* X *L. hirsutum* F_1 hybrids showed the symptoms.

Materials and Methods

The parent commercial tomato was a selfed line of the Sioux variety, which was well adapted to Idaho conditions (8). The resistant *L. hirsutum* came from a seed introduction of Blood and Tremelling (9). The *L. hirsutum* selfed progeny was compared with the other groups in order to evaluate the homozygosity of this parent. The F_1 hybrid was Sioux (female) crossed with *L. hirsutum* (male). The two back crosses were Sioux X (Sioux X *L. hirsutum*) and (Sioux X *L. hirsutum*) X *L. hirsutum*. These crosses were made in the field and greenhouse under controlled pollination and were grown in the field during the 1950 season. This minimized any interference that environmental or cultural conditions might have on the character studies.

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The tobacco mosaic virus strains present in the area served as the source of inoculum. The initial spread of the virus was due to normal handling and cultivating operations. Due to the rank growth of these plants, it was necessary to cut pathways between every other row to facilitate readings of individual plants. This cutting further served as an effective means of inoculating the plants.

All plants not showing symptoms at the time of the first field mosaic readings were inoculated by the carborundum method using the expressed juice of affected plants. A second mosaic reading was taken approximately one month after inoculation. As many cuttings as time and greenhouse space would permit were made from these plants. An adequate sample for further greenhouse readings and virus concentration studies were obtained. In the back cross to Sioux, special emphasis was placed on selecting all of the plants that did not show symptoms in the field; however, this selection was a small per cent of the total number of plants taken from this line. The large majority of plants were taken at random throughout the field.

Computing Virus Infectivity

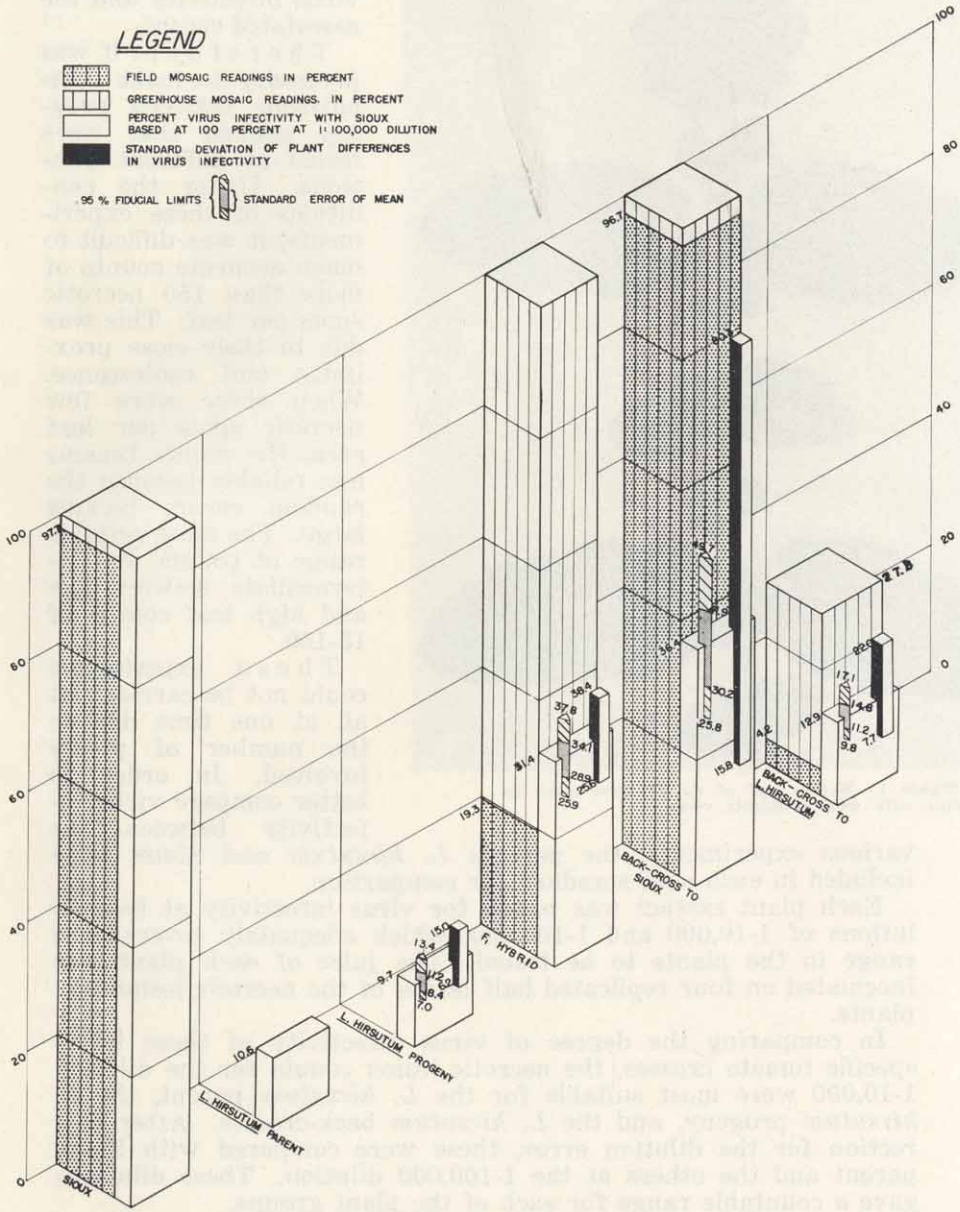
The necrotic lesion method (1, 4, 11, 12) was used to compare virus infectivity in the plant cuttings under greenhouse conditions. Since the necrotic lesion method does not measure virus concentration directly, but rather measures the virus extract's ability to develop necrotic spots on the test plant, the term "virus infectivity" has been used throughout this paper.

The hybrid *Nicotiana tobaccum L.* X. *N. glutinosa L* (5) was used for the necrotic lesion test plant. The special advantages of this cross were the reduced genetic variability in the F_1 test plants which had a better leaf surface, size, and quality than the *N. glutinosa* type.

Certain of the factors causing variable results in evaluating virus infectivity with the necrotic lesion method were standardized in order to minimize the inherent errors. The tobacco test plants were grown in a uniform mixture of pasteurized soil, were selected to a uniform size and age, and were pruned to remove the growing points for each experiment. Care was used to prevent errors in extracting and diluting the juice of the tomatoes and inoculating the test plants. Carborundum was spread uniformly over the leaf surfaces and enough inoculum was used to wet each leaf (13).

The size of the half-leaf areas in which the spots were counted was kept constant through the experiments. This was accomplished by placing a half-disc cut out of transparent cellulose acetate over the area containing the greatest number of evenly distributed spots. This area was marked off, and the spots counted. Some of the other sources of error were minimized by randomization and replication. It was necessary to compare virus infectivity over a wide range between the susceptible parent (Sioux) which contained 9.4 times as much virus as the resistant parent (*L. hirsutum*). These comparisons could not be made at the same dilution due

Chart 1



A COMPARISON OF THE SYMPTOM EXPRESSION OF TOBACCO MOSAIC IN THE FIELD AND GREENHOUSE WITH THE RELATIVE INFECTIVITY IN THE SIOUX AND L. HIRSUTUM PARENTS AND PROGENY

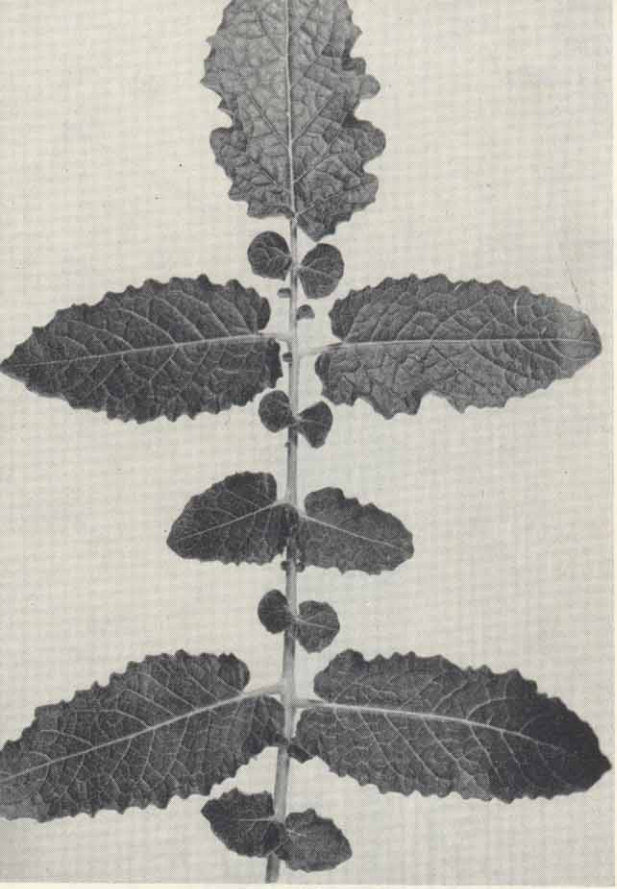


Figure 1.—Mature leaf of *L. hirsutum* plant infected with tobacco mosaic virus.

to the wide difference in virus infectivity and the associated errors.

Therefore, it was necessary to make comparisons between progeny groups that were tested at different dilutions. Under the conditions of these experiments, it was difficult to make accurate counts of more than 150 necrotic spots per leaf. This was due to their close proximity and coalescence. When there were few necrotic spots per leaf area, the counts became less reliable because the random errors became large. The most suitable range of counts was intermediate between low and high leaf counts of 15-150.

These experiments could not be carried out all at one time due to the number of plants involved. In order to better compare virus infectivity between the various experiments, the parents *L. hirsutum* and Sioux were included in each as a standard for comparison.

Each plant extract was tested for virus infectivity at two dilutions of 1-10,000 and 1-100,000, which adequately covered the range in the plants to be tested. The juice of each plant was inoculated on four replicated half leaves of the necrotic lesion test plants.

In comparing the degree of virus infectivity of these interspecific tomato crosses, the necrotic lesion counts for the dilution 1-10,000 were most suitable for the *L. hirsutum* parent, the *L. hirsutum* progeny, and the *L. hirsutum* back-crosses. After correction for the dilution error, these were compared with Sioux parent and the others at the 1-100,000 dilution. These dilutions gave a countable range for each of the plant groups.

The data indicate a correction, for dilution was necessary before the necrotic counts could be compared between plants having a relatively low virus infectivity, like *L. hirsutum,* and those having a high virus infectivity, like Sioux. Holmes (4) first indicated the need for such a correction.

Figure 2.—Symptom expression on the young leaves of the parent plants infected with Tobacco mosaic virus, Sioux on the left and *L. hirsutum* parent with no evident symptoms on the right.

The factor for correcting the results of necrotic tests made at different dilutions was derived from the data. Plant means of necrotic lesion counts which had been made for each plant tested at both 1-10,000 and 1-100,000 dilutions were used to determine the correction factor, with the exception of a few plants that had one replicate below 10 or above 150 necrotic spots per leaf. The plant means for each dilution were totalled and averaged. The average number of spots counted at the 1-100,000 dilution was divided by the average number of spots counted at the 1-10,000 dilution to obtain the correction factor of 0.2037. This factor, multiplied by the necrotic lesion counts for the *L. hirsutum, L. hirsutum* progeny, and the *L. hirsutum* back-cross which were made at the 1-10,000 dilution, corrected them to the 1-100,000 dilution for comparison with the other crosses. There were twice as many necrotic spots with the 1-100,000 dilution as there were when the 1-10,000 dilution was adjusted, for dilution. This condition made some corrections necessary before comparisons could be made. However, any errors inherent in this correction seemed small when compared to the errors in direct comparisons between samples with a different virus content.

The results of virus infectivity were analyzed by analysis of variance. Due to the obvious correlation between the mean and variance, the logarithms of the individual counts were used without Kleczkowski's (7) arbitrary corrective factor of 15-80. This resulted in a slight over-correction of the correlation between the mean and variance (Tables 9 and 10). Because of the lack of greenhouse space, and in order to simplify the analysis, equal numbers from each symptom class were tested. Each class was based on the field mosaic readings. The means, Chart 1 and Table 10, were weighed according to the total number of plants in the various symptom groups.

To facilitate note taking, the plants tested were consecutively numbered in the row. The line numbers were as follows: 1 for

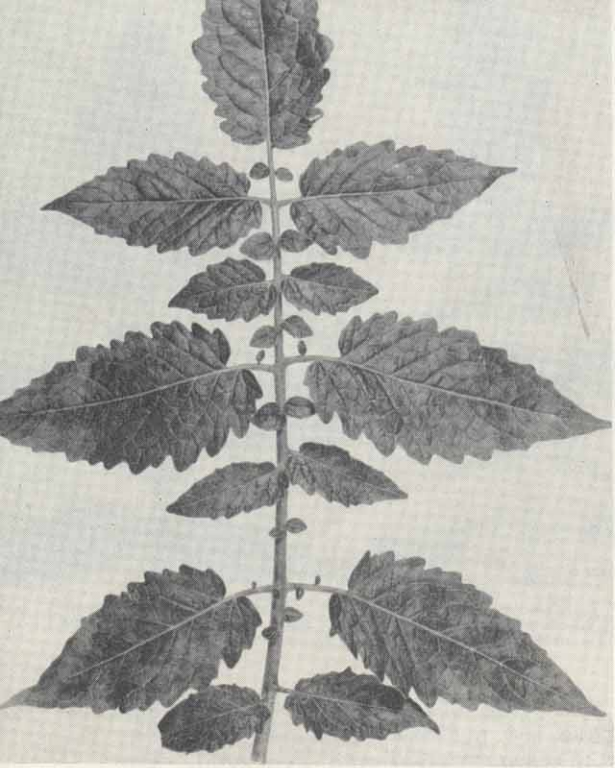


Figure 3.—Symptom expression of the F_1 hybrid (Sioux x *L. hirsutum*) infected with tobacco mosaic virus.

Sioux parent, 2 for *L. hirsutum* parent (cuttings from a single plant), 3 for *L. hirsutum* progeny, 4 for the F_1 (Sioux X *L. hirsutum*), 5 for the back-cross to the Sioux parent, and 8-15 for the back-cross to the *L. hirsutum* parent.

The back-cross was used to study segregation in these interspecific tomato crosses because of the difficulty of producing seed of selfed F_1 plants. Approximately 5000 selfs of F_1 flowers were attempted, and many of these flowers produced fruit but contained no seed. Two slightly different crosses, such as *L. hirsutum* x Sioux and *L. hirsutum* x Danmark produced viable seed, but no seed was produced by a single F_1 plant.

Results

In both field and greenhouse the symptom expression varied in the back-cross plants from the severe mottle with leaf distortion typical of the Sioux parent to that of the *L. hirsutum* parent with no evident symptoms (Figures 1 and 2).

In Sioux, tobacco mosaic virus produced a uniformly severe mottling with leaf distortion (Figure 2). Of the Sioux plants from which field readings were made, only one plant failed to exhibit symptoms. This plant was markedly healthy, giving the field percentage of 97.7 instead of the expected 100 per cent (Chart 1, Table 1). Cuttings made of this plant and grown in the greenhouse produced symptoms typical for Sioux, indicating the plant was a field escape. Greenhouse reading on 200 inoculated Sioux seedlings gave 100 per cent mosaic (Chart 1, Table 1). The expression of symptoms by the *L. hirsutum* parent and its selfed progeny were not evident either in the field or greenhouse and were classed for convenience as symptomless (Table 1, Figure 1).

The F_1 hybrid (Sioux x *L. hirsutum*) produced symptoms on 19.3 per cent of the plants in the field and 100 per cent in the greenhouse (Table 1). The symptoms in both tests, a very flat mottle of the leaves, were very mild (Figure 3). This symptom expression

of the F_1 was intermediate between Sioux and *L. hirsutum* but appeared more like the mild symptom group of the *L. hirsutum* back-cross. Cuttings were made from all the F_1 plants for greenhouse studies. Only nine survived. This poor cutting survival was due in part to the reduced vigor of these infected plants.

In the back-cross to Sioux, field symptoms were observed on 96.7 per cent of the plants examined (Table 1). All of the 332 plants grown in the greenhouse produced symptoms, including all 15 plants which showed no field symptoms. Symptom expression varied from very mild to severe. Those classed as severe were as severe in many cases as the symptoms on the Sioux parent. These plants were divided into three symptom classes: Severe, moderate, and mild. However, symptom expression varied continuously, and no clear-cut boundaries were evident.

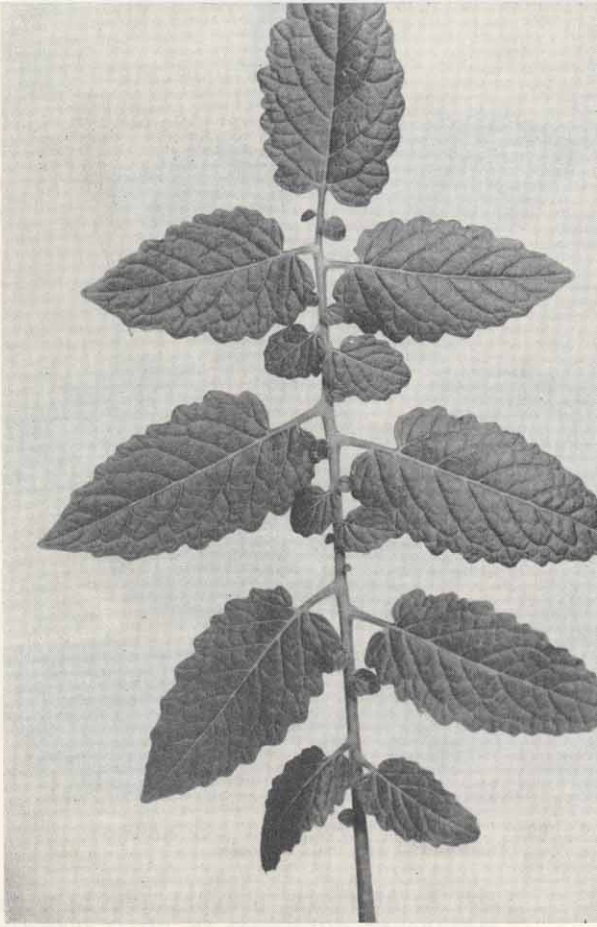


Figure 4.—The back-cross, (Sioux x *L. hirsutum*) x *L. hirsutum* with no evident symptoms.

In the *L. hirsutum* back-cross, there were two clear-cut symptom classes: the mild symptom class similar to the F_1 and a class with no evident symptoms either in the field or greenhouse. In the field 4.2 per cent of the 795 plants classified showed symptoms, while in the greenhouse 27.8 per cent of the 123 plants classified produced symptoms (Table 1). The ratio of 89 symptomless plants to 34 with symptoms in the greenhouse shows a very good fit to a 3:1 ratio in the back-cross by the Chi-square test of goodness of fit (Chart 1).

The percentage of plants with mosaic symptoms was greater in the greenhouse than in the field (Table 1 and shown graphically in Chart 1). This general increase in percentage of plants with symptoms in the greenhouse on all of these lines was due in part to the more ideal environmental conditions, to a regrowth from cuttings which were inoculated again in the process, and to klendusity. Klendusity (the ability of susceptible varieties to escape

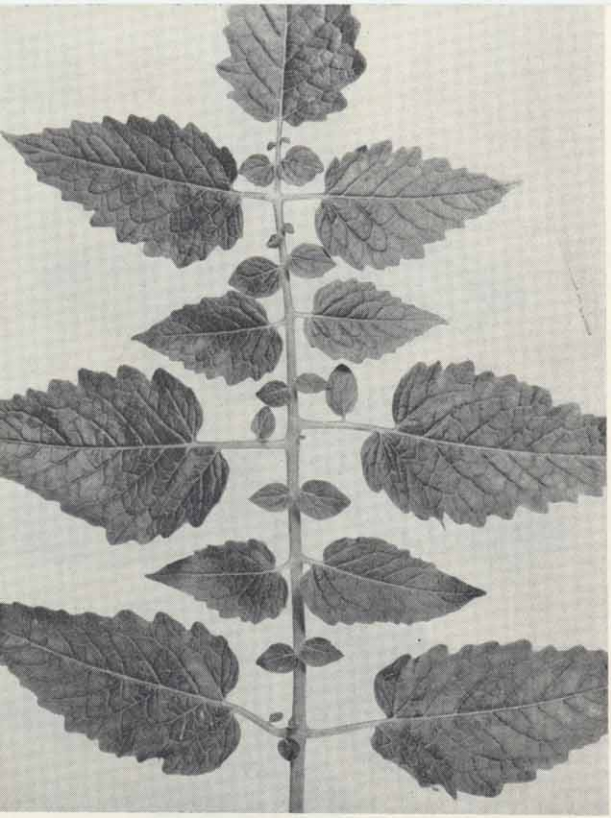


Figure 5.—The back-cross (Sioux x *L. hirsutum*) x *L. hirsutum* with very mild symptoms.

infection) was evident following natural infection and mechanical inoculation of the different lines and crosses (Table 1). The Sioux and its back-cross escaped inoculation in the field by about 3 per cent. The F_1 escaped field infection by 80 per cent. The back-cross to *L. hirsutum* showed about 4 per cent mosaic in the field, an escape of 24 per cent as compared to greenhouse symptom expression.

Relative Virus—Infectivity

The tobacco mosaic virus from the Sioux parent caused about nine times more necrotic spots to develop on the test plant leaves than did the virus from the *L. hirsutum* parent (Tables 2, 9, 10, Figure 6). All the *L. hirsutum* progeny plants tested contained the virus. No significant difference in virus infectivity was found between the *L. hirsutum* parent plant and its selfed progeny plants (Tables 2, 3, Chart 1).

The virus infectivity of the F_1 hybrid plants was significantly lower than that of Sioux and significantly higher than that of *L. hirsutum* (Table 3). The average virus concentration of these plants was closer to that of *L. hirsutum* than to that of Sioux (Chart 1).

An attempt was made to classify subjectively the plants in the back-cross to Sioux into three classes (mild, medium, and severe) on a basis of observed symptom expression. A measurable difference in virus concentration was established between the mild and severe symptom groups (Tables 4 and 5). There did not seem to be any basis for a medium symptom group, since the virus concentration of the individual plants within this group merged into the mild or severe groups. The mild symptom group did not differ in virus concentration from the *L. hirsutum* control. The Sioux control was higher in virus infectivity at both dilutions (Tables 4 and 5) than was the severe symptom group in the back-cross to Sioux. This difference was significant at the March 20 test date.

In the back-cross to *L. hirsutum*, plants having symptoms were

tested against plants not showing symptoms. No differences in virus concentration were established between symptom and non-symptom groups as a whole (Tables 6, 7, and 8). In one test (Table 8), however, the symptom group had a significantly higher virus concentration than the non-symptom group and the *L. hirsutum* control.

Tomato plant differences were found to be from twenty to twenty-five times greater in the two back-crosses than among the plants in the F_1 (Table 9). Tomato plant differences in the *L. hirsutum* progeny were about four to five times greater than among plants in the F_1. Necrotic test plant differences, although generally positive, were not significant in any case.

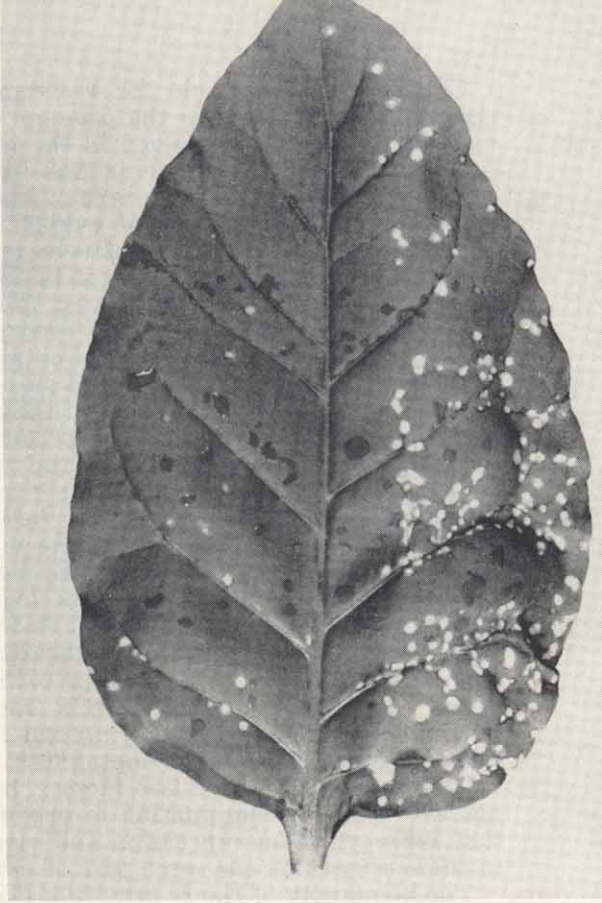


Figure 6.—Leaf of the test plant showing necrotic lesions from *L. hirsutum* on the left half-leaf and from Sioux on the right half-leaf. Dilution: 1:10,000.

Discussion

Symptoms of tobacco mosaic virus infection were not observed under either field or greenhouse conditions on the *L. hirsutum* parent. Cuttings from the *L. hirsutum* parent plant produced only 10.6 per cent as much virus, on the average, as was produced by the Sioux parent. Therefore, the *L. hirsutum* parent plant was much more resistant to both the disease and to virus production than was the Sioux parent. Both the *L. hirsutum* parent and the selfed progeny were found to contain the virus, but none of these showed any symptoms.

Chart 1 shows that a correlation existed between field symptom expression and virus infectivity. This relationship is shown in Tables 2, 3, 4, and 5. In general, the severity of the symptom expression can, therefore, be used as a fairly reliable criterion of resistance. However, when symptom expression was intermediate the virus concentration seemed to be a much better criterion of resistance, since it is more accurately determined than the severity of the symptoms can be subjectively classified. The two primary reasons for a reduced correlation between field symptom expression and virus infectivity were field escapes and the rough subjective classification.

Characters responsible for resistance to tobacco mosaic were shown to be inherited in the progeny of the crosses. At least two pairs of genes were involved in the inheritance of this resistance to tobacco mosaic virus. This was indicated in the back-cross to *L. hirsutum* by the ratio of three symptomless plants to one having symptoms. Three sources of evidence from the back-crosses indicated that there were relatively few pairs of genes affecting resistance to tobacco mosaic virus in these crosses, namely: (1) the wide variation of symptom classes, (2) the wide variation in virus infectivity, and (3) the ease of recovery of the parental types in the first back-cross. The results obtained in these studies can be explained on the basis of only two pairs of genes.

The factors for resistance contributed by the *L. hirsutum* parent seemed to have a dominant effect on virus infectivity of the F_1 hybrid and the back-cross. If the genes of both parents contributed equally, the average virus concentration of the F_1 hybrids would be approximately half way between the two parents. This was not the case, since the average virus concentration of the F_1 hybrid lies approximately one-third closer to the *L. hirsutum* than the Sioux. In the back-crosses the average virus content is lower than would be expected if the influence of the genes were additive.

The F_1 produced symptoms indicating that symptom production was dominant. In the back-cross to Sioux, all of the plants produced symptoms supporting this conclusion. The *L. hirsutum* back-cross plants developed symptoms in one-third of their number, and two-thirds remained symptomless.

This indicated at least two factors, both of which were dominant and necessary in combination to produce symptoms. It is possible that both symptom expression and virus infectivity are controlled in these crosses by the same pair of genes.

The klendusity of the *L. hirsutum* plant and the crosses as shown in field infection and artificial inoculation appears to be distinct and different from the resistance to the disease. Doolittle and Porte (2) reported observing both a "tolerance" and a tendency of the plants to escape natural infection in the field. These data would indicate that both klendusity and resistance are inherited and that the escape tendency more nearly follows the *L. hirsutum* type. No further work was done with the klendusity factor.

The Sioux parent was produced from a commercial tomato variety by selfing for several generations and was presumed to be a pure line and homozygous for the characters under investigation. The *L. hirsutum* homozygosity was open to some question due to the tendency of this species to be cross pollinated in nature. For that reason a selfed progeny was used in these tests to evaluate the genetic segregation in the *L. hirsutum* parent. The uniformity of reaction as to symptom expression and virus concentration in the *L. hirsutum* progeny and the F_1 hybrid would indicate that the *L. hirsutum* parent was relatively homozygous for the characters studied.

Table 1.—A comparison of field and green house mosaic readings of the Sioux and *L. hirsutum* parent plants, the *L. hirsutum* progeny plants, the F_1 and the back-cross plants.

Plant Lines	First Field Reading			Second Field Reading			Greenhouse Reading		
	Total Plants	No. Plants Mosaic	Percent Mosaic	Total Plants	No. Plants Mosaic	Percent Mosaic	Total Plants	No. Plants Mosaic	Percent Mosaic
	Number		Percent	Number		Percent	Number		Percent
Sioux	44	36	81.8	43	42	97.7	200	200	100.0
L. hirsutum (parent)	12*	0	0.0	12	0	0.0	12	0	0.0
L. hirsutum (progeny)	58	0	0.0	58	0	0.0	31	0	0.0
F_1 hybrids	31	2	6.4	31	6	19.3	9	9	100.0
B-C to Sioux	943	770	81.9	453	438	96.7	332	332	100.0
B-C to L. hirsutum†	795	32	4.2	‡	‡	‡	123	34	27.8

* Cuttings from one individual plant.

† Chi-square for ratio of 3:1 in back-cross to *L. hirsutum*, greenhouse reading=0.388; 5 per cent point =3.841. A very good fit of the data to the 3:1 ratio.

‡ The first field reading was made late due to the time required to cover the field; and no second reading was made.

Table 2.—Relative tobacco mosaic virus infectivity in parent *L. hirsutum* and Sioux checks at the various dates.
Infectivity measured by number of local lesions

Symptom group	Dates read	Dilution 1-10,000 Plant means	Dilution 1-10,000 Logarithmic means	Dilution 1-100,000 Plant means	Dilution 1-100,000 Logarithmic means
		Numbers			
L. hirsutum (no symptoms)	March 6	19.5	1.2864	4.5	
	March 11	45.5	1.6517	9.5	
	March 13	28.2	1.4345	4.2	
	March 18	57.5	1.7513	12.2	
	March 20	25.0	1.3865	5.5	
	March 22	20.0	1.2840	2.5	
Group means—		32.6	1.4674	6.4	
Sioux (Severe symptoms)	March 6	235.0		75.7	1.8742
	March 11	234.5		74.7	1.8697
	March 13	215.7		63.2	1.7983
	March 18	214.7		50.7	1.6927
	March 20	182.7		34.7	1.5306
	March 22	208.7		56.5	1.7389
Group means—		215.2		59.2	1.7508
* L.S.D. Dates 0.05			0.1523		0.1440
L.S.D. Dates 0.01			0.2087		0.1972

* Least significant differences for individual date means.

Table 3.—Relative tobacco mosaic virus infectivity in *L. hirsutum* progeny (Line 3) and Sioux X *L. hirsutum* F_1 hybrids (line 4.) (Tested March 11). Infectivity measured by number of local lesions

Symptom group	Plant no.	Dilution 1-10,000 Plant means	Dilution 1-10,000 Logarithmic means	Dilution 1-100,000 Plant means	Dilution 1-100,000 Logarithmic means
		Numbers			
	L. hirsutum progeny				
	3-2	35.8	1.5472	5.0	
1	4	18.7	1.2630	3.5	
(No symptoms)	5	31.0	1.4824	8.0	
	6	39.7	1.5777	5.5	
	7	40.0	1.5938	10.5	
	9	22.2	1.3391	4.0	
	10	38.2	1.5784	5.0	
	12	39.5	1.5942	9.5	
	13	25.0	0.9937	2.2	
	14	20.5	1.2997	3.2	
Group means—		29.6	1.4269	5.7	
	F_1 hybrid				
	4- 1	80.5		19.5	1.2781
	4	90.5		21.2	1.3245
	6	105.7		26.5	1.4166
2	11	107.5		18.5	1.2591
(Symptoms)	18	65.2		12.0	1.0714
	20	78.5		13.5	1.1188
	23	78.0		16.5	1.1971
	26	110.5		17.7	1.2414
	30	116.7		21.0	1.3156
Group means—		92.5		18.4	1.2470
3 (No symptoms)	*L. hirsutum*	45.5	1.6517	9.5	0.9747
4 (Severe symptoms)	Sioux	234.5		74.7	1.8697
L.S.D. Plants 0.05			0.1752		0.1763
L.S D. Plants 0.01			0.2389		0.2415
L.S.D. Symp. 1 and 3, 0.05			0.1838		
L.S.D. Symp. 2 and 3 or 2 and 4, 0.01					0.1384

Table 4.—Relative tobacco mosaic virus infectivity in Sioux back-cross. (Tested March 6).
Infectivity measured by number of local lesions

Symptom group	Plant No.	Dilution 1-10,000 Plant means	Dilution 1-100,000 Plant means	Logarithmic means
		Numbers		
	5- 9	48.0	7.5	0.8618
	59	43.7	6.7	0.8261
1	116	38.5	5.7	0.7508
(Mild	215	47.0	6.5	0.7751
symptoms)	228	36.2	4.5	0.6118
	407	35.7	4.2	0.6901
Group means—		41.5	6.0	0.7526
	5-136	50.7	7.7	0.8682
	198	46.0	7.7	0.8261
2	199	43.0	6.5	0.7583
(Medium	326	25.5	4.2	0.6193
symptoms)	395	81.0	23.5	1.3645
	398	65.0	12.0	1.0808
Group means—		51.8	10.3	0.9195
	5- 28	201.0	49.5	1.6862
	142	136.5	24.0	1.3723
3	182	225.0	33.0	1.7218
(Severe	293	151.7	42.0	1.6011
symptoms)	319	250.0	133.2	2.1153
	486	250.0	86.7	1.9360
Group means—		202.3	64.7	1.7388
4 (No symptoms)	*L. hirsutum*	19.5	4.5	0.63975
5 (Severe symptoms)	Sioux	235.0	75.7	1.8742
L.S.D. Plants 0.05				0.2232
L.S.D. Plants 0.01				0.2994
L.S.D. Symp. 1, 2, and 3. 0.05				0.2714
L.S.D. Symp. 1, 2, and 3. 0.01				0.3754
L.S.D. Symp. 1, 2, or 3 and 4 or 5. 0.05				0.2180
L.S.D. Symp. 1, 2, or 3 and 4 or 5. 0.05				0.3014

Table 5.—Relative tobacco mosaic virus infectivity in Sioux back-cross. (Tested March 20).
Infectivity measured by number of local lesions

Symptom group	Plant No.	Dilution 1-10,000 Plant means	Dilution 1-100,000 Plant means	Logarithmic means
		Numbers		
	5-536	45.7	9.0	0.9309
	918	61.7	12.5	1.0836
1	919	59.7	8.2	0.8944
(Mild)	940	48.2	7.7	0.8721
symptoms	975	22.7	5.0	0.6945
Group means—		47.5	8.5	0.8951
	5-503	155.2	40.5	1.6038
	507	94.5	23.5	1.3642
2	513	117.2	30.0	1.4574
(Medium)	558	106.2	18.2	1.2569
symptoms	585	92.0	22.0	1.3216
Group means—		113.0	26.8	1.4008
	5-538	174.7	46.2	1.6539
	579	77.2	11.2	1.0206
3	763	94.7	18.7	1.2636
(Severe)	799	98.7	22.0	1.3204
symptoms	787	88.7	20.2	1.2769
Group means—		106.7	23.7	1.3071
4 (No symptoms)	*L. hirsutum*	25.0	5.5	0.72134
5 (Severe symptoms)	Sioux	182.7	34.7	1.5306
L.S.D. Plants 0.05				0.2335
L.S.D. Plants 0.01				0.3159
L.S.D. Symp. 1, 2, and 3. 0.05				0.2372
L.S.D. Symp. 1, 2, and 3. 0.01				0.3326
L.S.D. Symp. 1, 2, or 3, and 4, or 5. 0.05				0.1982
L.S.D. Symp. 1, 2 or 3, and 4, or 5. 0.01				0.2779

Table 6.—Relative tobacco mosaic virus infectivity in *L. hirsutum* back-cross. (Tested March 13).
Infectivity measured by number of local lesions

Symptom group	Plant No.	Dilution 1-10,000 Plant means	Dilution 1-10,000 Logarithmic means	Dilution 1-100,000 Plant means
		Numbers		
	8- 3	33.5	1.4771	5.2
	5	40.2	1.5916	5.2
	17	30.2	1.4728	6.2
	20	16.5	1.2057	2.0
1	21	38.2	1.5819	7.7
(No symptoms)	23	29.5	1.4352	4.2
	25	18.2	1.2336	3.7
	26	41.2	1.6069	8.7
	28	35.5	1.5376	5.2
	29	43.0	1.6200	7.5
	31	33.0	1.5150	6.2
	32	88.2	1.9414	13.0
	33	30.2	1.4641	5.7
Group means—		36.7	1.5141	6.2
	8- 2	41.2	1.5832	7.2
	6	25.2	1.3774	4.5
	16	29.2	1.4562	5.5
	24	25.0	1.3948	7.0
	36	48.5	1.6811	11.0
2	42	17.7	1.2343	2.5
(Symptom)	52	16.0	1.1993	2.7
	61	33.2	1.4993	5.0
	69	41.2	1.5944	6.0
	80	29.2	1.4587	7.5
	86	15.7	1.1892	1.7
	94	53.0	1.7200	11.2
	95	82.2	1.9114	11.0
Group means—		35.2	1.4846	8.3
3 (None)	*L. hirsutum*	28.2	1.4345	4.2
4 (Symptom)	Sioux	215.7		63.2
L.S.D. Plants 0.05			0.2444	
L.S.D. Plants 0.01			0.3303	

Table 7.—Relative tobacco mosaic virus infectivity in *L. hirsutum* back-cross. (Tested March 18).
Infectivity measured by number of local lesions

Symptom group	Plant No.	Dilution 1-10,000 Plant means	Dilution 1-10,000 Logarithmic means	Dilution 1-100,000 Plant means
		Numbers		
	9- 5	45.0	1.6402	8.0
	9	26.5	1.4126	5.2
	11	39.0	1.5754	5.0
	13	21.0	1.3013	4.2
1	14	28.2	1.4391	5.0
(No symptoms)	15	88.5	1.9459	22.5
	20	77.0	1.8720	19.5
	30	39.7	1.5819	7.2
	32	97.7	1,9808	24.0
	42	50.2	1.6919	10.0
	43	102.0	2.0045	22.0
Group means—		55.9	1.6770	13.2
	9- 4	37.0	1.5528	8.0
	6	57.7	1.7552	8.7
	8	55.5	1.7330	11.0
2	18	38.0	1.5642	7.5
(Symptom)	24	55.0	1.7235	8.5
	27	43.5	1.6147	7.2
	29	26.5	1.3996	4.2
	31	38.2	1.5556	6.5
	45	93.5	1.9637	18.5
	61	83.0	1.9135	13.7
	72	90.2	1.9508	16.2
Group means—		56.1	1.7024	9.8
3 (None)	*L. hirsutum*	57.5	1.7513	12.2
4 (Symptom)	Sioux	214.7		50.7
L.S.D. Plants 0.05			0.1710	
L.S.D. Plants 0.01			0.2276	

Table 8.—Relative tobacco mosaic virus infectivity in *L. hirsutum* back-cross. (Tested March 22).
Infectivity measured by number of local lesions

Symptom group	Plant No.	Dilution 1-10,000 Plant means	Dilution 1-10,000 Logarithmic means	Dilution 1-100,000 Plant means
		Numbers		
1 (No symptoms)	10- 2	23.2	1.3505	4.2
	6	18.2	1.2370	3.0
	16	17.5	1.2247	3.7
	17	41.5	1.5887	8.7
	18	7.2	0.8503	1.7
	24	30.7	1.4754	5.5
	30	35.7	1.5414	6.7
	35	77.0	1.8697	13.7
	36	37.5	1.5497	8.0
	59	20.0	1.2830	4.0
Group means—		30.8	1.3970	5.9
2 (Symptom)	10-13	20.5	1.2914	5.0
	15	30.0	1.4358	5.0
	20	83.2	1.9158	13.0
	21	37.5	1.5426	8.0
	28	59.2	1.7599	12.0
	32	74.7	1.8728	12.0
	37	26.0	1.4027	4.2
	39	101.7	1.9903	17.2
	45	51.7	1.6898	8.2
	53	35.0	1.5314	8.2
Group means—		51.9	1.6432	9.3
3 (None)	*L. hirsutum*	20.0	1.2840	2.5
4 (Symptom)	Sioux	208.7		56.5
L.S.D. Plants 0.05			0.2785	
L.S.D. Plants 0.01			0.3755	
L.S.D. Symp. 1 and 2, 0.05			0.2414	
L.S.D. Symp. 1 and 2, 0.01			0.3306	
L.S.D. Symp. 1 or 2 and 3, 0.05			0.2018	
L.S.D. Symp. 1 or 2 and 3, 0.01			0.2765	

Table 9.—Estimates of variance components and standard errors of means for virus infectivity in logarithms of necrotic spots

Plant groups	Source of variation: Leaves (error)	Test plants	Tomato plants	Test dates	Standard error of weighed mean
	Numbers				
Parents:					
Sioux	.0094	.0000	....	.0144**	.0528
L. hirsutum	.0105	.0000	....	.0348**	.0790
L. hirsutum progeny	.0107	.0017	.0362**	....	.0630
Crosses:					
F_1	.0075	.0033	.0078*	....	.0354
B. C. to Sioux	.0194	.0027	.1600**	....	.0710
B. C. to *L. hirsutum*	.0135	.0061	.2271**	....	.0605

* Significant at 5 percent level
** Highly significant at 1 percent level

Table 10.—Geometric means of virus infectivity at 1-100,000 dilution and number of plants or dates on which the means are derived.

Plant Groups	Symptoms			No symptoms	Weighed means and total numbers
	Mild	Intermediate	Severe		
Parents:		Numbers			
Sioux	....	....	56.3	....	56.3
Number of dates tested	....	....	6	....	6
L. hirsutum	....	....	....	6.6	6.6
Number of dates tested	....	....	....	6	6
L. hirsutum progeny	....	....	....	6	6
Number of plants classified	....	....	....	10	10
Number of plants tested	....	....	....	10	10
Crosses:					
F_1	17.7	....	....	....	17.7
Number of plants classified	9	....	....	....	9
Number of plants tested	9	....	....	....	9
Back cross to Sioux	6.6	13.8	34.9	....	20.5
Number of plants classified	11	127	69	....	207
Number of plants tested	11	11	11	....	33
Back cross to *L. hirsutum*	8.1	....	....	6.9	7.3
Number of plants classified	34	....	....	89	123
Number of plants tested	32	....	....	34	66

Summary

1. This paper deals with the genetics of the transfer of resistance to tobacco mosaic virus in an interspecific tomato cross through F_1 and the two back-crosses.

2. Tobacco mosaic resistance was shown to be inherited and recoverable in the back-crosses along with commercially desirable characters. The native resistance of the *L. hirsutum* plant to tobacco mosaic virus was due to two types of plant response. One was klendusic in nature, and the other was plant resistance. This resistance was not complete in the *L. hirsutum* parent plant used in these studies.

3. The inheritance of resistance as observed in these interspecific crosses could be explained on the basis of two dominant genes, both required for maximum resistance as present in the *L. hirsutum* parent plant.

4. Symptom expression in the back-cross progeny varied considerably. In the back-cross to Sioux all plants developed symptoms which varied from a mild to severe mottle. In the back-cross to *L. hirsutum*, one third of the plants had a very light mottle and two thirds developed no symptoms.

5. After repeated inoculations all plants were found to contain virus. The commercial Sioux contained 9.4 times more virus than the resistant *L. hirsutum* parent. The F_1 virus content was intermediate but more closely approached that of the *L. hirsutum* than the Sioux. Plants with severe symptoms had more virus than plants with mild symptoms. The mild symptom plants had more virus, on the average, than those plants with no symptoms.

6. The necrotic test plant differences were small and insignificant statistically, indicating the value of the hybrid (*N. tobaccum* x *N. glutinosa*) as a necrotic test plant for evaluation of virus infectivity.

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