A RELATIONSHIP BETWEEN IMMUNITY AND LOCALIZED REACTION TO VIRUS X IN THE POTATO (*SOLANUM TUBEROSUM*)

By E. M. Hutton* and D. C. Wark*

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Summary

The pattern of virus X development in the inoculated leaves of immune, localized reacting, and susceptible phenotypes in the potato has been studied. The results indicate that immunity is not absolute. Phenotypes giving a localized reaction cannot be regarded as hypersensitive. The evidence shows that an inactivating system restricts the development of the virus as soon as infection takes place.

All the results, including those from the X inoculation of first-generation seedlings, raised from intercrosses between immune, localized reacting, and susceptible phenotypes, indicate that a common virus-inactivating system determines resistance. The difference between localized resistance and immunity may be determined by different tetraploid conditions of a common major gene.

I. Introduction

Immunity to virus X in potatoes was first described by Schultz *et al.* (1934) in the American seedling U.S.D.A. 41956. Later, Stevenson, Schultz, and Clark (1939) found that in crosses between 41956 and susceptible parents, 37-42 per cent. of the progenies were immune and that selfing immune types resulted in 72-78 per cent. of the progenies being immune. On this basis they assumed two genes, one in the duplex and the other in the simplex condition, to be necessary for immunity to virus X.

Cadman (1942) studied the inheritance of the top-necrotic reaction to virus X following grafting in a number of hybrid potato progenies and found most necrotic-reacting varieties to be simplex for the dominant allele of a gene. Phenotypes reacting in this way give only localized necrotic lesions when the leaves are inoculated, and both Cockerham (1943) and Cadman (1942) regard these reactions as evidence of extreme susceptibility or hypersensitivity. Under field conditions of infection with virus X, potato varieties and seedlings with a localized reaction remain free of this virus.

Little work has been done on the nature of the immune and localized reactions to virus X in the potato, in spite of their importance in this crop and their bearing on the general problem of virus resistance. Clinch (1942) used Seedling 41956 as the stock or scion in grafts with X-infected potatoes, and also as the intermediate scion in double grafts with infected and virus-free material above and below. She found that 41956 failed to become infected

* Division of Plant Industry, C.S.I.R.O., Canberra, A.C.T.

with virus X but allowed the virus to pass unchanged through its stem. She concluded that the non-multiplication of virus X in 41956 was due to the lack in its cells of some substance or physical condition necessary for virus X synthesis. The course of infection and subsequent localization and death of the virus in hypersensitive phenotypes has not been studied. It is difficult to see how extreme susceptibility can account for the resistance of these phenotypes to systemic invasion by virus X.

At Canberra a study of the pattern of virus X development has been made in both immune and hypersensitive phenotypes. The results indicate that both reactions have a common basis and are dependent on a similar major gene.

II. Materials and Methods

A virulent strain of virus X, cultured in *Datura stramonium,* was used as described previously (Hutton 1948). The pattern of virus X development was followed in the immune 11-84, the localized reacting Epicure and 47-20, and in a virus-free clone of the susceptible Factor. The hybrids 11-84 and 47-20 derived their X resistance from 41956 and Epicure respectively.

Vigorous plants, 12 in. high were each inoculated on six leaves during the summer in the glass-house. At intervals up to 4 or 8 weeks after inoculation, according to the experiment, discs of tissue were removed from inoculated leaves with a cork borer (diam. 9 mm.). For each plant at any one interval, one disc of tissue was removed from each of the six inoculated leaves, and the discs macerated together to provide inoculum for transfers to two young *D. stramonium* plants and duplicate globe amaranth leaves (cf. Wilkinson and Blodgett 1948).

For the studies involving the inheritance of the localized and immune reactions in hybrid progenies, a series of potato crosses were made to include all combinations between selected hybrids with either immune, localized, or susceptible reactions to virus X. To prevent indirect effects on the types of inheritance, only hybrids with well-defined parental backgrounds of immunity, localized reaction, or susceptibility were selected for crossing. First-generation seedlings were raised from the hybrid seed in the autumn, and were inoculated with virus X on the third unfolded leaf from the tip when 3 in. high. Reactions were observed at weekly intervals. Seedlings that developed systemic necrosis following a localized reaction were discarded. Eight weeks after inoculation, the tips of the seedlings that had been retained were tested for the presence of virus X by transfers to globe amaranth.

III. Pattern of Virus X Development in Immune, Localized Reacting, and Susceptible Phenotypes

After the plants of 11-84, 47-20, Epicure, and Factor were inoculated, the samplings and transfers to indicators were made at intervals of 2 or 3 days for the first 2 weeks, and then at two further weekly intervals. At the final transfer, tips of all the potato plants were inoculated to the indicators.

In Table 1 the *D. stramonium* results show the presence or absence of virus X. The lesion numbers on globe amaranth indicate both presence and concentration of virus. There was a marked contrast between the different types of reaction. In the susceptible Factor, virus X quickly became established in relatively high concentration when compared with the resistant Epicure and 47-20, in which virus concentration never reached a high level, and from which virus was recovered in only a low percentage of cases. The fact that an early limited development of virus X occurred in the immune 11-84 was of considerable interest.

TABLE 1

VIRUS X RECOVERIES FROM DISCS TAKEN AT INTERVALS FROM INOCULATED LEAVES OF IMMUNE, LOCALIZED REACTING, AND SUSCEPTIBLE PHENOTYPES

A = number of potato plants out of six which gave a positive reaction on *D. stramonium**; *B* = mean number of lesions on globe amaranth from six potato plants

Intervals After Inoculation at Which Transfers Made (days)	Factor Susceptible		Epicure Localized Reacting		47-20 Localized Reacting		11-48 Immune	
	A	*B*	*A*	*B*	*A*	*B*	*A*	*B*
2	1	0.5	0	0.2	0	0.0	0	3.8
5	4	7.8	1	3.6	2	6.3	1	0.2
7	6	29.2	1	1.0	0	0.7	0	0.0
9	6	34.5	4	3.3	2	0.3	0	0.0
12	6	17.8	2	0.2	2	0.3	0	0.0
14	6	29.3	1	2.3	0	0.0	0	0.0
21	6	43.0	2	0.5	1	0.2	0	0.0
28	6	18.0	5	0.2	3	0.8	0	0.0
28 (Tips)	6	4.5	2	0.0	1	0.0	0	0.0

* In Factor, except for two transfers, both duplicates reacted in every case. In others, 72-100 per cent. of the transfers gave a reaction in only one of the duplicates.

The results of Table 1 give no indication of an extreme susceptibility being present in Epicure and 47-20, but rather the presence of an inactivating system which restricts virus development and concentration as soon as infection takes place. In view of the results with 11-84 it is possible that the difference between immune and localized-reacting phenotypes is only one of degree.

IV. THE IMMUNE REACTION TO VIRUS X

In view of the importance of the previous finding that the immune 11-84 allowed a very restricted development of virus X in inoculated leaves, another and similar experiment was done with this hybrid, using virus-free Factor as the control. To obviate any possibility of adhering tissue from the inoculum causing the results described, the six leaves on each of the six inoculated plants of both 11-84 and Factor were washed thoroughly with water several times after inoculation.

The results in Table 2 confirm those obtained previously. The recoveries shown for 11-84 are all from different plants, so that half the plants of this immune hybrid allowed a very restricted development of virus X, one of the recoveries being made 3 weeks after inoculation.

TABLE 2

VIRUS X RECOVERIES FROM INOCULATED LEAVES OF 11-84 AND FACTOR

		Intervals After Inoculation at Which Transfers Made (days)						Intervals After Inoculation at Which Transfers Made (weeks)							
Variety	*D. stramonium*	1	2	3	4	5	7	2	3	4	5	6	7	8	Final
11-84 (immune)	No. out of 12 which reacted	0	0	1	0	0	0	1	1	0	0	0	0	0	0
Factor (susceptible)		0	1	2	5	7	12	12	12	12	12	12	12	12	12

V. Immunity, Resistance, and Susceptibility to Virus X Dependent on Different Tetraploid Conditions of a Common Major Gene

The experiments described have indicated that in 11-84 the immunity to virus X derived from 41956 is not absolute and is dependent on the inheritance of a highly efficient virus-inactivating system. The reaction of Epicure or 47-20, usually described as hypersensitivity, appears to be a form of general resistance dependent on the operation of a similar virus-inactivating system, in fact the difference between this reaction and immunity could well be one of degree. In order to find whether such relationship could be established genetically, segregations for the three X reactions were recorded in the hybrid progenies raised and inoculated as described in Section II. The results are given in Table 3.

The main features of Table 3 are the high proportion of localized reacting resistant seedlings from crosses involving only X-immune parents, and the appearance of immune phenotypes from crosses between localized reacting parents. These findings are further substantiated by the isolation of localized reacting phenotypes in the progeny of immune-susceptible crosses, and immune phenotypes from localized-susceptible crosses. A further point of interest is the reduction in the percentage of resistant phenotypes resulting when the immune parent was male in the two combinations, immune-localized and immune-susceptible.

These results support those obtained in the previous experiments, and establish that immune parents carry genetic factors for localized necrosis, while localized reacting ones carry factors for immunity. They also suggest that the same virus-inactivating system is being inherited by the resistant phenotypes in the various progenies. Whether this system functions as the highly

TABLE 3

PERCENTAGES OF PHENOTYPES WITH IMMUNE, RESISTANT, AND SUSCEPTIBLE REACTIONS TO VIRUS X RESULTING FROM CROSSES BETWEEN HYBRIDS WITH THESE DIFFERENT REACTIONS

Type of Parentage (Female first, Male second)	No. of Different Hybrid Progenies	No. of Seedlings Tested	Susceptible Seedlings			Resistant or Immune Seedlings			Range in Resistant or Immune Between Different Hybrid Progenies (%)
			Lesions Absent (%)	Lesions Present (%)	Total (%)	Lesions Absent (%)	Lesions Present (%)	Total (%)	
Immune × immune	5	542	25.0	26.6	51.6	12.4	36.0	48.4	29 to 56
Immune × localized	3	381	57.2	7.6	64.8	28.0	7.2	35.2	13 to 41
Localized × immune	4	425	68.5	13.6	82.1	10.1	7.8	17.9	10 to 26
Immune × susceptible	4	165	46.7	23.0	69.7	14.0	16.3	30.3	13 to 62
Susceptible × immune	4	597	75.8	19.0	94.8	4.5	0.7	5.2	3 to 25
Localized × localized	2	67	79.1	3.0	82.1	16.4	1.5	17.9	7 to 26
Localized × susceptible	3	190	64.2	14.8	79.0	14.2	6.8	21.0	14 to 31
Susceptible × susceptible	3	333	87.0	13.0	100	0.0	0.0	0.0	0

efficient immune one, or as the less effective localized necrotic one is considered to be dependent on different autotetraploid conditions of a common major gene. That using first-generation seedlings in the manner described was necessary for revealing these relationships was shown by the fact that the majority of the tuber progeny from the resistant ones gave an apparently immune reaction to virus X during the summer. It is apparent that the drastic methods used have been highly selective for immune and nearly immune phenotypes.

VI. Discussion

Some of the implications of these results have been discussed generally elsewhere (Hutton 1951). The results emphasize the need for a biochemical understanding of the virus-inactivating system involved, as this would be the only way to prove or disprove the relationships shown. There is little doubt that the term hypersensitivity is inappropriate for the reaction to X of Epicure and its derivatives, and that the term resistance should take its place. It is contended that the necrotic reaction is not necessary to the primary virus inactivation process, but is a side reaction. This is supported by the fact that the majority of resistant first-generation seedlings, which reacted necrotically, did not do so later as tuber progeny.

Cadman (1942) has summarized the evidence for the tetraploid nature of the potato. Taking into consideration his results and those of Stevenson, Schultz, and Clark (1939), as well as the ratios of resistant or immune to susceptible phenotypes obtained in our experiments, it is suggested that the recessive allelomorph of a gene in the nulliplex condition results in immunity, while the dominant allelomorph in the quadruplex condition gives complete susceptibility. The simplex and duplex conditions could give phenotypes with localized reactions, the one resulting from the former being the more efficient. Phenotypes reacting with severe systemic necrosis would be dependent on the triplex condition. There is no doubt that the operation of the major gene as suggested is tempered by polygenes.

VII. Acknowledgment

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