A RECESSIVE TYPE OF IMMUNITY TO VIRUS X IN THE POTATO¹

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IN *Solanum tuberosum* L. two types of resistance to potato virus X (JOHNSON 1925; SMITH 1931) have been reported, *viz.*, field immune type and immunity type, both following tetrasomic inheritance. The first is controlled by dominant genes *Nx* and *Nb* present in simplex or duplex condition (CADMAN 1942; COCKERHAM, 1943 a,b; 1945). KOHLER and ROSS (1951) designated almost similar isolates as *X^N* and *X^B*. The second type of resistance is controlled by two dominant complementary genes (STEVENSON, SCHULTZ and CLARK 1939). KEHR and HORTON (1959, 1960) observed that these two complementary genes could exist separately in a dominant condition in some susceptible varieties and combine to impart immunity when such two susceptible varieties are crossed. A case of immunity control by a single dominant gene (inherited on a disomic basis) from *Solanum acaule* Bitt. has also been reported (ROSS 1954).

HUTTON (1951) suggested that immunity to virus X could be conditioned by a recessive gene but no data were provided.

A large number of strains of virus X have been described. Those causing hypersensitive responses have been divided into five groups (COCKERHAM 1954, 1960) on the basis of phenotypic expression of symptoms on four potato varieties. In the case of strains isolated from varieties in which resistance is controlled by immunity type of genes, a number of distinct strains have been reported (LADEBURG, LARSON and WALKER 1950; HANSEN and LARSON 1957, 1959). Most of these appear identical in serological cross absorption tests but a few differ from others (MATTHEWS 1949). However, it is interesting that the different immunity or hypersensitive types of resistance (described above) have not so far been overcome by any strains of virus X.

In the present investigation, a new pattern of immunity response controlled by a recessive gene, not hitherto described, was observed in one variety of *S. tuberosum*. The possible genetic constitution and nature of inheritance of this new gene in this variety and its relationship to the complementary genes described by STEVENSON *et al.* (1939) in two *S. tuberosum* varieties are discussed in the present paper.

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MATERIALS AND METHODS

Potato Varieties: Three hybrids were selected from the University of Wisconsin potato breeding stock for the present investigation. Of these, X 137 and X 143 are derivatives of S. 41956 and are immune to virus X. The third, AG 54.55 is not related to S. 41956 and is susceptible to virus X.

The population of seedlings in different generations of selfed lines of these varieties and their crosses screened for resistance to the virus is given in Table 1.

The seeds were germinated in furrows in small trays lined with "black" sand above vermiculite. Seedlings about 4 cm high were transplanted to 8 cm pots, in the greenhouse at 16° C to 20° C.

Virus X: Five different strains of virus X were tested on *Nicotiana glutinosa* L., *Datura stramonium* L., *D. tatula* (L) Torr. and *S. tuberosum*. On the basis of the behavior on different hosts, a Ring Spot Strain X²¹ of Wisconsin stock (LADEBURG *et al.* 1950) was selected for use as a tester strain as it was observed to be the most stable and severe.

A pure culture of the virus was maintained on *Nicotiana rustica* L. Stock cultures were dehydrated and stored at freezing temperatures. In order to protect the infectivity, the virus was periodically recovered after passage through potato seedlings. It was multiplied on *N. rustica* and *D. tatula*. For resistance tests, the third and fourth leaves of one month old potato seedlings were inoculated with fresh sap expressed from leaves of *Nicotiana tabacum* L. var. Havana 38 (on which the virus culture was maintained) diluted 1:10. To ensure infection, inoculation was done twice at weekly intervals. The infectivity and purity of culture of each preparation of X²¹ was tested by inoculating at least 25 plants of *N. tabacum* var. Havana 38 and 5 plants of *N. rustica* which acted as check.

Method of testing for systemic infection of virus X: The inoculated seedlings were allowed to grow for one month. Thereafter the sap from the newly-developed leaves of such seedlings was taken for testing the presence of virus serologically. The results were confirmed by biological testing on *Gomphrena globosa* L.

In order to detect the pattern of resistance in the resistant seedlings of AG 54.55 S₁, about 175 cm high single stem seedlings of 1st tuber generation of S₁ were grafted on to (1) virus X infected susceptible seedlings, using them as stocks and (2) young healthy *D. tatula* plants (used as both stock and scion). When the graft on *Datura* was established, the *Datura* leaves were in-

TABLE 1

Population of seedlings in different generations screened for resistance

Cross details	Generation	Number of seedlings tested for resistance to virus X
<i>Parents:</i>		
1. AG.54.55 selfed	S ₁	509
2. X 137 selfed	S ₁	579
3. X 143 selfed	S ₁	815
4. Four selections from the S ₁ of X 143	S ₂	433
<i>Crosses:</i>		
5. AG.54.55 × X 137	F ₁	879
6. AG.54.55 × X 143	F ₁	1385
7. Seventeen selections from (AG 54.55 × X 143) F ₁	F ₁ -S ₁	1898

S₁ = First selfed generation.

S₂ = Second selfed generation.

F₁ = First filial generation from crossing.

F₁-S₁ = Generation from selfing F₁.

oculated with the virus. Three weeks later the leaves of potato (stock or scion) were tested for the presence of virus by sap inoculation on *G. globosa*, *Capsicum annuum* L. and *N. debneyi* L. A few S_1 resistant selections of X 143 were also tested in this way.

Preparation of antiserum for serological tests and method of testing: The virus cultured on *N. tabacum* var. Havana 38 was purified after BAWDEN and PIRIE (1938) or by repeated ultracentrifugation. The purified virus suspension in normal saline was injected into selected rabbits intravenously in 8 to 10 doses of $1\frac{1}{2}$ to 2 ml. each, at 3-day intervals. The titer of the antiserum was determined after absorption with freshly extracted sap of healthy leaves of *N. tabacum* var. Havana 38. The precipitin tests with leaf sap of virus X inoculated seedlings were made on slides. On each slide a control test using normal rabbit serum was also run. The drops on the slide were examined after 10 min and observations taken at $50\times$ magnification using a dark field condensor.

EXPERIMENTAL RESULTS

The results on the segregation of progenies (Table 1) into resistant and susceptible classes are presented in Tables 2, 3, 4 and 5. In the case of AG 54.55 S_1 , 118 seedlings were resistant on the basis of serological and local lesion tests (Table 2). Out of this population a random sample of 24 seedlings was selected for graft tests. Of these, virus could be detected in new shoots of two plants. These two plants apparently carried a high degree of resistance. The remaining 22 seedlings in the graft test did not show any virus even when repeatedly tested for a further period of 3 months. This confirmed that the plants carried genes of immunity type conferring resistance to the virus.

Observations on graft tests with selected resistant plants of X 143 S_1 revealed that this variety also carried genes of the immunity type for resistance.

DISCUSSION

Hypersensitivity vs. Immunity: No S_1 seedling of X 143 or AG 54.55 exhibited a hypersensitive reaction on graft inoculation. It can be concluded from these observations that (1) the parental potato varieties possess immunity genes to virus X (See SCHULTZ *et al.* 1933; COCKERHAM, 1943b), and (2) hypersensitivity and immunity reactions are probably controlled by different genes. Further, it is also clear from the observations (which were recorded at temperature ranges of 16° to 24°C) that immunity is not an extreme form of hypersensitivity as considered by some authors (HUTTON 1951; HOOKER, 1954; ROSS 1954), but both are independent types of reactions. This observation is in agreement with the view of HOLMES (1955) and B. KASSANIS (private communication).

Genetic pattern of resistance in the varieties: An analysis of the data on the S_1 , S_2 , F_1 and F_1 - S_1 population of the varieties and crosses between them provides information on the genetic nature of the immunity genes in the parental varieties.

Pattern in AG 54.55: The population of 509 seedlings of AG 54.55 segregated into 118 immune and 391 susceptible types (Table 2). The segregation ratios fit nicely with HALDANE's (1930) simplex random chromosome segregation, indicating the presence of a dominant gene for susceptibility. Designating the immunity gene in this variety with a letter *c*, the genotype of AG 54.55 in relation to virus X should be *Cccc*. Such a gene will impart immunity to any variety

TABLE 2

Values of P from χ^2 with different genotypes for the observed values of S_1 of X 137, X 143 and AG.54.55

Possible genotypes	Resistant	Observed Susceptible	Total	Resistant	Expected Susceptible	Total	P from χ^2
a. Segregation in X 137— S_1							
<i>AaaaBbbb</i>	461	118	579	326	253	579	Very low
<i>AAaaBbbb</i> <i>AaaaBBbb</i>	461	118	579	422	157	579	.0003
<i>AAaaBbbbCCCC</i> <i>AaaaBBbbCCCC</i>	461	118	579	422	157	579	.0003
<i>AAaaBbbbCCCc</i> <i>AaaaBBbbCCCc</i>	461	118	579	422	157	579	.0003
<i>AAaaBbbbCCcc</i> <i>AaaaBBbbCCcc</i>	461	118	579	422	157	579	.001
<i>AAaaBbbbCccc</i> <i>AaaaBBbbCccc</i>	461	118	579	461	118	579	1.0
b. Segregation in X 143— S_1							
<i>AaaaBbbb</i>	615	200	815	458	357	815	Very low
<i>AAaaBbbb</i> <i>AaaaBBbb</i>	615	200	815	594	221	815	0.1
<i>AAaaBbbbCCCC</i> <i>AaaaBBbbCCCC</i>	615	200	815	594	221	815	0.1
<i>AAaaBbbbCCCc</i> <i>AaaaBBbbCCCc</i>	615	200	815	594	221	815	0.1
<i>AAaaBbbbCCcc</i> <i>AaaaBBbbCCcc</i>	615	200	815	600	215	815	0.24
<i>AAaaBbbbCccc</i> <i>AaaaBBbbCccc</i>	615	200	815	650	165	815	0.004
c. Segregation in AG 54.55— S_1							
<i>aaaabbbbCccc</i>	118	391	509	149	360	509	0.001†
<i>A—bbbbCccc</i>	118	391	509	127	382	509	0.4*
<i>aaaaB—Cccc</i>	118	391	509	146	363	509	0.006‡

† Segregation when $a = \frac{1}{3}$.

* Chromosome segregation.

‡ Chromatid segregation.

against virus X when present as a recessive nulliplex *cccc*. STEVENSON *et al.* (1939) described an immunity type resistance in *S. tuberosum* controlled by two complementary genes *A* and *B* present in dominant condition. But the present investigation reveals the existence of a new gene *c* for immunity.

Pattern in X 137 and X 143 and the segregation in crosses with AG 54.55: These two hybrids are related to S 41956 and it is therefore logical to assume that both may have genes *A* and *B* in dominant condition for resistance to virus X. These two genes are inherited in these varieties through the maternal parent B.595-76, a progeny of a cross with S. 41956 (both immune to virus X). The

genotype of S. 41956 has been determined to be *AAaaBbbb* (STEVENSON *et al.* 1939) where presence of both *A* and *B* is necessary to impart immunity. The other parent of B. 595-76 is a virus X susceptible variety, Cherokee. Therefore, for immunity to virus X, B595-76 must inherit the *Bb* complex and the *AA* or *Aa* complex from S. 41956. The observed segregation in S_1 of X 137 and X 143 shows a better fit when the genotype is *AAaaBbbb* than *AaaaBbbb* (Table 2). However, a glance at the goodness of fit when different gene constitutions are assigned to these varieties reveals that deviations from expected ratios are sufficiently large to suggest the presence of some other factor, such as an additional gene.

Since a new gene *c* controlling immunity to virus X has been proposed to explain the type of resistance in AG 54.55, this gene can also be present, in addition to genes *A* and *B*, in varieties X 137 and X 143. In both these varieties, the gene *c* might have come from the parent Minn.133.43-1-45 common in the ancestry of X 137, X 143 and AG 54.55. An examination of the different expected ratios when this gene is present in X 137 and X 143 in quadruplex, triplex, duplex and simplex condition with *A*---- and *B*---- and comparing the same for goodness of fit with the observed segregations, reveals that the segregation ratios of S_1 of X 137 are best explained if its genotypic constitution is *AAaaBbbbCccc* and that of X 143 is *AAaaBbbbCCcc* (Table 2). An analysis of the goodness of fit for observed segregations in F_1 of the crosses (AG 54.55 $\times$ X 137) and (AG 54.55 $\times$ X 143) (Table 3) compared to the expected ratios for F_1 with different genotypic combinations of genes *A* and *B* for AG 54.55, which can be *aaaaB*--- *Cccc* or *A*-- *bbbbCccc* or *aaaabbbbCccc*, shows that the data are best explained by accepting the genetic constitution of AG 54.55 as *aaaaBbbbCccc* and the genetic constitution of X 137 and X 143 as *AAaaBbbbCCcc* (Table 3).

This proposal for the genetic constitution of X 143 is also supported by the expected and observed segregations in F_2 of 17 random selections of the (AG 54.55 $\times$ X 143) F_1 (Table 5), and the observed occurrence of different frequencies of the random sample (Table 6). Further support for the proposed genotypic constitution of X 143 is given by the proposed constitutions for the segregating genotypes observed in S_2 of resistant selections from X 143 S_1 (Table 4).

The marked deviations from the expected autotetraploid ratios of chromosome segregations in the case of observed values of S_2 selection No. 343 of X 143 S_1 (Table 4) and F_2 selection nos. 1537, 1761 and 1923 (Table 5) is due to the increase in the proportion of recessive phenotypes. Such deviations were also observed by LUNDEN (1937) and CADMAN (1942). An analysis of possible causes leading to such situations has been given by CATCHESIDE (1956, 1959).

No precise conclusion can be drawn about the genotypic constitution of X 137 on account of the large range of variation in the P-values in its S_1 and F_1 of the cross AG 54.55 $\times$ X 137 for the genotypes *AAaaBbbbCCcc* and *AAaaBbbbCccc* (Tables 2, 3). This deviation in segregation may be due to the action of one or more of the different variables mentioned by CATCHESIDE (1959).

The question arises how best a recessive gene such as *c* can be utilized in genetic investigations on the potato, and what is its value in a potato improve-

TABLE 3
*Segregation ratios and values of P from χ^2 with the proposed genotypes in the F₁ of
 (AG 54.55 $\times$ X 137) and (AG 54.55 $\times$ X 143)*

Possible genotypes	Segregation in (AG 54.55 $\times$ X 137) F ₁			Segregation in (AG 54.55 $\times$ X 143) F ₁		
	Resistant	Observed Susceptible	Total	Resistant	Observed Susceptible	Total
1. <i>aaabbbbCccc</i> <i>A AaaBbbbCCcc</i>	577	302	879	409	470	879
2. <i>AaaabbbbCccc</i> <i>A AaaBbbbCCcc</i>	577	302	879	455	424	879
3. <i>aaaaBbbbCccc</i> <i>A AaaBbbbCCcc</i>	577	302	879	577	302	879
4. <i>aaaaBBBBCccc</i> <i>A AaaBbbbCCcc</i>	577	302	879	689	190	879
5. <i>aaaaBbbbCccc</i> <i>A AaaBbbbCccc</i>	577	302	879	632	247	879
6. <i>AaaabbbbCccc</i> <i>A AaaBbbbCccc</i>	577	302	879	522	357	879

N.B. P values in most cases have not been calculated the deviation in the observed and expected segregation is high enough to indicate that the genotypes proposed will not fit.

TABLE 4

Segregation in S₂ populations derived from selections of X 143 S₁

Selection No.	Reaction to virus	Observed segregation			Expected segregation			P from χ^2	Possible genotype
		Resist.	Suscep.	Total	Resist.	Suscep.	Total		
26 selfed	Resistant	86	31	117	86	31	117	1.0	<i>AAaaBbbbCCcc</i> or <i>AaaaBBbbCCcc</i>
93 selfed	Resistant	92	2	94	90	4	94	0.33	<i>AAaaBBbbCccc</i>
343 selfed	Resistant	121	16	137	129	8	137	0.004	<i>AAaaBBbbCCcc</i>
921 selfed	Resistant	68	17	85	68	17	85	1.0	<i>AAaaBbbbCccc</i>

ment program. The use of nulliplex individuals in test crosses would considerably simplify the study of inheritance in tetraploids. Its value is further enhanced for a highly heterozygous crop like potato, because it behaves as a single recessive gene controlling immunity to virus X, and acts independently of, as well as in addition to, genes *A* and *B*, while not interfering with the reaction of either.

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SUMMARY

A new recessive gene designated *c* imparts immunity to potato virus X in nulliplex condition to the offspring in an American potato hybrid AG 54.55 (susceptible to virus X). The known complementary genes *A* and *B* for immunity to virus X are also present in two other hybrids X 137 and X 143 (both immune to virus X). Hybridization of AG 54.55 with X 137 and X 143 and segregation of the resulting populations revealed that the gene *c* is present in these two hybrids as well. It is suggested that this gene may have originated in all three hybrids from a common parent, Minn. 113.43-1-45. Gene *c* acts independently of the complementary genes *A* and *B*.—The genetic constitution of the three hybrids in relation to virus X is proposed to be *aaaaBbbbCccc* for AG 54.55, *AAaaBbbbCCcc* or *AAaaBbbbCccc* for X 137, and *AAaaBbbbCCccc* for X 143.

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TABLE 5

Segregation ratios and proposed genotypes for selected S₁ of (AG 54.55 × X 143) F₁

Selection No.	Reaction to virus	Observed segregation			Expected segregation			P from χ^2	Possible genotype
		Resist.	Suscep.	Total	Resist.	Suscep.	Total		
1.1488 selfed	Susceptible	8	37	45	6	39	45	0.25	<i>A—bbbbCccc</i> or <i>aaaaB—Cccc</i>
2.1489 selfed	Susceptible	2	78	80	2	78	80	0.9	<i>A—bbbbCCcc</i> or <i>aaaaB—CCcc</i>
3.1502 selfed	Susceptible	6	177	183	5	178	183	0.65	<i>A—bbbbCCcc</i> or <i>aaaaB—CCcc</i>
4.1537 selfed	Susceptible	20	138	158	...	...	...	...	
5.1543 selfed	Susceptible	19	52	71	18	53	71	0.85	<i>A—bbbbCccc</i> or <i>aaaaB—Cccc</i>
6.1569 selfed	Susceptible	7	149	156	5	151	156	0.25	<i>A—bbbbCCcc</i> or <i>aaaaB—CCcc</i>
7.1633 selfed	Susceptible	6	155	161	5	156	161	0.3	<i>A—bbbbCCcc</i> or <i>aaaaB—CCcc</i>
8.1923 selfed	Susceptible	5	50	55	2	53	55	0.007	<i>A—bbbbCCcc</i> or <i>aaaaB—CCcc</i>
9.1390 selfed	Resistant	173	55	228	168	60	228	0.5	<i>AaaaBBbbCCcc</i> or <i>AAaaBbbbCCcc</i>
10.1393 selfed	Resistant	89	62	151	87	64	151	0.75	<i>AaaaBbbbCccc</i>
11.1567 selfed	Resistant	107	30	137	109	28	137	0.7	<i>AAaaBbbbCccc</i> or <i>AaaaBBbbCccc</i>
12.1597 selfed	Resistant	58	22	80	60	20	80	0.65	<i>AAaaBbbbCCcc</i> or <i>AaaaBBbbCCcc</i>
		58	22	80	58	22	80	1.00	<i>AAaaBbbbCCCC</i> or <i>AaaaBBbbCCCC</i>
13.1659 selfed	Resistant	63	5	68	64	4	68	0.5	<i>AAaaBBbbCCcc</i>
14.1678 selfed	Resistant	136	46	182	134	48	182	0.75	<i>AAaaBbbbCCcc</i> or <i>AaaaBBbbCCcc</i>
15.1714 selfed	Resistant	39	8	47	37	10	47	0.65	<i>AAaaBbbbCccc</i> or <i>AaaaBBbbCccc</i>
16.1761 selfed	Resistant	55	7	62	59	3	62	0.05	<i>AAaaBBbbCCcc</i> or <i>AAaaBBbbCCCC</i>
17.1946 selfed	Resistant	27	7	34	27	7	34	0.9	<i>AAaaBbbbCccc</i> or <i>AaaaBBbbCccc</i>

TABLE 6

Frequency of distribution of different genotypes in S_1 of ($AG\ 54.55 \times X\ 143$) F_1 when genotypic constitution of $X\ 143$ is $AAaaBbbbCCcc$

Genotypes	Percent expected ratio of		Percent expected distribution	Observed distribution of the 17 selections of table 5*
	Resistant	Susceptible		
A. Resistant types				
1. $A-B-cccc$ $a-B-cccc$ $A-b-cccc$ $aaaabbbbcccc$	100.0	0.0	8.3	
2. $AAaaBbbbCccc$	96.3	3.7	1.7	Group I†
3. $AAaaBbbbCCCc$ $AAaaBbbbCCcc$	94.5	5.5	2.1	
4. $AAaaBbbbCccc$ $AaaaBbbbCccc$	79.7	20.3	10.4	Group II
5. $AAaaBbbbCCcc$ $AaaaBbbbCCcc$	73.6	26.4	10.4	
6. $AAaaBbbbCCCc$ $AaaaBbbbCCCc$	72.9	27.1	2.1	Group III
7. $AaaaBbbbCccc$	67.2	32.8	14.0	
8. $AaaaBbbbCCcc$	57.5	42.5	14.0	Group IV
9. $AaaaBbbbCCCc$	56.3	43.7	2.8	
B. Susceptible types				
10. $aaaaB-Cccc$ $A-bbbbCccc$	25.0	75.0	15.6	2 2 (Inter)
11. $aaaaB-CCcc$ $A-bbbbCCcc$	2.8	97.2	15.6	4
12. $aaaaB-CCCc$ $A-bbbbCCCc$	0.0	100.0	3.0	

* Eight selections from the susceptible F₁ and nine selections from the resistant F₁ were chosen at random for this study.

† Groups I-IV represent the groups which fit with χ^2 limits.

* Eight selections from the susceptible F_1 and nine selections from the resistant F_1 were chosen at random for this study.

† Groups I-IV represent the groups which fit with χ^2 limits.

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