The relationship of genes X^i and N_b for resistance to potato virus X

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The relationship of genes X^i and N_b , which confer resistance to strains of potato virus X, was investigated using the progeny of a cross between a potato clone with both genes and a susceptible clone. The two genes were apparently inherited at separate unlinked loci.

INTRODUCTION

Cockerham (1970) investigated the relationships of various genes for resistance to potato virus X (PVX) and potato virus Y. He found indirect evidence that the genes X^i and N_b were non-allelic: a third gene X^n was found to be allelic with X^i but appeared independent of N_b . This would suggest that the genes X^i and N_b are non-allelic, though there was no direct evidence. The present study examines the relationship between X^i and N_b directly.

The gene X^i from *Solanum acaule* controls extreme resistance to group 1, 2, 3 and 4 strains of PVX (Cockerham, 1958; Ross, 1954a, b). It is probably identical with Rx_{act} (Cockerham, 1970). The gene N_{bibr} or N_b in *Solanum tuberosum* controls necrosis to group 2 (or B) and 1 strains of PVX (Cadman, 1942; Cockerham, 1954, 1970). Both genes are dominant over their alleles for susceptibility (Cockerham, 1970; Ross, 1951, 1954b).

MATERIALS AND METHODS

The potato clone G5399(4) contains the gene X^i , derived from its parent 44/1016/10 (Ross) (Cockerham, 1970), and the gene N_b derived from its grandparent cultivar Catriona, which is susceptible to PVX common strain (fig. 1). In order to investigate directly the relationship between the genes X^i and N_b , G5399(4) was crossed with the susceptible cultivar Flourball, and the progeny G6063 was examined.

Figure 1 Pedigree of progeny G6063

In a glasshouse, two plants of each of 84 clones of the progeny were sap-inoculated with PVX common strain (group 3 strain) (X_3), and two of each clone with a B strain (group 2 strain). Of each of a further 22 clones, only two plants were available so one was used for each strain. The common strain of PVX was maintained in *Nicotiana tabacum* cv White Burley and the B strain in the potato cv King Edward, which has the gene N_x conferring hypersensitivity to the common strain, which prevents contamination with the latter. White Burley tobacco plants inoculated with B from King Edward were used for inoculum, for comparability of virus concentration in the inocula.

Sap-inoculations were made by hand, by gently rubbing infected sap diluted with tap water on leaves dusted with 300 grit carborundum. The plants were examined for their response at intervals, starting 10 days after inoculation, and after 4 to 5 weeks non-inoculated leaves were tested for infection by chloroplast agglutination (Gibbs and Harrison, 1976). Where no response was seen, the plants were either sap-inoculated again or graft-inoculated (de Bokx, 1972) by top-grafting with

an infected scion, using King Edward for B and *Solanum stoloniferum* for common X. Responses to grafting were observed in the stock from 3 weeks after grafting. Tubers from plants giving an apparently resistant response to sap- or graft-inoculation were grown on and inoculated and tested again to confirm their status. The phenotypes conferred by each gene with respect to each virus strain used are summarised in table 1.

Table 1 Resistance conferred by the genes X^i and N_b to the PVX strains used

PVX strain	Resistance gene	
	X^i	N_b
Common (or 3)	res	sus
B (or 2)	res	res

res = resistant.
sus = susceptible.

RESULTS AND DISCUSSION

Sap-inoculation either produced mosaic symptoms and a positive result when the plants were tested for infection, confirming susceptibility, or elicited various resistant responses. These latter included necrotic lesions on the inoculated leaves only, systemic necrotic spots and stem necrosis, fine necrotic spots, fine halo necrosis where each fine necrotic spot was surrounded by a chlorotic area, and null responses where no reaction was seen. All these gave a negative result when tested for infection, except the tuber progeny of one plant which had shown necrosis after sap-inoculation and grafting with X_3 . Similar cases of infection of plants carrying the gene Rx_{acl} were reported by Delhey (1974).

Resistant responses (in the stock) to grafting with B included necrotic flecking, fine necrotic spots and lethal top necrosis. Resistant responses to grafting with X_3 included necrotic flecking, fine necrotic spots, halo necrosis and larger necrotic spots. The susceptible response to grafting is a mosaic symptom and a positive infection test.

Clones showing resistance to B alone (i.e., carrying the gene N_b but not X^i) showed a necrotic response to inoculation with B. Although the gene X^i is said to confer extreme resistance (Ross, 1954a) rather than hypersensitivity, the various necrotic responses described above were seen as well as null responses in plants inoculated with X_3 . This phenomenon was also reported by Cockerham (1970) and Delhey (1974).

Table 2 Theoretical segregation ratios for genes X^i and N_b at independent loci

(i) Individual loci (general case, R = any dominant gene for resistance)

Cross	Progeny phenotypic ratio res:sus
simplex $R \times sus$	1:1
duplex $R \times sus$	5:1

(ii) Hence for two loci

Cross	Progeny phenotypic ratio res X_3 res B:sus X_3 res B:sus both
simplex $X^i \times sus$	2:1:1
simplex $N_b \times sus$	6:5:1
simplex $X^i \times sus$	6:5:1
duplex $N_b \times sus$	10:1:1
duplex $X^i \times sus$	30:5:1
duplex $N_b \times sus$	30:5:1

res = resistant (to).

sus = susceptible (to).

X_3 = PVX common strain.

B = PVX strain B.

The theoretical segregation ratios for independent loci, for alleles and for linked loci are derived in tables 2–4 assuming autotetraploid (tetrasomic) segregation with no disturbance of meiosis (Cadmán, 1942). The numbers of clones showing resistance to both strains, resistance to B only and susceptibility to both are given in table 5. All ratios in this discussion refer to the numbers of clones in these three categories respectively (resistant to X_3 and to B; resistant to B only; susceptible to both). Some theoretical ratios and their χ^2 values from the data are also shown in table 5. Other theoretical ratios in tables 3 and 4 are omitted from table 5 because they include zeros in categories where some clones did in fact occur.

From the χ^2 tests (table 5), it appears that the parent G5399(4) was duplex with respect to the gene N_b , and that the genes X^i and N_b are independent (i.e., non-allelic and not linked) since the theoretical ratio 6:5:1 fits very well ($P = 0.7-0.8$), whilst the next closest, 3:2:1 (simplex for both genes, allelic) does not ($P = 0.01-0.02$). The source of X^i , 44/1016/10 (Ross), was simplex (Cockerham, 1970), so G5399(4) was most unlikely to be duplex with respect to X^i and the segregation ratio bears this out (10:1:1, $P < 0.001$; 30:5:1, $P < 0.001$).

The theoretical ratios if the two genes were allelic are shown in table 3. Apart from the case

Table 3 Theoretical segregation ratios for genes X^i and N_b allelic or linked in repulsion phase

Cross	Progeny genotypic* ratio	Progeny phenotypic ratio	
		res X_3 res B :sus X_3 res B :sus both	
simplex X^i simplex N_b × sus	$1X^iN_b:2X^i:2N_b:1$ sus	3:2:1 (2:3:1)	
simplex X^i duplex N_b × sus	$2X^iN_b:1X^i:1N_bN_b:2N_b$	1:1:0 (1:5:0)	
duplex X^i simplex N_b × sus	$1X^iX^i:2X^i:2X^iN_b:1N_b$	5:1:0 (3:2:1)	
duplex X^i duplex N_b × sus	$1X^iX^i:4X^iN_b:1N_bN_b$	5:1:0 (1:5:0)	

Ratios in brackets would occur if N_b were dominant over X^i (if allelic).

* Mentioning (dominant) alleles for resistance only.

res = resistant (to).

sus = susceptible (to).

X_3 = PVX common strain.

B = PVX strain B.

Table 4 Theoretical segregation ratios for genes X^i and N_b at linked loci in coupling phase (following recombination)

Cross		Progeny genotypic* ratio	Progeny phenotypic ratio	
			res X_3 res B :sus X_3 res B :sus both	
coupled once	simplex X^i simplex N_b × sus	$1X^iN_b:1$ sus	1:0:1	
	simplex X^i duplex N_b × sus	$1X^iN_bN_b:2X^iN_b:2N_b:1$ sus	3:2:1	
	duplex X^i simplex N_b × sus	$1X^iX^iN_b:2X^iN_b:2X^i:1$ sus	5:0:1	
	duplex X^i duplex N_b × sus	$1X^iX^iN_b:1X^iN_bN_b:2X^iN_b:1X^i:1N_b$	5:1:0	
	duplex X^i duplex N_b × sus	$1X^iX^iN_bN_b:4X^iN_b:1$ sus	5:0:1	
coupled twice				

* Mentioning (dominant) alleles for resistance only.

res = resistant (to).

sus = susceptible (to).

X_3 = PVX common strain.

B = PVX strain B.

of simplex for both genes (mentioned above), all these ratios specify no clones susceptible to both strains, (whereas in fact seven clones were susceptible to both), assuming that individuals carrying both genes are resistant to both strains. If they were resistant to B only (*i.e.*, if N_b were dominant over X^i), the expected ratio would be 3:2:1 if the parent were duplex X^i and simplex N_b , or further still from the observed segregation if it were any other genotype (table 3). It therefore appears that X^i and N_b are not allelic.

If the two genes were linked in repulsion phase, the segregation ratio would tend towards those

expected if they were allelic (table 3). Since the genes X^i and N_b came from different sources in the pedigree, they were most unlikely to be linked in coupling phase; this could only occur if there had been recombination between them. The expected segregation ratios in this event are given in table 4, and none of them fits the data. Hence there is no evidence for linkage.

These data therefore suggest that the genes X^i and N_b are at two separate loci and are not linked.

Table 5 Segregation of progeny G6063 with respect to resistance to PVX common and B strains

		Phenotype		χ^2	P
		res X_3 res B:sus X_3 res B:sus both			
Observed nos. of clones		55:44:7			
Theoretical ratios:					
Resistant	X^iN_b , independent	2: 1:1	25.98	<0.001	
parent*	$X^iN_bN_b$, independent	6: 5:1	0.457	0.7-0.8	
	$X^iX^iN_b$, independent	10: 1:1	152.96	<0.001	
	$X^iX^iN_bN_b$, independent	30: 5:1	76.39	<0.001	
	X^iN_b , allelic or linked in repulsion;	3: 2:1	8.64	0.01-0.02	
	$X^iN_bN_b$, linked (once) in coupling phase				
	X^iN_b , allelic, N_b dominant				
		2: 3:1	18.92	<0.001	

* genotype mentioning (dominant) alleles for resistance only.

res = resistant to.

sus = susceptible to.

X_3 = PVX common strain.

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