Euphytica 2 (1953): 197–206

EXPERIMENTS ON THE INHERITANCE OF BLIGHT IMMUNITY IN POTATOES DERIVED FROM SOLANUM DEMISSUM LINDL.

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Received 30 Jan. 1953

1. INTRODUCTION

In previous publications (4,5) the author has discussed the amount of losses, caused by the potato late blight fungus, *Phytophthora infestans*, in the Netherlands. When in 1943 breeding for immunity started at the Plant Breeding Station of the "Centraal Bureau", inoculations of potato seedlings were performed with two races, viz. *0* and *1*[1]). Afterwards six new races differing definitely from each other in their spectrum were discovered and isolated. This was illustrated in the reactions of the test series used in differentiating the races found in the Netherlands (5, table 1). Relationships and differences between the races were outlined in a diagram (5, fig. 1). The observed segregations upon inoculation with various races were explained by the assumption of three independent dominant factors: R_1, R_2, R_3. The presence of a fourth gene R_4, preliminarily labelled $R_{2,5}$ (5), and also behaving dominantly, will be demonstrated below.

2. INHERITANCE OF IMMUNITY

The immunity of clone 4431–5 of the test series (5) could not be explained by the presence of one of the three genes identified previously. Experiments were performed in order to demonstrate the mode of inheritance of immunity in this clone. 79 seedlings of cross 52117 (= 4431–5 × Koopmans Blauwe) were grown in pots in the greenhouse. Immunity or susceptibility was determined by inoculating detached leaves on moist filter paper with suspensions of races *0; 1; 2* and *4* (table 1).

TABLE 1. SEGREGATION IN $R_4 \times r$ PROGENY 52117 (4431–5 × KOOPMANS BLAUWE)

Number of seedlings	Race			
	0	*1*	*2*	*4*
41	s	s	s	s
38	R	R	R	s

Thus it appeared that half of the seedlings were susceptible to all races used. The other half was immune from *0; 1* and *2* but susceptible to race *4*, just like the mother plant 4431–5. This may be explained in assuming a dominant gene R_4 in simplex condition in 4431–5, controlling immunity from the races *0; 1* and *2*.

Four dominant genes derived from *S. demissum* have now been identified. Interrelationships of genes and races are given in table 2.

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[1]) The international nomenclature proposed in (2) is used throughout this publication.

TABLE 2. INTERRELATIONSHIPS OF GENES FOR IMMUNITY AND RACES OF P. INFESTANS, FOUND IN THE NETHERLANDS

	0	*1*	*2*	*4*	*1,4*	*2,4*	*1,2,4*	*2,3,4*
R_1	R	s	R	R	s	R	s	R
R_2	R	R	s	R	R	s	s	s
R_3	R	R	R	R	R	R	R	s
R_4	R	R	R	s	s	s	s	s

From table 2 it is evident, that immunity from all races is expected if the genes R_1 and R_3 are brought together because of the dominance of immunity to susceptibility. The other two factors are not important as far as immunity from the races known in the Netherlands is concerned. However, it is possible that new races will be found in future. In fact, some strains isolated by BLACK (1) have already been demonstrated to be different from those found in our country (2, 4). Therefore it is thought recommendable to combine all genes.

Methods of inoculation were essentially the same as outlined before (4, 5). In the following tables the significant terms only are indicated.

A. Progenies of $R_1 \times R_3$ crosses

TABLE 3. SEGREGATION IN $R_1 \times R_3$ PROGENIES

(1949) Cross	Series	1st inoculation				2nd inoculation				3rd inoculation				4th inoculation			
		Race	s	R	%R	Race	s	R	%R	Race	s	R	%R	Race	s	R	%R
4735 ¹)	A	*2*	15	42	74	*2,4*	0	12	100	*1*	4	8	67	*1,4*	0	8	100
	B	*0*	6	13	68	*1*	4	9	69	*2,4*	0	9	100	*1,4*	0	9	100
	C	*0*	7	19	73	*1,4*	6	13	68	*2,4*	0	9	100				
4764 ²)	A	*0*	30	80	73	*1*	28	52	65	*1,4*	0	52	100	*2,4*	0	49	100
	B	*0*	12	33	73	*1*	8	19	70	*2,4*	0	19	100				
	C	*0*	10	33	77	*1,4*	10	17	63	*2,4*	0	17	100				

¹) 4735 = 442–8 × 43160–12
²) 4764 = 4428–2 × 43160–12

Clones 442–8 and 4428–2 were shown to be simplex R_3 and clone 43160–12 simplex R_1 (4, 5). The factorial scheme of these crosses will, simplified, run as follows:

$$\begin{array}{lll} \text{Parents:} & r_1R_3 & R_1r_3 \\ \text{Gametes:} & r_1 + R_3 & R_1 + r_3 \\ \text{Zygotes:} & \multicolumn{2}{l}{R_1R_3 + R_1r_3 + r_1R_3 + r_1r_3} \end{array}$$

Thus, R_1R_3, R_1 and R_3 individuals or 75 % of the seedlings will be immune from the races *0; 2; 4* and *2, 4;* only R_1 R_3 or 25 % of the seedlings will be immune from *1, 2, 4* and *2, 3, 4*. An inoculation with *1*; *1, 4* or *1, 2, 4* following one with *0*; *2*; *4* or *2, 4* is expected to give a 1 : 2 (susc.: imm.) segregation. The χ^2-test (table 4) reveals that the hypothesis agrees well with the observed data.

TABLE 4. χ^2-TEST OF THE DATA OF TABLE 3

Cross	Ratio	Expected	Observed	χ^2	P
4735	1 : 3	25.5 : 76.5	28 : 74	0.327	> 0.50
	1 : 2	14.7 : 29.3	14 : 30	0.050	> 0.80
4764	1 : 3	49.5 : 148.5	52 : 146	0.168	> 0.60
	1 : 2	44.7 : 89.3	46 : 88	0.057	> 0.80

Seedlings out of a number of crosses of this type were inoculated with a mixture of zoospores of the races *1*, *2*, *4* and *2*, *3*, *4* in 1951 and 1952 (table 5 A).

TABLE 5. SEGREGATION IN PROGENIES OF CROSSES OF VARIOUS TYPES UPON INOCULATION WITH A MIXTURE OF RACES *1*, *2*, *4* AND *2*, *3*, *4*

Section	Type of progeny	Number of progenies inoculated (1951+1952)	Segregation					
			Observed			Expected		
			s	R	%R	s	R	%R
A	$R_1 \times R_3$	42	7021	2267	24.4	6966	2322	25.0
B	$R_1R_3 \times r$	114	27753	8705	23.9	27343.5	9114.5	25.0
C	$R_1R_3 \times R_3$	20	5974	3666	38.0	6025	3615	37.5
D	$R_1R_3 \times R_1$	21	3888	2192	36.1	3800	2280	37.5
E	$R_3 \times R_1R_2$	3	496	143	22.4	479.25	159.75	25.0
F	$R_3 \times R_1R_3$	12	92	36	28.1	80	48	37.5
G	$r \times R_1R_3$	6	52	19	26.8	53.25	17.75	25.0
H	$R_1R_3 \times R_1R_2$	1	20	10	33.3	18.75	11.25	37.5
I	$R_1R_3 \times R_1R_3$	2	167	95	36.3	114.625	147.375	56.25
K	R_1R_3 S.P. 1)	10	1604	1410	46.6	1318.625	1695.375	56.25

1) S.P. = spontaneous progeny (natural selfing).

In general the observed segregations agree closely with the theoretically expected ones, though segregations in some crosses are slightly deviating. In most of these cases a relatively small number of seedlings were inoculated and divergences might have occurred to either side of the theoretical ratio. The usually small number of seedlings suggests chance to be the cause, but other reasons cannot be excluded, as no cytological investigations concerning meiosis were performed.

B. Progenies of R_1R_3 × r crosses

Progenies of crosses of this type are theoretically expected to segregate in exactly the same ratio as $R_1 \times R_3$ progenies, dealt with in the previous section. A factorial scheme will be superfluous. Quite a number of these progenies were inoculated with races *1*, *2*, *4* + *2*, *3*, *4* during 1951 and 1952 (table 5, B).

Again there is in general sufficient agreement between observation and expectation.

Upon inoculation with race *1*, *2*, *4* half of the seedlings are expected to resist the fungus, as is shown in fig. 1 by 5022, segregating in 46 attacked and 49 non-attacked plants.

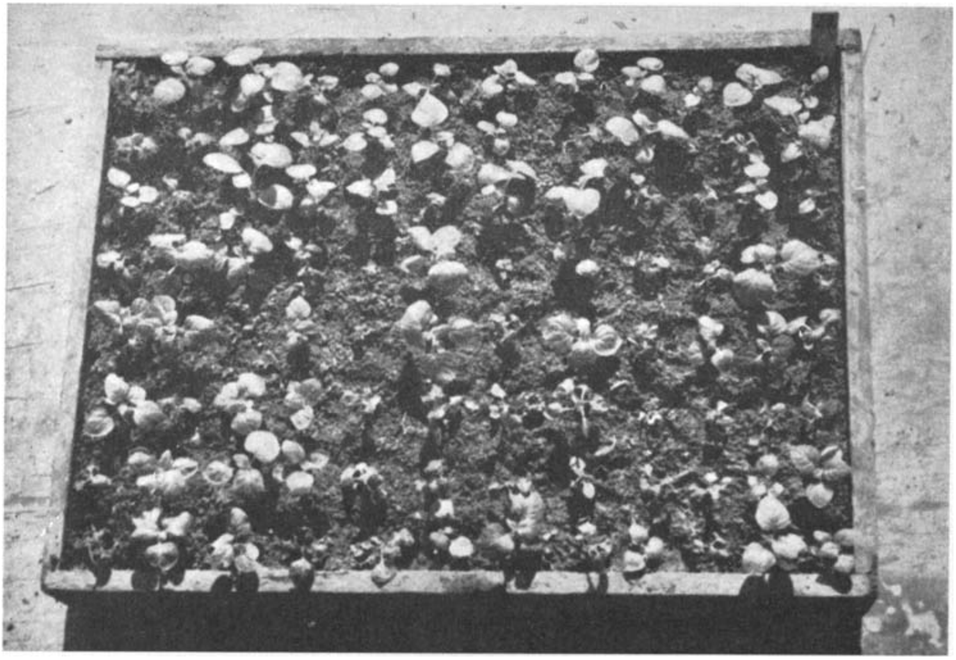

Fig. 1. Segregation (s 46, R 49) in the R_1R_3 × r cross 5022 (4737–34 × ultimus) upon inoculation with race *1, 2, 4.*

C. Progenies of R_1R_3 × R_3 crosses

The factorial scheme of these crosses will be:

Parents: R_1R_3 $\qquad$ r_1R_3
Gametes: $R_1R_3 + R_1r_3 + r_1R_3 + r_1r_3$ $\qquad$ $r_1R_3 + r_1r_3$
Zygotes: $R_1r_1R_3R_3 + r_1r_1R_3R_3 + 2\ R_1r_1R_3r_3 + 2\ r_1R_3 + R_1r_3 + r_1r_3$

Upon inoculation with races *1, 2, 4* + *2, 3, 4* only the $R_1R_3R_3$ and R_1R_3 genotypes will be immune; thus $\frac{3}{8}$ or 37.5 % will be expected, provided everything goes regularly. Seedlings of a number of crosses of this type were inoculated in 1952 (table 5, C).

D. Progenies of R_1R_3 × R_1 crosses

In general outlines the factorial scheme of these crosses is very similar to that of the previous section, the male parent being simplex R_1 instead of simplex R_3. Genotypes $R_1R_1R_3$ and R_1R_3 will be immune from *1, 2, 4* + *2, 3, 4*, thus $\frac{3}{8}$ will be expected to survive infection (table 5, D).

E. Progenies of R_3 × R_1R_2 crosses

One such cross was investigated more closely by means of successive inoculations with various races (table 6).

TABLE 6. SEGREGATION IN A $R_3 \times R_1R_2$ PROGENY

(1952) Cross	Series	1st inocuation				2nd inoculation				3rd inoculation			
		Race	s	R	%R	Race	s	R	%R	Race	s	R	%R
49111	A	*0*	4	22	85								
	B	*4*	9	87	91	*2, 3, 4*	33	47	59	*1, 2, 4*	20	21	51
	C	*2*	20	75	79	*1, 4*	10	65	87	*2, 3, 4*	20	35	64

49111 = 4642–16 × 4538–4

Clone 4642–16 was shown to give 49 % (s 930, R 889) seedlings immune from race *1, 2, 4* in crosses with the *S. tuberosum* varieties Earlaine, Fransen, Frühmölle, Katahdin, Record and Sirtema. Since 4642–16 is susceptible to race *2, 3, 4* it does not possess factor R_1. From the segregations in cross 49111 the presence of a factor other than R_3 cannot be demonstrated, so clone 4642–16 is suggested to be simplex R_3. Clone 4538–4 was demonstrated to be of the R_1R_2 genotype (4, table 39). It is not thought necessary to write down the complete factorial scheme in detail. It will be evident that 8 different genotypes will occur, theoretically in equal proportions, viz. $R_1R_2R_3$, R_1R_2, R_1R_3, R_2R_3, R_1, R_2, R_3 and r. Thus, upon inoculation with *0* or *4* $^7/_8$ or 87.5 % of the seedlings is expected to be immune, only the recessive genotypes being susceptible. Actually 85 % and 91 % were found. When *2, 3, 4* is inoculated after *4*, genotypes R_2R_3, R_2 and R_3 will be susceptible; a 3 : 4 segregation is expected, 57 % being immune. In fact 59 % was observed. In a third inoculation with *1, 2, 4* genotypes R_1R_2 and R_1 will be susceptible and genotypes $R_1R_2R_3$ and R_1R_3 immune. A 2 : 2 segregation is expected; 51 % immune seedlings were found.

Upon inoculation with race *2* the r and R_2 genotypes will prove susceptible, thus a 2 : 6 ratio is expected; 79 % was recorded. A second inoculation with race *1, 4* will show the R_1 genotypes to be susceptible, thus a 1 : 5 segregation is expected; 87 % (theoretically 83 %) was observed. Race *2, 3, 4* in a third inoculation will attack the R_2R_3 and R_3 genotypes, the $R_1R_2R_3$, R_1R_2 and R_1R_3 genotypes being immune. Thus a 2 : 3 segregation is expected; 64 % (theoretically 60 %) was observed.

Upon inoculation with races *1, 2, 4* + *2, 3, 4* the genotypes $R_1R_2R_3$ and R_1R_3 only will prove to be immune; this is 25 % of the seedlings. Actually 22.4 % was found in 3 crosses in 1951 (table 5, E).

F. Progenies of $R_3 \times R_1R_3$ crosses

In progenies of this type 37.5 % of the seedlings are expected to be immune from *1, 2, 4* + *2, 3, 4*, these crosses being the reciprocal ones of those of section C. However, only 28.1 % was found (table 5, F). It is true that the numbers of inoculated seedlings were low. Table 7 gives some further information and allows more detailed analysis.

The crosses 50237 and 5136 are dealt with in section F of table 5. It is shown by the χ^2-test that the segregation in 50237 is close to expectation; however, that in 5136 is not. Clone 449–8 seems to give female gametes in normal proportions, as is illustrated by the segregation in 5139. Thus the abnormal low percentage of immune seedlings may be attributed to 4768–15. Clone 4768–15, when used as a mother plant, gives normal segregations (only in 51198 there is an excess of immune seedlings). However, this does not necessarily imply that the male gametes are produced in normal propor-

TABLE 7. SEGREGATION IN PROGENIES OF VARIOUS TYPES OF CROSSES

Cross	Parentage	Genotypes	Inoculation with races	Segregation						χ^2	P
				Observed			Theoretical				
				s	R	%R	s	R	%R		
50237	4428–34 × 4768–41	$R_3 \times R_1R_3$	*1, 2, 4 + 2, 3, 4*	13	8	38.1	5	3	37.5	0.003	> 0.95
5136	449–8 × 4768–15	$R_3 \times R_1R_3$	*1, 2, 4 + 2, 3, 4*	79	28	26.2	5	3	37.5	5.49	< 0.02
5139	449–8 × 47237–116	$R_3 \times r$	*1, 2, 4*	95	105	52.5	1	1	50.0	0.50	> 0.40
51194	4768–15 × 47237–116	$R_1R_3 \times r$	*1, 2, 4 + 2, 3, 4*	175	63	26.5	3	1	25.0	0.27	> 0.50
51198	4768–15 × Agnes	$R_1R_3 \times r$	*1, 2, 4 + 2, 3, 4*	499	197	28.3	3	1	25.0	3.99	< 0.05
51199	4768–15 × Katahdin	$R_1R_3 \times r$	*1, 2, 4 + 2, 3, 4*	37	17	31.5	3	1	25.0	1.21	> 0.20
51200	4768–15 × Marktredwitzer Frühe	$R_1R_3 \times r$	*1, 2, 4 + 2, 3, 4*	365	115	24.0	3	1	25.0	0.28	> 0.80
51201	4768–15 × Koopmans Blauwe	$R_1R_3 \times r$	*1, 2, 4 + 2, 3, 4*	246	89	26.6	3	1	25.0	0.44	> 0.50
51202	4768–15 × Oberarnbacher Frühe	$R_1R_3 \times r$	*1, 2, 4 + 2, 3, 4*	724	240	24.8	3	1	25.0	0.005	> 0.90
51203	4768–15 S.P.	R_1R_3 S.P.	*1, 2, 4 + 2, 3, 4*	49	78	61.4	7	9	56.25	1.55	> 0.20

tions also. From progeny 51203 (spontaneous pollination of 4768–15) no indications can be obtained that the R_1R_3 gametes in the pollen are formed less frequently than the other gametes. Thus it must be assumed that either chance or a preferential pairing is the cause of the low percentage of immune seedlings in 5136.

G. Progenies of r × R_1R_3 crosses

Only very few seedlings from six crosses were inoculated with races *1, 2, 4 + 2, 3, 4* (table 5, G). The observed segregation is in close agreement with the theoretically expected one. In one of the four crosses involved clone 4768–41 was the male parent. The normal segregation agrees closely with the segregation in 50237 (table 7).

H. A progeny of a R_1R_3 × R_1R_2 cross

In inoculations with races *1, 2, 4 + 2, 3, 4* gene R_2 is of no importance, so 37.5 % immune seedlings is expected as in section D. Actually 33.3 % was observed, which may be regarded as close to expectation, taking in account the small number of seedlings (table 5, H).

I. Progenies of R_1R_3 × R_1R_3 crosses

The factorial scheme of this type of crosses may be set out in a diagram, in which, for the sake of simplicity only significant terms are mentioned.

	r	R_1	R_3	R_1R_3
r	r	R_1	R_3	R_1R_3
R_1	R_1	R_1R_1	R_1R_3	$R_1R_1R_3$
R_3	R_3	R_1R_3	R_3R_3	$R_1R_3R_3$
R_1R_3	R_1R_3	$R_1R_1R_3$	$R_1R_3R_3$	$R_1R_1R_3R_3$

Upon inoculation with a *1, 2, 4 + 2, 3, 4* mixture all individuals possessing one or two genes R_1 and R_3 are immune; seedlings lacking R_1 or R_3 genes or both will be susceptible. Thus a 7: 9 (s: R) segregation is expected theoretically.

Table 5, I, however, shows a definite deviation from the expected ratio. More information concerning the clones involved is given in tables 7 and 8.

TABLE 8. SEGREGATIONS IN PROGENIES OF VARIOUS TYPES OF CROSSES UPON INOCULATION WITH RACES *1, 2, 4 + 2, 3, 4*

Cross	Parentage	Genotypes	Segregation						χ^2	P
			Observed			Theoretical				
			s	R	% R	s	R	% R		
51124	4739-58 × 4768-15	$R_1R_3 \times R_1R_3$	92	25	21.4	7	9	56.25	58.22	< 0.01
51192	4768-15 × 4768-42	$R_1R_3 \times R_1R_3$	75	70	48.3	7	9	56.25	4.05	< 0.05
50168	4739-58 × Alpha	$R_1R_3 \times r$	263	93	26.1	3	1	25.0	0.24	> 0.60
50170	4739-58 × Noordstar	$R_1R_3 \times r$	181	57	23.9	3	1	25.0	0.14	> 0.70
50171	4739-58 × Record	$R_1R_3 \times r$	127	39	23.5	3	1	25.0	0.20	> 0.60
50172	4739-58 × Ysselster	$R_1R_3 \times r$	46	13	22.0	3	1	25.0	0.28	> 0.50
51131	4739-58 × Alpha	$R_1R_3 \times r$	243	92	27.4	3	1	25.0	1.08	> 0.20
51135	4739-58 × Cayuga	$R_1R_3 \times r$	463	172	27.1	3	1	25.0	1.47	> 0.20
51138	4739-58 × Katahdin	$R_1R_3 \times r$	412	132	24.3	3	1	25.0	0.16	> 0.60
51141	4739-58 × Noordstar	$R_1R_3 \times r$	337	136	28.7	3	1	25.0	3.55	> 0.05

The data of table 8 illustrate well the normal genetic behaviour of clone 4739-58. In all eight crosses with recessives, cited there, segregations are in agreement with expectation. In all, progenies of 19 crosses of this type having 4739-58 as a mother plant, were inoculated with *1*, *2*, *4* + *2*, *3*, *4* during 1951 and 1952, with a total of 7781 seedlings and a segregation of 5857 susceptible and 1924 immune (% R = 24.7), which is close to expectation ($P > 0.50$). Thus there seems to be no doubt about the normal formation of gametes in 4739-58.

In section F, table 7, the normal behaviour of 4768-15 as a mother plant has already been shown. There also appeared to be no reason to assume an abnormal ratio of the genotypes in the pollen of 4768-15. Nevertheless, the percentage of immune seedlings in 5136 was too low. This is still more so in 51124, as is illustrated by $P < 0.01$. However, in 51192 there is only a slight deficit of immune seedlings. Unfortunately, it was impossible to check the genetic behaviour of 4768-42 both as a mother and as a father plant; there were crosses and also a S.P. progeny available, but because of a low germination of the blight spores used the segregations were not reliable.

K. Spontaneous progenies of R_1R_3 individuals

If pollination has actually taken place by pollen of the plant itself, then 56.25 % immune seedlings are expected as in the previous section, supposing random pairing and segregation. However, there is, as is shown in table 5, K, an excess of susceptible genotypes. In connection with the data of section I it would be interesting to study additional information (tables 9 and 10).

From table 9 it is evident that in the spontaneous progenies 50261, 50233, 5171 and 51203 the assumption of self-pollination and normal segregation fits in well with the observed data. However, in other progenies there is an excess of susceptible seedlings, the percentage of immune seedlings even falling to 16.7 % in 51113.

Table 9. Segregation in a number of spontaneously pollinated progenies of R_1R_3 individuals upon inoculation with races *1, 2, 4* + *2, 3, 4*

Spontaneous progeny	Parentage	Observed segregation			χ^2	P
		s	R	%R		
50173	4739–58	184	63	25.5	95.08	< 0.01
50261	4768–15	31	28	47.5	1.78	> 0.10
50233	4768–41	12	21	63.6	0.52	> 0.40
5171	4739–37	231	241	51.1	1.29	> 0.20
5195	4739–49	77	42	35.3	21.37	< 0.01
51113	4739–53	75	15	16.7	59.08	< 0.01
51145	4739–58	174	85	32.8	58.53	< 0.01
51163	4739–60	48	14	22.6	29.04	< 0.01
51203	4768–15	49	78	61.4	1.55	> 0.20
51269	4768–41	723	823	53.2	5.81	< 0.02
		1604	1410	46.6		

Table 10. Segregation in progenies of $R_1R_3 \times r$ and $r \times R_1R_3$ crosses upon inoculation with races *1, 2, 4* + *2, 3, 4*

Immune parent	Genotype $R_1R_3 \times r$						Genotype $r \times R_1R_3$					
	Number of crosses	Observed segregation			χ^2	P	Number of crosses	Observed segregation			χ^2	P
		s	R	%R				s	R	%R		
(1951) 4739–58	4	617	202	24.7	0.06	> 0.80						
(1951) 4768–41	2	171	61	26.3	0.21	> 0.60	3	25	10	28.6	1.54	> 0.20
(1952) 4739–37	2	199	72	26.6	0.32	> 0.50						
(1952) 4739–49	8	2257	794	26.0	1.68	> 0.10	1	6	2	25.0	0.00	1.00
(1952) 4739–53	6	2413	764	24.0	1.51	> 0.20						
(1952) 4739–58	15	5240	1722	24.7	0.26	> 0.60						
(1952) 4739–60	14	4595	1219	21.0	50.44	< 0.01						
(1952) 4768–15	6	2046	721	26.1	1.62	> 0.20						
(1952) 4768–41	6	1170	379	24.5	0.22	> 0.60	1	16	6	27.3	0.06	> 0.80

Table 10 illustrates the normal genetic behaviour in crosses of the clones figuring in table 9, the only exception being clone 4739–60. In both of the reciprocal types of crosses 25.0% immune seedlings are expected upon inoculation with races *1, 2, 4* + + *2, 3, 4*. Though the numbers of seedlings are small, the segregation in the $r \times R_1R_3$ crosses do not suggest a preferential pairing or formation of male gametes in abnormal proportions, e.g. caused by an unbalanced number of chromosomes. In the progenies of 4739–60, however, there is such an excess of susceptible individuals that a normal segregation is improbable, but, the percentage of immune seedlings in 51163 (table 9) is still lower than might be expected from the percentage of 21.0% in crosses with recessives.

It is not possible to conclude whether spontaneous cross-fertilization by R_1, R_3 and/or r pollen or preferential pairing or both took place at different degrees. Dorst (3) made several observations which indicate cross-pollination of potato flowers by small bumble bees. On the other hand, in view of the segregations in 51124 and 51192 (table 8) a preferential pairing, leading to a deficit of immune derivatives, is also a possible explanation.

Spontaneous progenies of 4768–15 were inoculated in 1951 and 1952, both segregating in agreement with expectation. Of the two spontaneous progenies of 4768–41 only that of 50233 seemed to be normal, that of 51269 showing a small deviation from standard ratios.

Spontaneous progenies of 4739–58 both are greatly deficient in immune seedlings.

3. DISCUSSION

In breeding potatoes for immunity from *P. infestans* progenies of a number of genetical types were inoculated with a mixture of the races *1*, *2*, *4* and *2*, *3*, *4* during 1951 and 1952 (table 5). In the greater part of these types segregations agreed closely with the hypotheses, postulated before. In some crosses, however, there was a deficit of immune seedlings. This occurred also in most of the spontaneous progenies tested.

There seems to be no obvious reason for this phenomenon. For instance, clone 4768–15 is segregating about normally in crosses with recessives and in spontaneous progenies; in crosses with 449–8 (5136, table 7) and 4739–58 (51124, table 8), however, there is an excess of susceptible seedlings. There seemed to be no support to the assumption of irregular formation of gametes in the pollen. Therefore linkage is not likely to be the cause. This possibility might be explored by means of successive inoculations with various races. Another possible explanation is preferential pairing of the gametes at fertilization, may be as a consequence of differences in growth rate of the pollen genotypes (certation). A slower growth of the pollen tubes of the R_1R_3 types must then be assumed. It is not clear, however, why this phenomenon should operate in certain cases and not in others. If certation actually occurs, its operation must be governed by (an) other factor(s).

In selfings (in which way obtained?) of genotypes with one or two different genes for immunity BLACK (1) did not encounter percentages of immune seedlings that were lower than might be expected with normal segregations, nor did he in crosses of two identical genotypes. On the contrary, an excess of immune derivatives was observed in crosses with individuals duplex in a certain factor (used as father plants).

However, the author investigated some crosses with plants interpreted to be duplex and observed segregations that strongly suggested pairing at random (5). In the opinion of the author the results of BLACK (1) on this type of crosses seem to agree better with the hypothesis of pairing at random between all genes than with the assumption of preferential pairing. An extensive discussion will not be given here, crosses of the type in question not being considered in this publication.

Segregations in spontaneously pollinated progenies cannot be regarded as substantial evidence, cross pollination by insects being possible (3). Further research regarding this problem may be done with progenies from controlled crosses and selfings.

4. SUMMARY

Progenies of crosses of the following genetical types were inoculated with and selected for immunity from the races *1*, *2*, *4* and *2*, *3*, *4* of *Phytophthora infestans*, viz. (dominant symbols only) $R_1 \times R_3$, $R_1R_3 \times r$, $R_1R_3 \times R_3$, $R_1R_3 \times R_1$, $R_3 \times R_1R_2$, $R_3 \times$

R_1R_3, r × R_1R_3, $R_1R_3 \times R_1R_2$, $R_1R_3 \times R_1R_2$ and R_1R_3 S.P. (spontaneously pollinated). One $R_3 \times R_1R_3$ progeny, two $R_1R_3 \times R_1R_3$ progenies and six (out of ten) S.P. progenies segregated with a larger or smaller deficit of immune seedlings as was expected according to the hypotheses that were postulated before and which appeared to be in agreement with the observed segregations in the other progenies. There are insufficient data of unquestionable reliability to explain the deviating segregations with certation, linkage or irregular chromosomal behaviour; cytological investigations were not performed.

5. SAMENVATTING

Onderzoekingen over de erfelijkheid van de resistentie tegen Phytophthora infestans bij aardappelen, afstammend van Solanum demissum Lindl.

Nakomelingschappen van kruisingen van de volgende genetische samenstellingen (wat de resistentiefactoren betreft) werden geïnoculeerd met en geselecteerd op resistentie tegen de physio's *1, 2, 4* en *2, 3, 4* van *P. infestans*, nl. $R_1 \times R_3$, $R_1R_3 \times r$, $R_1R_3 \times R_3$, $R_1R_3 \times R_1$, $R_3 \times R_1R_2$, $R_3 \times R_1R_3$, $r \times R_1R_3$, $R_1R_3 \times R_1R_2$, $R_1R_3 \times R_1R_3$ en R_1R_3 S.P. (spontaan bestoven). Enkele kruisingen werden nader geanalyseerd door middel van herhaalde inoculaties met verschillende physio's; zij bevestigden de conclusies, uit de splitsingen van de met *1, 2, 4* + *2, 3, 4* geïnoculeerde nakomelingschappen getrokken. Het merendeel der splitsingen was geheel in overeenstemming met de reeds eerder opgestelde hypothesen. In 9 nakomelingschappen, nl. één $R_3 \times R_1R_3$, twee $R_1R_3 \times R_1R_3$ en zes R_1R_3 S.P., was er een groter of kleiner tekort aan resistente zaailingen. Aangezien dit niet het geval is in alle kruisingen met R_1R_3-klonen als vader en dezelfde klonen als moeder bijna steeds geheel normale splitsingsgetallen geven, moeten de abnormaal lage percentages resistente zaailingen teweeggebracht worden door andere oorzaken. Koppeling en afstoting is niet waarschijnlijk, certatie is mogelijk (met dien verstande, dat r-stuifmeel het snelst zou moeten groeien), hoewel het al of niet optreden van certatie dan weer afhankelijk moet zijn van andere factoren. S.P. nakomelingschappen van R_1R_3-klonen vormen geen betrouwbaar studiemateriaal, omdat kruisbestuiving door insecten mogelijk wordt geacht (3). Verder onderzoek zal aan gecontroleerde zelfbestuivingen moeten worden gedaan.

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