STUDIES ON THE INHERITANCE OF RESISTANCE TO WART DISEASE (*SYNCHYTRIUM ENDOBIOTICUM* (SCHILB.) PERC.) IN POTATOES.

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CONTENTS.

Introduction.

The breeding work described in this article was carried out at the Scottish Plant Breeding Station and, with a few exceptions, the data presented were obtained from experiments which were undertaken primarily to obtain new economic types. The actual determinations of resistance or susceptibility to *Synchytrium endobioticum* (Schilb.) Perc., however, were carried out at the Seed Testing Station of the Department of Agriculture for Scotland. The writer had the privilege of studying the approved methods employed at that station and was provided with facilities for personally conducting determinations on particular progenies. The original method employed was by sprouting the tubers in sphagnum which was periodically impregnated with watery extract of wart, but from 1932 onwards the method of spore suspension described by Lemmerzahl (1930 and 1931) was adopted. Data have been collected since 1927 and, where possible, seedlings which remained unaffected in their first test were subjected to a second and occasionally a third infection. The proportion of seedlings which proved susceptible only on reinfection was relatively small and was insufficient to affect the ratios to a significant extent.

The possibility of contamination by foreign pollen in potato breeding, though small, is now generally recognised. In the present experiments, precautionary measures were taken and an endeavour was made to protect all flowers used as female parents by means of pergamine bags. The hybridisations were all carried out in this manner, but in the case of the self-fertilisations, natural berries were utilised when the protected flowers failed to set seed. The natural selfs are indicated by N.S. (natural self), and the protected selfs by B.S. (bagged self).

Nature of resistance.

Resistance to parasitic attack may be defined as the counteraction of a plant to the invasion of an organism. The phenomenon of resistance to diseases has been found in many plant species, and frequently there appear in literature discussions and observations on the nature of its inheritance. The resistance of potatoes to wart disease has been accepted as a biological fact by several authors, some of whom have attempted to explain its nature and mode of inheritance from various points of view.

In a discussion on immunity in plants Kostoff (1929) mentioned, in the first place, two kinds of immunity, viz. mechanical and physiological. With regard to the former, Cartwright, according to Garbowski and Leszczenko (1931), found by biochemical methods that no significant differences existed in the anatomical structure of the protective tissues on the sprouts of susceptible and resistant varieties of the potato. The thickness of the epidermis as well as the thickness and chemical constitution of the walls of the cuticular cells were absolutely the same in both cases. Further evidence on this point has been put forward by Köhler (1931) who observed that swarm spores and zygotes penetrated the tissue of immunes in the same manner, and in equal numbers as in susceptibles. Ripening and multiplication of the fungus was deranged in resistant varieties. It can consequently be concluded that mechanical resistance is not an important factor in the invasion of the potato by *S. endobioticum*.

There remains the other kind of immunity referred to by Kostoff (1929), viz. physiological, but he divided physiological immunity into natural and acquired.

Acquired physiological immunity in animals has long been recognised, but in plants the evidence is far from convincing with regard to fungous diseases. Carbone and Arnaudi (1930) discussed the analogies existing between plant and animal immunity and concluded, with reservations, that there was a closer connection between them than had hitherto been generally appreciated. The absence in plants of something equivalent to the blood stream in animals was found to be a serious obstacle to their artificial immunisation. Roach (1927) by making grafts of various sorts of potatoes immune and susceptible to wart disease found that no interaction occurred between immune and susceptible varieties, and no change of resistance took place. He expressed the view that resistance was a property of the non-diffusable elements of the protoplasm, probably the albumens. Kostoff (1929) tested acquired immunity by precipitin reactions. He found in certain species of the Solanaceae that the induced antibodies were specific although non-specific precipitins were also found. In intergeneric graft unions he found that starch which had accumulated above the callus failed to pass down into the stock. Ware (1931) in comparisons on immunity in plants and animals concluded that inoculations were of little value in plants since there was no blood stream to give immediate distribution of antibodies, and that a reaction to disease was usually localised and not found throughout the body. There is a possible exception to this in virus diseases. There is no evidence that superinfection or any other irregularity which is likely to occur in nature has any effect on the inherent resistance of potato varieties to *S. endobioticum*, and it can therefore be assumed that acquired immunity plays no part in the inheritance of resistance to that disease. It appears that resistance is due to a natural physiological state existing within the plant.

DEGREES OF RESISTANCE AND SUSCEPTIBILITY.

Köhler (1931) and others have observed that susceptible varieties show different degrees of infection and sizes of warts under similar environmental conditions. The differences are sufficiently great to justify the assertion that susceptible varieties may be resistant to a certain degree, but the degree is not the same in all such varieties.

In the laboratory, different types of immunes have been demonstrated by different kinds of infection behaviour. Köhler (1931 and 1931*a*) made arbitrary groups of resistant varieties and in certain cases found it difficult to decide to which of two groups a variety really belonged. Köhler (1930) and Lemmerzahl (1930) have expressed the view that all resistant varieties may be liable to infection under special conditions. So far it is not known whether a variety exists which is not liable to complete or sub-infection under suitable circumstances. The groups presented by Köhler (1931) are as follows:

Group I (all resistant): all, or nearly all infections die away.

Group II (all resistant): greater part of infections die away; very few ripen.

Group III (a few susceptible): fewer infections die away. Relatively many ripen.

Group IV (a large number susceptible): nearly all parasites ripen.

Wart-resistant varieties can be arranged in a series of increasing frequency of attack. In groups III and IV are to be found both wart-resistant and wart-susceptible varieties. The reason is that individual varieties react differently to the parasite in respect of the development of new tissue. Some varieties react very slowly or not at all to the hypertrophic stimulus of the parasite, *i.e.* a low degree of reaction; and do not form warts characteristic of susceptible varieties. Others react very readily and have, therefore, a high degree of reaction.

It may be concluded, therefore, that two different physiological factors at least are concerned in resistance, viz. "Infection degree" and "Reaction degree." Different contributions of these two factors make up the different groups. Köhler (1930) was of the opinion that the phenotypic multiplicity resulting from this corresponded to a no less great genotypic multiplicity.

Inheritance of resistance.

It is probable that the great majority of varieties, including those commonly recognised as susceptible, possess some degree of resistance determined by their genetic constitution. They, however, fall naturally into two classes: (I) those with high resistance, and (II) those with low resistance. The former remain practically unharmed in ordinary cultivation and are termed "resistant." The latter are to some extent affected by the disease and are termed "susceptible."

Resistants may consequently be made up of homozygous and heterozygous forms, and likewise susceptibles may be either homozygous or heterozygous. In view of the general heterozygous nature of the potato it is probable that very few homozygous forms of either kind are to be found in cultivation.

The question as to whether resistance or susceptibility is dominant has been discussed by several authors. The balance of opinion is swayed in favour of resistance by the conclusions of Orton and Weiss (1921), Salaman and Lesley (1921 and 1923), Müller (1925), Köhler (1931), Jørstad and Lunden (1932), and Lunden and Jørstad (1934). The dominance of susceptibility is supported only by Collins (1921).

In Table I are shown the numbers of resistant and susceptible offspring obtained in the families of self-fertilised resistant varieties. In each case a majority of resistant seedlings has appeared, and it may reasonably be considered that all resistant varieties produce a majority of resistant offspring when self-fertilised.

Similar progenies, derived from susceptible varieties, are shown in Table II, and in each case susceptible seedlings are in the majority. It therefore appears that all susceptible varieties in general give, on self-fertilisation, a majority of susceptible offspring.

In the hybridisation of resistant and susceptible varieties in the

TABLE I.

Progenies resulting from the fertilisation of resistant varieties.

Reference No.	Parentage		No. of seedlings: Resistant	Susceptible	Total
167*a*	105 (29)	N.S.	28	0	28
126	32 (17)	B.S.	26	0	26
101	31 (37)	B.S.	31	1	32
198	120 (64)	B.S.	16	1	17
47	Langworthy	N.S.	31	2	33
223	135 (10)	B.S.	55	4	59
284	233 (8)	N.S.	14	2	16
220	73 (12)	N.S.	12	2	14
218	Abundance	N.S.	64	13	77
199*a*	121 (11)	N.S.	75	19	94
203	135 (30)	B.S.	43	11	54
162	Flourball	B.S.	44	14	58
325	Bishop	N.S.	55	19	74
193	47 (21)	B.S.	32	13	45
196*a*	120 (3)	N.S.	49	20	69
127	56 (1)	N.S.	33	16	49
73	Majestic	B.S.	23	14	37
110	964*b* (5)	B.S.	27	19	46

TABLE II.

Progenies resulting from the self-fertilisation of susceptible varieties.

Reference No.	Parentage		No. of seedlings: Resistant	Susceptible	Total
200	123 (1)	N.S.	31	47	78
207*b*	168*a* (28)	B.S.	26	46	72
168*a*	105 (33)	N.S.	31	55	86
105	653*a* (4)	B.S.	8	22	30
306	42667	—	8	23	31
114	General	N.S.	17	49	66
165*a*	99 (7)	N.S.	13	54	67
174	114 (40)	N.S.	6	25	31
99	31 (8)	B.S.	2	16	18
170	110 (20)	B.S.	3	19	22
131	64 (2)	B.S.	8	61	69
178	98 (23)	N.S.	1	12	13
347	287*b* (41)	N.S.	1	15	16
173*a*	114 (39)	N.S.	1	32	33
128	56 (2)	N.S.	2	80	82

present experiments the progenies have always contained both resistant and susceptible individuals but, as a general rule, resistants have appeared in the majority. It seems probable, however, that extremely susceptible types are less liable to be present in any collection of varieties than extremely resistant ones, since the former would soon lose favour and their cultivation be discontinued. Breeding and selection work in the past have tended to eliminate the more susceptible varieties, and from that point of view it is not surprising that hybrid progenies of resistant and susceptible parents usually contain a majority of resistant seedlings.

It appears, therefore, that genetically it is not a case of simple dominance but, in view of the wide range of ratios obtained, rather the interaction of several factors which induce resistance. The ultimate number of factors required for a full explanation may be considerable.

In the literature on the subject several suggestions have been put forward. Orton and Weiss (1921) expressed the view that differences in the degree of resistance and susceptibility were dependent for their expression on more than a single factor difference. Salaman and Lesley (1921 and 1923) concluded that two factors were operative, each of which might produce immunity in the presence of a complementary factor. The presence of two inhibitors in certain varieties was also demonstrated. They concluded that the difference of genotype amongst immune plants is not reflected by any difference of degree in the immunity conferred. The aspect of the problem has, however, altered a great deal since then. Müller (1925) indicated that two complementary factors were required to produce immunity. In the light of later results that number is insufficient.

The experiments of Jørstad and Lunden (1932) and Lunden and Jørstad (1934) yielded approximate ratios of 3 immunes to 1 susceptible in families derived by self-fertilisation from several parents. They considered them heterozygous for a single dominant factor (**X**) inducing immunity, but indicated that the immunity factor may or may not be identical in the different varieties. Results obtained from hybrid progenies showed that in certain cases immunity seemed to be dependent upon two complementary factors (**Y** and **Z**) distinct from, and independent of the original **X**. In further crosses a fourth factor ($\mathbf{X}^1$) was found necessary to complete the elucidation of these experiments. The immunity factors **X** and $\mathbf{X}^1$ were considered to be independent of each other and of the complementary factors **Y** and **Z**. The effect of the factors and their interrelations as assumed by these authors is not in full accordance with the corresponding factors of Salaman and Lesley.

More or less simple inheritance of disease resistance has been postulated in other crop plants, *e.g.* oats, wheat, and barley (Hayes, 1930), flax (Henry, 1930) and maize (Mains, 1931). In potatoes, however, the power to create and maintain great genetic complexity in a stable clonal unit may in part account for the more complex mode of inheritance of disease resistance in cultivated varieties.

In connection with blight (*Phytophthora infestans* (Mont.) De By.) in potatoes, Müller (1930) found that resistance was inherited, but that a number of factors was involved. The hypothesis put forward to explain the inheritance was such that two factor pairs existed in a tetraploid plant in which each of the four allelomorphic genes acted independently. Each gene was given a value, *e.g.* $R1=1$, $R2=2$, $R3=3$, and $R4=4$, and resistance was only attained when the sum of the values of the genes was twelve or over. His segregation ratios agreed closely with the experimental results, with certain exceptions which he considered to be linked up with certain irregularities in cell division observed by other workers. The advantages of such a numerical system of computing the power of factors in a character of physiological nature is considerable.

In the investigation of characters of a physiological nature it is difficult to associate factors with any definite feature, and the action of individual factors cannot so far be distinguished by differences in phenotypic expression. It is obvious, however, that more than one factor is in operation as exemplified in the theory of Salaman and Lesley (1923) where five factors were employed, and in that of Jørstad and Lunden (1932) where four were introduced. The complexity of these factorial hypotheses suggests that, before a comprehensive scheme could be arrived at, the multiplicity of factors and their interrelationships might render it unworkable. It would seem advisable, therefore, before accepting such complex hypotheses, to ascertain whether some simpler explanation might not be found to fit all the facts. A three-factor scheme is presented below which appears adequately to meet the case.

In view of the nature of varietal reaction to infection, there is a possibility that the resistance factors do not all possess similar powers and consequently do not contribute equally toward the natural resistance which is characteristic of the plant. On that basis it is suggested that three factor pairs control the reaction to wart disease in the following manner. The three factors **A**, **B**, and **C** are each given a value, viz. **A** $=1$, **B** $=2$, and **C** $=3$, which represents the relative power of the factorial contribution towards resistance. In any particular plant the sum of the values must be seven or over to induce sufficient resistance to overcome infection in cultural conditions and consequently the presence of at least two factors is required. On that basis, a plant heterozygous for all three factors would be susceptible, the sum of its factorial values being only six.

Varieties with the following genotypic constitutions should be resistant to wart disease and when self-fertilised should segregate resistants and susceptibles in the following proportions:

AABBCC	= all resistant.			
AaBBCC	=	,,		
AABbCC	=	,,		
aaBBCC	=	,,		
AAbbCC	=	,,		
AaBbCC	= 15	resistants	: 1	susceptible.
AABBCc	= 3	,,	: 1	,,
AaBBCc	= 3	,,	: 1	,,
aaBbCC	= 3	,,	: 1	,,
AabbCC	= 3	,,	: 1	,,
aaBBCc	= 3	,,	: 1	,,
AABbCc	= 5	,,	: 3	,,

Likewise varieties possessing the following constitutions should be susceptible and when self-fertilised should segregate resistants and susceptibles in the following proportions:

AaBbCc	= 27	resistants	: 37	susceptibles.
aaBbCc	= 5	,,	: 11	,,
AAbbCc	= 1	,,	: 3	,,
AabbCc	= 3	,,	: 13	,,
AaBbcc	= all susceptible.			
AaBBcc	=	,,		
AABBcc	=	,,		
AABbcc	=	,,		

In addition, all varieties with only one factor present in their constitutions are susceptible and produce only susceptible seedlings when self-fertilised.

In Table III are shown the segregations resulting from the self-fertilisation of resistant varieties and their probable constitutions. Similar data relating to susceptible varieties are given in Table IV. In several parents where alternative factorial constitutions present themselves, which so far cannot be checked by relationship, the one which appears most suitable has been used and indicated in the tables by an asterisk. This happens in those parents which produce nothing but resistants or susceptibles, and those which produce resistants and susceptibles in the proportion 3 : 1 respectively. Otherwise, either the ratios obtained offer no alternative factorial constitution than that utilised,

TABLE III.

Progenies resulting from the self-fertilisation of resistant varieties.

Reference No.	Parentage		No. of seedlings: Resistant	Susceptible	Total	Probable factorial formulae
325	Bishop, N.S.	O.	55	19	74	aaBbCC
		T.R.	3	1	4	
		E.	55·5	18·5	74	
162	Flourball, B.S.	O.	44	14	58	AABBCc
		T.R.	3	1	4	
		E.	43·5	14·5	58	
47	Langworthy, N.S.	O.	31	2	33	AaBbCC
		T.R.	15	1	16	
		E.	31	2	33	
193	47 (21), B.S.	O.	32	13	45	aaBbCC*
		T.R.	3	1	4	
		E.	34	11	45	
73	Majestic, B.S.	O.	23	14	37	AABbCc
		T.R.	5	3	8	
		E.	23	14	37	
220	73 (12), N.S.	O.	12	2	14	AABBCc
		T.R.	3	1	4	
		E.	10·5	3·5	14	
110	964*b* (5), B.S.	O.	27	19	46	AABbCc
		T.R.	5	3	8	
		E.	29	17	46	
101	31 (37), B.S.	O.	31	1	32	AaBbCC
		T.R.	15	1	16	
		E.	30	2	32	
127	56 (1), N.S.	O.	33	16	49	AABbCc
		T.R.	5	3	8	
		E.	31	18	49	
167*a*	105 (29), N.S.	O.	28	0	28	aaBBCC
		T.R.	×	0	×	
		E.	28	0	28	
249*a*	207*b* (19), B.S.	O.	18	1	19	aaBbCC*
		T.R.	3	1	4	
		E.	14	5	19	
218	Abundance, N.S.	O.	64	13	77	AaBBCc
		T.R.	3	1	4	
		E.	58	19	77	
223	135 (10), B.S.	O.	55	4	59	AaBbCC
		T.R.	15	1	16	
		E.	55	4	59	
203	135 (30), B.S.	O.	43	11	54	AABBCc*
		T.R.	3	1	4	
		E.	40·5	13·5	54	
196*a*	120 (3), N.S.	O.	49	20	69	AABbCc
		T.R.	5	3	8	
		E.	43	26	69	
198	120 (64), B.S.	O.	16	1	17	AaBbCC
		T.R.	15	1	16	
		E.	16	1	17	
284	233 (8), N.S.	O.	14	2	16	AabbCC
		T.R.	3	1	4	
		E.	12	4	16	
126	32 (17), B.S.	O.	26	0	26	AABbCC*
		T.R.	×	0	×	
		E.	26	0	26	
199*a*	121 (11), N.S.	O.	75	19	94	AABBCc*
		T.R.	3	1	4	
		E.	70·5	23·5	94	

Note. In this and the following tables: O. = observed, T.R. = theoretical ratio, E. = expected or the results of related families provide an indication of what the constitution should be. Such related families are contained in each table, and in some cases in both tables, while many of them are directly connected with hybrid progenies in Tables V–XII inclusive.

The four different segregations obtainable from resistant varieties by self-fertilisation and the five from susceptibles have been observed.

For simplicity, the available results are sorted into eight groups of related progenies and are shown in Tables V–XII. Each group is centred round a particular parent variety and those used for the purpose are: Flourball, Abundance, 135 (10), Bishop, Kerr's Pink, Up-to-Date, Great Scot, and British Queen. The constitutions of the other varieties concerned are assessed in relation to them. This method involves a certain amount of repetition of figures but, to be comprehensive, it is unavoidable.

Discussion.

A test for resistance or susceptibility to wart disease presents difficulties which must be brought into consideration in the elucidation of experimental ratios. In view of the various degrees of resistance observed by a number of authors on standard varieties it is not expected that susceptible seedlings will react to infection in a uniform manner, and consequently those which are most likely to escape detection are the very slightly susceptible ones. Also, when testing a large number of single specimens there is the possibility that a few may not be exposed to adequate infection. Consequently, apart from the laws of chance in the assortment of factors, ratios of resistants and susceptibles are liable to be weighted in favour of resistants, but never in favour of susceptibles. In the tables the proportions observed are fairly consistent in showing a slight balance in favour of resistant as compared with the theoretical ratio; a deviation which must be expected in cases where it was found impossible to repeat the test on all the unaffected seedlings.

The majority of authors are of the opinion that resistance is dominant to susceptibility. In view of the nature of the reaction to the disease it cannot be said that either resistance or susceptibility is dominant. On the present basis the reaction is controlled by dominant factors inducing resistance but nevertheless the complete heterozygote is classed as a susceptible type, suggesting thereby that susceptibility is the dominant character. Since the reaction to the disease is a question of balance between host and parasite, it may be more appropriate to consider its inheritance intermediate. The characters "resistant" and "susceptible" are not direct or primary characters; they are dependent upon physio-

TABLE IV.

Progenies resulting from the self-fertilisation of susceptible varieties.

Reference No.	Parentage		No. of seedlings: Resistant	Susceptible	Total	Probable factorial formulae
99	31 (8), B.S.	O.	2	16	18	**AabbCc**
		T.R.	3	13	16	
		E.	3	15	18	
165*a*	99 (7), N.S.	O.	13	54	67	**AabbCc**
		T.R.	3	13	16	
		E.	13	54	67	
105	653*a* (4), B.S.	O.	8	22	30	**aaBbCc**
		T.R.	5	11	16	
		E.	9	21	30	
168*a*	105 (33), N.S.	O.	31	55	86	**aaBbCc**
		T.R.	5	11	16	
		E.	27	59	86	
207*b*	168*a* (28), B.S.	O.	26	46	72	**aaBbCc**
		T.R.	5	11	16	
		E.	22·5	49·5	72	
114	General, N.S.	O.	17	49	66	**AabbCc**
		T.R.	3	13	16	
		E.	12	54	66	
174	114 (40), N.S.	O.	6	25	31	**AabbCc**
		T.R.	3	13	16	
		E.	6	25	31	
173*a*	114 (39), N.S.	O.	1	32	33	**aabbCc***
		T.R.	0	×	×	
		E.	0	33	33	
347	287*b* (41), N.S. ex 173*a*	O.	1	15	16	**aabbCc***
		T.R.	0	×	×	
		E.	0	16	16	
131	64 (2), B.S.	O.	8	61	69	**AaBbcc***
		T.R.	0	×	×	
		E.	0	69	69	
178	98 (23), N.S.	O.	1	12	13	**AABbcc**
		T.R.	0	×	×	
		E.	0	13	13	
170	110 (20), B.S.	O.	3	19	22	**AABbcc***
		T.R.	0	×	×	
		E.	0	22	22	
128	56 (2), N.S.	O.	2	80	82	**AaBbcc***
		T.R.	0	×	×	
		E.	0	82	82	
306	42667	O.	8	23	31	**AAbbCc**
		T.R.	1	3	4	
		E.	8	23	31	
200	123 (1), N.S.	O.	31	47	78	**AaBbCc**
		T.R.	27	37	64	
		E.	33	45	78	

TABLE V.

Progenies related to Flourball.

Reference No.	Parentage	Description of parents		No. of seedlings: Resistant	Susceptible	Total	Probable factorial formulae
162	Flourball, B.S.	Resistant	O.	44	14	58	AABBCc
			T.R.	3	1	4	
			E.	43·5	14·5	58	
134	Abundance	Resistant	O.	27	7	34	AaBBCc
	×	×	T.R.	3	1	4	×
	Flourball	Resistant	E.	25·5	8·5	34	AABBCc
218	Abundance, N.S.	Resistant	O.	64	13	77	AaBBCc
			T.R.	3	1	4	
			E.	58	19	77	
154*a*	Majestic	Resistant	O.	32	1	33	AABbCc
	×	×	T.R.	3	1	4	×
	Flourball	Resistant	E.	25	8	33	AABBCc
73	Majestic, B.S.	Resistant	O.	23	14	37	AABbCc
			T.R.	5	3	8	
			E.	23	14	37	
144*abc*	Epicure	Susceptible	O.	75	77	152	aabbCC
	×	×	T.R.	1	1	2	×
	Flourball	Resistant	E.	76	76	152	AABBCc
182*a*	Ally	Resistant	O.	86	11	97	AaBbCC
	×	×	T.R.	7	1	8	×
	Flourball	Resistant	E.	85	12	97	AABBCc
142*a*	Champion	Resistant	O.	93	16	109	AaBbCC
	×	×	T.R.	7	1	8	×
	Flourball	Resistant	E.	95	14	109	AABBCc
187	King Edward VII	Susceptible	O.	12	14	26	aaBBcc
	×	×	T.R.	1	1	2	×
	Flourball	Resistant	E.	13	13	26	AABBCc
43	Up-to-Date	Susceptible	O.	23	16	39	aabbCC
	×	×	T.R.	1	1	2	×
	Flourball	Resistant	E.	19·5	19·5	39	AABBCc
146	Kerr's Pink	Resistant	O.	74	5	79	AaBbCC
	×	×	T.R.	7	1	8	×
	Flourball	Resistant	E.	69	10	79	AABBCc
140*a*	British Queen	Susceptible	O.	5	5	10	aabbCC
	×	×	T.R.	1	1	2	×
	Flourball	Resistant	E.	5	5	10	AABBCc
139*ab*	Bishop	Resistant	O.	79	37	116	aaBbCC
	×	×	T.R.	3	1	4	×
	Flourball	Resistant	E.	87	29	116	AABBCc
325	Bishop, N.S.	Resistant	O.	55	19	74	aaBbCC
			T.R.	3	1	4	
			E.	55·5	18·5	74	

TABLE VI.

Progenies related to Abundance.

Reference No.	Parentage	Description of parents		No. of seedlings: Resistant	Susceptible	Total	Probable factorial formulae
218	Abundance, N.S.	Resistant	O.	64	13	77	AaBBCc
			T.R.	3	1	4	
			E.	58	19	77	
134	Abundance	Resistant	O.	27	7	34	AaBBCc
	×	×	T.R.	3	1	4	×
	Flourball	Resistant	E.	25·5	8·5	34	AABBCc
162	Flourball, B.S.	Resistant	O.	44	14	58	AABBCc
			T.R.	3	1	4	
			E.	43·5	14·5	58	
135	Abundance	Resistant	O.	16	6	22	AaBBCc
	×	×	T.R.	5	3	8	×
	Majestic	Resistant	E.	14	8	22	AABbCc
73	Majestic, B.S.	Resistant	O.	23	14	37	AABbCc
			T.R.	5	3	8	
			E.	23	14	37	
311*ab*	Abundance	Resistant	O.	60	15	75	AaBBCc
	×	×	T.R.	13	3	16	×
	135 (10)	Resistant	E.	61	14	75	AaBbCC
223	135 (10), B.S.	Resistant	O.	55	4	59	AaBbCC
			T.R.	15	1	16	
			E.	55	4	59	
136	Abundance	Resistant	O.	52	11	63	AaBBCc
	×	×	T.R.	13	3	16	×
	Shamrock	Resistant	E.	51	12	63	AaBbCC
180	Abundance	Resistant	O.	56	10	66	AaBBCc
	×	×	T.R.	13	3	16	×
	120 (56)	Resistant	E.	54	12	66	AaBbCC
138	Abundance	Resistant	O.	40	36	76	AaBBCc
	×	×	T.R.	1	1	2	×
	121 (6)	Susceptible	E.	38	38	76	aabbCC
308*a*	Abundance	Resistant	O.	17	1	18	AaBBCc
	×	×	T.R.	13	3	16	×
	Herald	Resistant	E.	15	3	18	AaBbCC

TABLE VII.

Progenies related to 135 (10).

Reference No.	Parentage	Description of parents		No. of seedlings: Resistant	Susceptible	Total	Probable factorial formulae
223	135 (10), B.S.	Resistant	O.	55	4	59	AaBbCC
			T.R.	15	1	16	
			E.	55	4	59	
311*ab*	Abundance	Resistant	O.	60	15	75	AaBBCc
	×	×	T.R.	13	3	16	×
	135 (10)	Resistant	E.	61	14	75	AaBbCC
218	Abundance, N.S.	Resistant	O.	64	13	77	AaBBCc
			T.R.	3	1	4	
			E.	58	19	77	
316*ab*	British Queen	Susceptible	O.	43	8	51	aabbCC
	×	×	T.R.	3	1	4	×
	135 (10)	Resistant	E.	38	13	51	AaBbCC
212*abc*	Epicure	Susceptible	O.	49	4	53	aabbCC
	×	×	T.R.	3	1	4	×
	135 (10)	Resistant	E.	40	13	53	AaBbCC
319	Up-to-Date	Susceptible	O.	33	6	39	aabbCC
	×	×	T.R.	3	1	4	×
	135 (10)	Resistant	E.	29	10	39	AaBbCC

TABLE VIII.

Progenies related to Bishop.

Reference No.	Parentage	Description of parents		No. of seedlings: Resistant	Susceptible	Total	Probable factorial formulae
325	Bishop, N.S.	Resistant	O.	55	19	74	aaBbCC
			T.R.	3	1	4	
			E.	55·5	18·5	74	
139*ab*	Bishop	Resistant	O.	79	37	116	aaBbCC
	×	×	T.R.	3	1	4	×
	Flourball	Resistant	E.	87	29	116	AABBCc
965, 966	Bishop	Resistant	O.	51	11	62	aaBbCC
	×	×	T.R.	3	1	4	×
	724 (2)	Resistant	E.	46·5	15·5	62	AABBCc
967	Bishop	Resistant	O.	15	10	25	aaBbCC
	×	×	T.R.	5	3	8	×
	800 (2)	Resistant	E.	16	9	25	AABbCc
184*a*	Bishop	Resistant	O.	12	0	12	aaBbCC
	×	×	T.R.	×	0	×	×
	120 (42)	Resistant	E.	12	0	12	AABbCC

TABLE IX.

Progenies related to Kerr's Pink.

Reference No.	Parentage	Description of parents		No. of seedlings			Probable factorial formulae
				Resistant	Susceptible	Total	
146	Kerr's Pink	Resistant	O.	74	5	79	AaBbCC
	×	×	T.R.	7	1	8	×
	Flourball	Resistant	E.	69	10	79	AABBCc
162	Flourball, B.S.	Resistant	O.	44	14	58	AABBCc
			T.R.	3	1	4	
			E.	43·5	14·5	58	
96	Kerr's Pink	Resistant	O.	122	12	134	AaBbCC
	×	×	T.R.	7	1	8	×
	Bell	Resistant	E.	117	17	134	AABBCc
151	Kerr's Pink	Resistant	O.	119	12	131	AaBbCC
	×	×	T.R.	7	1	8	×
	966*b* (4)	Resistant	E.	115	16	131	AABBCc
185	Kerr's Pink	Resistant	O.	9	1	10	AaBbCC
	×	×	T.R.	7	1	8	×
	120 (45)	Resistant	E.	9	1	10	AABBCc
147	Kerr's Pink	Resistant	O.	13	6	19	AaBbCC
	×	×	T.R.	5	3	8	×
	39 (15)	Susceptible	E.	12	7	19	AAbbCc
317*a*	Kerr's Pink	Resistant	O.	26	2	28	AaBbCC
	×	×	T.R.	15	1	16	×
	Herald	Resistant	E.	26	2	28	AaBbCC
262*a*	Kerr's Pink	Resistant	O.	44	3	47	AaBbCC
	×	×	T.R.	7	1	8	×
	70 (13)	Resistant	E.	41	6	47	AABBCc

TABLE X.

Progenies related to Up-to-Date.

Reference No.	Parentage	Description of parents		No. of seedlings			Probable factorial formulae
				Resistant	Susceptible	Total	
43	Up-to-Date	Susceptible	O.	23	16	39	aabbCC
	×	×	T.R.	1	1	2	×
	Flourball	Resistant	E.	19·5	19·5	39	AABBCc
162	Flourball, B.S.	Resistant	O.	44	14	58	AABBCc
			T.R.	3	1	4	
			E.	43·5	14·5	58	
319	Up-to-Date	Susceptible	O.	33	6	39	aabbCC
	×	×	T.R.	3	1	4	×
	135 (10)	Resistant	E.	29	10	39	AaBbCC
223	135 (10), B.S.	Resistant	O.	55	4	59	AaBbCC
			T.R.	15	1	16	
			E.	55	4	59	
160	Up-to-Date	Susceptible	O.	3	46	49	aabbCC
	×	×	T.R.	0	×	×	×
	98 (23)	Susceptible	E.	0	49	49	AABbcc
178	98 (23), N.S.	Susceptible	O.	1	12	13	AABbcc
			T.R.	0	×	×	
			E.	0	13	13	
216	Up-to-Date	Susceptible	O.	10	19	29	aabbCC
	×	×	T.R.	3	5	8	×
	160 (28)	Susceptible	E.	11	18	29	AaBbCc

TABLE XI.

Progenies related to Great Scot.

Reference No.	Parentage	Description of parents		No. of seedlings: Resistant	Susceptible	Total	Probable factorial formulae
93, 94	Great Scot	Resistant	O.	196	18	214	AaBbCC
	×	×	T.R.	7	1	8	×
	Bell	Resistant	E.	187	27	214	AABBCc
120	Great Scot	Resistant	O.	23	4	27	AaBbCC
	×	×	T.R.	7	1	8	×
	993*a* (4)	Resistant	E.	24	3	27	AABBCc
196*a*	120 (3), N.S.	Resistant	O.	49	20	69	AABbCc
			T.R.	5	3	8	
			E.	43	26	69	
191*a*	94 (93)	Resistant	O.	32	14	46	AABBCc
	×	×	T.R.	3	1	4	×
	120 (3)	Resistant	E.	34·5	11·5	46	AABbCc
183	Ally	Resistant	O.	16	5	21	AaBbCC
	×	×	T.R.	3	1	4	×
	120 (3)	Resistant	E.	16	5	21	AABbCc

TABLE XII.

Progenies related to British Queen.

Reference No.	Parentage	Description of parents		No. of seedlings: Resistant	Susceptible	Total	Probable factorial formulae
140*a*	British Queen	Susceptible	O.	5	5	10	aabbCC
	×	×	T.R.	1	1	2	×
	Flourball	Resistant	E.	5	5	10	AABBCc
162	Flourball, B.S.	Resistant	O.	44	14	58	AABBCc
			T.R.	3	1	4	
			E.	43·5	14·5	58	
316*ab*	British Queen	Susceptible	O.	43	8	51	aabbCC
	×	×	T.R.	3	1	4	×
	135 (10)	Resistant	E.	38	13	51	AaBbCC
223	135 (10), B.S.	Resistant	O.	55	4	59	AaBbCC
			T.R.	15	1	16	
			E.	55	4	59	
314	British Queen	Susceptible	O.	23	4	27	aabbCC
	×	×	T.R.	3	1	4	×
	Herald	Resistant	E.	20	7	27	AaBbCC
259*ac*	British Queen	Susceptible	O.	11	7	18	aabbCC
	×	×	T.R.	1	1	2	×
	70 (13)	Resistant	E.	9	9	18	AABBCc
117	British Queen	Susceptible	O.	6	5	11	aabbCC
	×	×	T.R.	1	1	2	×
	993*a* (4)	Resistant	E.	5·5	5·5	11	AABBCc

logical qualities in the plant which, in turn, are presumed to be controlled by definite hereditary factors. It is the combined effect of these physiological qualities which determines the degree of resistance, and since they are tentatively considered to possess unequal powers the net result seems to accrue from the blend of their respective contributions.

Köhler (1931) found that resistance to wart disease involved, in the first place, two different physiological factors, viz. "infection degree" and "reaction degree," the former being the counteraction of the plant towards the invading organism, and the latter the reaction of the plant to the hypertrophic stimulus of the parasite. It may be possible to correlate such physiological entities with genetic factors.

The theoretical ratios obtained by Salaman and Lesley (1923) applicable to the self-fertilisation of resistant varieties are in close agreement with those existing in the present hypothesis. In fact, they are identical except in one case where a 5 : 3 ratio is obtained by the present system in place of a 9 : 7 ratio suggested by Salaman and Lesley. Both theories allow for the possibility of four different ratios of resistants and susceptibles resulting from the self-fertilisation of resistant varieties. With regard to susceptible varieties Salaman and Lesley found various sorts but did not attempt to enumerate them.

The experimental results obtained by Jørstad and Lunden (1932) and Lunden and Jørstad (1934) are in some respects similar to those of Salaman and Lesley (1923), but they fail to agree in the nature of the effect and the interrelations of the factors which are similarly designated in both theories. The conclusive data, however, could be explained as readily by the present system.

The fact that, in Lunden and Jørstad's experiments, the selfing and crossing of susceptible varieties having yielded nothing but susceptible offspring does not, however, preclude the existence of susceptible varieties giving widely different ratios. If Centifolia is one of the extremely susceptible types, then such results would be expected. Likewise the ratio of 3 immunes : 1 susceptible obtained from all the self-fertilised immunes is probably a coincidence, particularly since all the parents except one are closely related. This preponderance of 3 : 1 ratios is amply provided for in the present scheme by the existence of five different genotypes giving such ratios. Only one self-fertilised variety, viz. Flourball, is common to both series of experiments and in each case a 3 : 1 ratio was obtained.

If the present scheme be applied to the data of Lunden and Jørstad, the following genotypes may be tentatively suggested: Centifolia **AABbcc**;

Jubel, Hindenburg **AABBCc**; Dukker **AaBbCC**; and Golden Lass **AABbCc**. On that basis Sagerud, Marius, Louis Botha, and Early Puritan might be represented by **AABBcc** and Flourball, Abundance and Kerr's Pink by the formulae already used in this paper. The factorial constitutions of the remaining parents thereupon become obvious and can easily be filled in to complete the explanation. The theoretical ratios obtained therefrom are found to fit the experimental ratios identically with the exception of three progenies in which Jubel appears as male parent. Two of these exceptions, viz. Sagerud × Jubel and Early Puritan × Jubel, should under the present scheme give immunes and susceptibles in the ratio of 1 : 1 instead of 5 : 3 as observed. The third, viz. Kerr's Pink × Jubel, should give a ratio of 7 immunes : 1 susceptible by the present scheme instead of the observed 15 : 1 ratio. These differences are all due to a scarcity of susceptible plants in the progenies, a divergence which in practice is much more likely to occur than a scarcity of immunes. In view of the fact that Jubel on selfing segregates immunes and susceptibles in the ratio of 3 : 1, Kerr's Pink would require to be extremely resistant to give a 15 : 1 ratio with it on hybridisation. Such a high degree of resistance is not borne out in the present experiments.

The experiments of Salaman and Lesley led them to conclude that a difference of genotype amongst "immune" plants is not reflected by any difference of degree in the immunity conferred. Recent work, however, has shown that several different degrees of immunity are conferred and it appears that different genotypes are responsible. In many resistant varieties, the invasion of the fungus has been demonstrated. In the more highly resistant types the fungus was found to die but in less highly resistant forms, radial galls may be formed, with or without summer sporangia. In moderately resistant varieties radial galls have been found to coalesce, with subsequent proliferation of tissue, and summer sporangia are generally produced. The less resistant varieties have been observed to show proliferation of tissue and malformation of sprouts which, in appearance, are like true warts. In this type, winter sporangia may sometimes be formed. It can consequently be accepted that there are different kinds of resistant phenotypes.

It can also be demonstrated that amongst susceptible varieties there are several different phenotypes. In ordinary field cultivation, the difference in degree of infection and size of the resulting warts can be taken as an indication of the degree of susceptibility of the variety. In uniformly inoculated soil some susceptible types are more or less completely destroyed by the fungus while others are but little affected. Similar results are obtained under laboratory conditions.

These different phenotypes, both resistant and susceptible, are likely to be controlled by corresponding genotypes, and it is tentatively suggested that the numerical values assigned to the various genotypes correspond to phenotypic reaction in such a manner that the higher the numerical value of the genotype the more resistant is the phenotype.

SUMMARY.

It is concluded that there are various kinds of resistant varieties as illustrated by differences in toleration and reaction towards the fungus. Similarly, there are various kinds of susceptible varieties: these differences are due to physiological qualities in the plant which in turn are controlled by definite hereditary factors.

The inheritance of resistance to wart disease is dependent upon the cumulative interaction of three factors inducing resistance. The three factors are designated **A**, **B**, and **C**, and each is given a value, viz. **A** = 1, **B** = 2, and **C** = 3, which represents approximately the relative power of the factorial contributions towards resistance. In any particular plant the sum of the values must be seven or over to induce sufficient resistance to overcome infection under cultural conditions, and consequently the presence of at least two factors is required. The numerical values assigned to genotypes correspond to phenotypic reaction in such a manner that the higher the value, the more resistant is the phenotype.

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