GENETIC STUDIES IN POTATOES; THE INHERITANCE OF IMMUNITY TO WART DISEASE.

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A preliminary account of the work undertaken by the joint authors to elucidate the inheritance of immunity to wart disease by the potato was read before the International Potato Conference in November 1921. Since then another year's results are to hand, and the combined results are such as to support in general the views put forward on that occasion. Notwithstanding the fact that unresolved difficulties still present themselves, the importance of the problem under investigation is such that it seems desirable to put forward the facts and the conclusions to which they have led, without further delay. This course seems the more advisable when it is remembered that to carry out a test for wart on any particular desired mating requires at least three years to obtain a tentative result and a further year to confirm it.

It is generally recognised that once the immunity of a variety is established it has never been found to break down. The immunity is under the conditions of normal horticulture constant. Professor Schaffnit (1) has stated that degenerate plants of a hitherto immune variety will succumb to wart disease under normal conditions. We have found no evidence of such an occurrence during the ten years in which trials for wart immunity have been conducted at Ormskirk. Indeed, Sutton's Abundance has retained its immunity, under trial, for 14 consecutive years. We have, however, very frequently found rogues in immune stocks which have succumbed and which, had they not been identified by constant inspection during the growing period, would have been overlooked and given rise to just such a view as Professor Schaffnit advances. At Ormskirk it has been laid down that a trial in two consecutive years is necessary to determine the existence of immunity, and that the number of plants examined should not be less than forty. The experience we have gained undoubtedly supports this view, and although forty plants may be greater than is really essential, it is a wise measure of precaution. There are several conditions which affect the incidence of the disease in a susceptible variety. It is, above all, necessary that

the soil should be thoroughly infected with the spores of the pathogen, *Synchytrium endobioticum*, Schilb. Perc. This is assured at Ormskirk. The plants should be well grown and healthy. Infection with the virus diseases such as Leaf Roll and Mosaic, if severe, will produce such feeble plants with tubers so small and few that they may escape infection or at least the infection may escape detection. The effect of virus diseases is to hasten the maturity of the plant and this early ripening is to a considerable extent a protection against attack, especially in a cold and dry season. Not least important, as the season of 1921 taught, is that the rainfall should be normal, as moisture hastens and increases infection, whilst drought may so hinder the growth of the organism as to allow many susceptible plants to escape. This was exemplified in a very marked way in our cultures in 1921 and 1922. In the latter year all those which escaped infection in the abnormally warm dry season of 1921 were replanted and the result showed that many of those stocks grown in the open field which had so escaped fell readily to the disease in the cooler and moister season of 1922. On the other hand, certain extremely vigorous families were grown in 1921 in a small highly infected garden which, owing to trees and hedges and the very rich deep soil, had been protected from the intense heat and consequent evaporation which had taken place generally in the open in that year. In a family of 79 individuals, 76 were free from wart and not one of the 76 succumbed when grown in the trial grounds again in 1922. The families 318*Bb*/20 and 321*Bb*/20, both very vigorous, were also grown in this garden and although the non-warted seedlings of 1921 were not regrown in 1922, there is probably no reason to doubt the substantial accuracy of the figures then obtained. In the case of all the families which did not enjoy such exceptional advantages it was found that a considerable modification of the 1921 result was occasioned by the further test undertaken in 1922. The incidence of wart disease in 1922 was most severe and it is unlikely that the results obtained would be materially altered by a further year's test.

The series of families tested for their susceptibility or otherwise to wart disease arose from fertilizations made by hand under parchment paper bags and with all precautions. The families fall into six groups, seedlings of immune parents selfed, seedlings arising from the mating of two different immunes, seedlings of susceptible selfed parents, seedlings arising from the mating of two different susceptibles, seedlings of the mating immune by susceptible and, finally, seedlings of the mating susceptible by immune.

An examination of the tables reveals at once the fact that whereas an immune selfed or mated to another may produce, as found in one family, all immunes, it generally gives rise to a large majority of immunes and to a minority of susceptibles. On the other hand, susceptibles, with one notable exception, give rise to families composed entirely of susceptibles or at most contain a few per cent. of non-warted individuals. It can be accepted at once that immunity is dominant and susceptibility recessive. This view is directly opposed to that of Collins (2) who, however, at that time was not in possession of any consistent body of first hand facts, but it is in agreement with the indications obtained by Orton and Weiss (3).

Table II, giving the mating of the two immunes, Kerr's Pink and Champion the Second, deals with a family of 79 individuals who have been tested thoroughly in two consecutive years and the result may be taken as absolutely reliable. The ratio of 3 susceptible to 76 immune suggests at once a 1 : 15 ratio brought about by two factors independently capable of inducing immunity. We may call these factors *X* and *Y*. The existence of a 1 : 15 ratio is also supported by the evidence afforded in the mating of the Flourball F_2 seedling (3*Cb*23) Table I.

TABLE I.

Immune Selfed.

Name	Class Number	Number of Seedlings Tested		Non-warted		Susceptible		Dead
Flourball Seedling ...	3 *Cb*/19, 6 *Cb*/21	10		6		3		1
,, ,, ...	3 *Cb*/19, 23 *Cb*/21	26		22		3		1
Leinster Wonder ...	307 *Bb*/20	10	18	5	10	5	8	0
,, ,, ...	307 *Cb*/20	8		5		3		0
Leinster Wonder Seedling	307 *Cb*/20, 4 *Cb*/21	12		9		0		3
*Golden Wonder × Leinster Wonder F^2 Seedling	305 *Cb*/20, 125/21	9		9		0		0
Majestic	309 *Bb*/21	25		10		9		6
Edzell Blue	302 *Bn*/20	13	28	12	22	1	6	0
,, ...	302 *Cn*/20	15		10		5		0
Edgecote Purple × Edzell Blue Seedling	315 *Cb*/20, 31 *Cb*/21	13		10		3		0

* Only this relatively small proportion of the family was tested.

TABLE II.

Immune × Immune.

Name	Class Number	Number of Seedlings Tested	Non-warted	Susceptible	Dead
Kerr's Pink × Champion II ...	306 *Bb*/20	79	76	3	0
*Golden Wonder × Leinster Wonder	305 *Cb*/20	27	18	9	0

* Only this relatively small proportion of the family was tested.

The late John Snell (4) undertook some experiments on the inheritance of wart in 1919. The seedlings were raised from natural berries. The notes containing Mr Snell's observations came into the hands of Mr W. Cuthbertson, from whose published letter the following facts are taken. The results from the following selfed plants, viz. Priory Queen, Favourite and Admiral, all synonyms of and doubtless identical with Abundance, showed 7 to be warted out of 80, figures again suggesting a 1 : 15 ratio. Possibly also Flourball is an *Xx Yy* plant because we have seedlings of it giving indications of both a 1 : 3 and a 1 : 15 family ratio derived from it. (See Table I.) In addition to an immune plant having a formula *Xx Yy*, the selfed immunes in Table I give at least one clear example of a 3 : 1 ratio—such immunes having the formula *Xxyy* or *xxYy*. Whilst the families of pure immunes derived from Leinster Wonder F_2 and Golden Wonder × Leinster Wonder F_2 seedlings, though small, are evidence of some weight in favour of the existence of a homozygous immune plant, none of the six crosses of immune and susceptible produce a family of all immunes which points to the relative rarity of the homozygous immune parent.

If we regard the families 307 *Cb*, 4 *Cb* and 305 *Cb* 125 as homozygous types they would presumably have the formula *XX YY*. To these may be added the types *Xx yy* or *xx Yy* which have already been identified.

There are, however, two immune parents which do not fit into this scheme, viz., Majestic and Leinster Wonder. The family of Majestic tested at Ormskirk in 1922 produced 10 immunes to 9 susceptibles. These numbers would not by themselves carry very much weight were it not that in the notes of the late J. Snell already alluded to, Majestic seedlings obtained from natural berries behaved in an almost identical manner, viz. 38 non-warted to 22 susceptible. The combined numbers would be 48 : 31, a close approximation to a 9 : 7 ratio which is not to be expected from the presence of two factors either of which, acting independently, can confer immunity. Similarly, Leinster Wonder selfed produced 10 non-warted to 8 susceptible individuals, a result which, in view of the Majestic findings, must be considered of some significance. The deviations from a 3 : 1 ratio are approximately three times the standard error which, together with the fact that both families exhibit ratios which approximate to 9 : 7, suggests the existence of two factors which produce immunity only when both are present. If, therefore, adhering to the two factors *X* and *Y* which independently were assumed capable of inducing immunity to wart, we make the further assumption that in the absence of a complementary factor, which we will call *Z*,

neither X nor Y alone can induce immunity but that the combined action of either X or Y with Z will induce immunity equally as does the combination of X and Y together without Z, then a plausible explanation is found. Under such an hypothesis a plant heterozygous for X and Y and homozygous for the absence of Z would produce 9 immune to 7 susceptible plants.

Susceptible plants as judged from the selfed families, Table III, and the crosses of susceptible by susceptible, Table IV, would appear to be

TABLE III.

Susceptible Selfed.

Name	Class Number	Number of Seedlings Tested		Non-warted		Susceptible		Dead
Congo × Flourball F_2 Seedlings	*K*23 *Cb*/19, 23 *Cb*/21	16		0		10		6
Edgecote Purple	147 *Bb*/20	31		2*		27		2
Myatt's Ashleaf	333 *Bb*/21	22	50	11	22	9	26	2
,, ,, ...	333 *Cb*/21	28		11		17		0

* Very poor small plants: probably too feeble to have contracted the disease.

TABLE IV.

Susceptible × *Susceptible.*

Name	Class Number	Number of Seedlings Tested			Non-warted			Susceptible			Dead
Congo-Flourball Seedling × Edgecote Purple	330 *Bb*/21	14			0			14			6
May Queen × Edgecote Purple	332 *Bb*/21	33			1			31			1
Eclipse × Sharpe's Victor	326 *Bb*/21	6			0			6			0
Myatt's Ashleaf × Edgecote Purple	334 *Bb*/21	22	59	151	2	11	24	20	48	122	0
	334 *Cb*/21	37			9			28			0
Edgecote Purple × Myatt's Ashleaf	338 *Bb*/21	39	92		5	13		31	74		3
	338 *Cb*/21	53			8			43			2

divided into those which produce only susceptibles and those which produce a considerable number of immunes also. This latter group is seen to include the selfed and crossed families in which Myatt's Ashleaf is a parent. The former group includes families in which an occasional immune is noted, viz., in Edgecote Purple 147 *Bb*/20 where there are 27 susceptibles and 2 immunes, and in May Queen by Edgecote Purple where there are 37 susceptibles to 1 immune. In the former family the immune plants are very poor ones and may be left out of consideration,

and in the latter, although the immune plant was not abnormal in growth it is not improbable that its immunity in 1922 is due to some fortuitous circumstance, and that it will not be maintained.

When susceptibles are crossed to immunes or vice versa the results are again of two kinds, a larger class where the resultant family is made up of equal numbers of immune and susceptible individuals, and another of which we have but one example, viz. Arran Rose × Sharpe's Victor (324*Bb*/21, Table V), where there is a large majority of immunes.

TABLE V.

Immune × *Susceptible.*

Name	Class Number	Number of Seedlings Tested	Non-warted	Susceptible	Dead
Arran Rose × Sharpe's Victor	324 *Bb*/21	16	11	4	1
Witchhill * × Myatt's Ashleaf	316 *Bb*/20	25, 32 → 57	9, 16 → 25	16, 16 → 32	0
	316 *Cb*/20				0
Snowdrop* × Myatt's Ashleaf	313 *Cb*/20	25, 25 → 82	14, 14 → 39	9, 9 → 41	2
Edzell Blue × Edgecote Blue	304 *Bb*/20	27, 38 → 65	11, 21 → 32	16, 17 → 33	0
	304 *Cb*/20				0
Edgecote Purple × Edzell Blue	315 *Cb*/20	28, 28 → 93	16, 16 → 48	12, 12 → 45	0
Edzell Blue × Myatt's Ashleaf	303 *Cb*/21	44	23	21	0

* Synonyms for one and the same plant.

The susceptible individuals who on selfing produce no immunes and behave in crossing as pure recessives must, on the *X* and *Y* hypothesis be represented as *xx yy*, whilst the immune parents with which they are mated will be examples of the *Xx yy* or *xx Yy* types of immune plants when the resultant family consists of half immune and half susceptible plants.

In Tables V and VI there are several examples which illustrate this mating, but attention is in particular drawn to the mating 316/20 and

TABLE VI.

Susceptible × *Immune.*

Name	Class Number	Number of Seedlings Tested	Non-warted	Susceptible	Dead
Kew 2 × E. Regent 63, 78 × Shamrock	318 *Bb*/20	38	17	21	0
Kew 3 × *K* 23, 17 × Leinster Wonder	321 *Bb*/20	37	15	22	0

313/20. In these examples Myatt's Ashleaf is used to cross Witchhill and Snowdrop. The resulting families were identical in appearance and are seen to be similar also in their reaction to wart disease. It was further found also that their heritable cropping capacity as exhibited by the graphs of the curves of their offsprings' crops was also identical[1](5). It is well known that Witchhill and Snowdrop, though considered by most experts to be but one and the same variety—an example of synonymity amongst potatoes—are by others still regarded as distinct. We are now in a position to say that not only are these two varieties identical morphologically, but that in respect to two most important physiological reactions, viz. that of immunity to wart disease and heritable cropping capacity, they are also identical.

It may here be pointed out that the reciprocal crosses Myatt's Ashleaf and Edgecote Purple (Table IV) are also identical in respect to their susceptibility to wart disease. Indeed, identical results from the reciprocal crosses 304*Cb*/20, 304*Bb*/20 and 315*Cb*/20 were obtained, which would tend to confirm the view that there is no linkage or other effect induced by sex on the inheritance of immunity in the potato.

The families in which Myatt's Ashleaf enter differ in their reaction to wart disease.

Whilst other susceptible plants which have been tested appear to give all warted offspring on selfing, Myatt's Ashleaf produces a family in which the ratio of susceptible to non-warted is 26 : 22. Further, in its matings with the susceptible Edgecote Purple, the resultant family consists of 122 susceptible individuals and 24 immunes, a result deviating from a 3 : 1 ratio by twice the standard deviation.

Both results suggest that Myatt's Ashleaf is really an immune variety whose immunity is being held up by one or more inhibiting factors. Indeed, in a previous publication (5) evidence was adduced that Myatt's Ashleaf contained a factor "*B*" which inhibits its own immunity factor *Y*. However, the ratio 26 : 22 in the selfed family now available indicates a 9 : 7 ratio, and seems to suggest that there may be not one, but two inhibitors, *A* and *B*, existent in an heterozygous state. With the existing data, the relation of these inhibitors with the factors *X*, *Y*, and *Z* cannot be further elucidated but it may well be that it is necessary for both of them to be present to inhibit either of the immune factors, though their combined presence is incapable of inhibiting the immunity conferred by the combined presence of both *X* and *Y*. On such an hypothesis Myatt's Ashleaf would have the formula *xx YY Aa Bb*.

[1] This refers to an unpublished work on the *Inheritance of Cropping*.

In Snell's notes are given the results of a test on 29 seedlings of a natural ball of President, with a result that 15 are susceptible and 14 not, which suggests that President is a susceptible variety similar in kind to Myatt's Ashleaf.

It has been seen that the mating of Myatt's Ashleaf × Edgecote Purple results in the production of 122 susceptible to 24 immune plants. This ratio is suggestive of 3 : 1, although its deviation is just over twice the standard error. If the formula *xx YY Aa Bb ZZ* be adopted for Myatt's Ashleaf, the corresponding formula for Edgecote Purple would be *xx yy Aa BB ZZ*, which would allow of 3 susceptible to 1 immune in crossing. The formulae both for Edzell Blue and Witchhill might be *xx Yy aa BB Zz*, which would allow for the production on crossing with Myatt's Ashleaf of a family composed of one half immune and one half susceptible seedlings.

The crosses in Table VI representing the matings of susceptibles by immunes present two results which may be interpreted as follows:

The first family 318 *Bb*/20 where the immune parent is Silver Shamrock produced 17 non-warted to 21 susceptible which is near enough to 19 : 19 or equality. This would be a probable result of the mating of a susceptible variety not containing *X* or *Y* or the inhibitors to an immune which is of the 3 : 1 type. Silver Shamrock, which is a Flourball seedling, is thus not unlikely to be just such a type of immune.

The second family 321 *Bb*/20 is crossed by Leinster Wonder which, it has been seen, is probably to be regarded as devoid of the complementary factory *Z* and as bearing the formula *Xx Yy zz*. If the susceptible is *xx Yy zz* and Leinster Wonder be as suggested then a ratio of 3 non-warted to 5 susceptible would result; actually in the family 321 *Bb* the ratio is 15 immunes to 22 susceptibles; on a 3 : 5 basis the number would be 14 : 23.

Sharpe's Victor in its reaction presents a further problem; itself it is susceptible but nevertheless offers sufficient resistance to wart disease as for some time to have been considered as an immune. The small family Eclipse × Sharpe's Victor is all warted, but the mating Arran Rose (immune) × Sharpe's Victor (Table V) gives rise to a family of 11 immunes to 4 susceptibles, an excess of immunes which suggests a 3 : 1 ratio. A result which might arise where Arran Rose owes its immunity to one of the *X* or *Y* factors, and Sharpe's Victor to contain the other but in an inhibited combination due to the combined presence of *A* and *B*.

It would appear that certain plants may offer a varying degree of resistance to the attacks of the pathogen, which is very possibly correlated with their genotypic composition. This resistance is, however, insufficient to protect the plant against the full force of a heavy attack, such as befell the plants at Ormskirk in 1922. On the other hand a plant which owing to its genotypic character is immune, remains constantly so under all the conditions of experimentation as yet employed. Indeed, a suggestion of the kind has been made by Orton and Weiss who state that "such differences in the degree of resistance or susceptibility shown are believed to be inherent in the variety itself and this would indicate that the extremes of resistance and susceptibility are dependent for their expression upon more than a single factor difference." The evidence we have brought forward as a result of our researches at Ormskirk would seem to afford the necessary proof of this contention, for whether we explain our facts by supposing that some plants might be susceptible because they have no immunity factors, or susceptible because the immunity factors are held in suspense by inhibitors, or susceptible because the immunity factor, though present, lacks its complementary factor, the essential fact remains that there is unmistakable evidence, that certain susceptible plants, such as Myatt's Ashleaf and Sharpe's Victor, behave quite differently both when selfed and when crossed as compared to other immunes.

We may summarise our results as follows:

(1) That immunity to wart disease in the potato is dependent upon segregating factors.

(2) That immunity is dominant to susceptibility: though this dominance may be inhibited by other factors.

(3) That there are at least four types of immunes, which may be described as:

(a) pure immunes,

(b) immunes which, on selfing, give 15 immunes to 1 susceptible,

(c) „ „ „ „ „ 3 „ „ 1 „

(d) „ „ „ „ „ 9 „ „ 7 „

and that the immunity they respectively possess may be due to the presence of one or more immune factors, the evidence for the co-presence of at least two immune factors in some varieties being particularly strong.

(4) That susceptibles may be of various sorts:

(*a*) due to the absence of either of the immune factors *X* or *Y*,

(*b*) due to the absence of the complementary factor *Z*, though either *X* or *Y* may be present,

(*c*) due to the presence of an inhibitor of the immunity factor.

(5) Difference of genotype amongst immune plants is not reflected by any difference of degree in the immunity conferred. Difference of genotype, however, amongst susceptibles does appear to confer considerable differences in degree of susceptibility. However, under the conditions of field experimentation the line between immune and susceptible once reached is absolute.

(6) No differences were discovered as regards the immunity in respect to reciprocal crosses.

(7) There is no evidence of any relation or linkage between wart disease and any other character of the plant.

We take this opportunity of thanking Mr Heber Smith for having carried through the 1922 field work at Ormskirk, and Mr H. Bryan, Superintendent of the National Institute of Agricultural Botany Potato Testing Station, for his assistance, and to the Ministry of Agriculture which has kindly allowed all the material to be tested free of charge.

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