INVESTIGATIONS ON THE INHERITANCE OF IMMUNITY TO WART DISEASE (*SYNCHYTRIUM ENDOBIOTICUM* [SCHILB.] PERC.) IN THE POTATO.

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Introduction.

The present results on the inheritance of wart immunity in the potato were obtained from indoor experiments, carried out at the Botanical Museum of the University, Oslo, in the years 1928–33.

The investigations were first planned in connection with some breeding work with potatoes, carried out at the College of Agriculture in Aas. The chief aim of the work has been to determine at an early stage the reaction to wart disease of the most promising breeding material. But since the method proved to give very reliable results and to be convenient in other respects (requiring comparatively little attention, labour and space), the investigations were extended so as to make possible also a genetic analysis of the varieties concerned, with regard to their reaction to wart.

We have thus tested the reaction to wart of all available seed plants in most of those families which have been segregating for immunity.

The heterozygous nature of most potato varieties, in respect of this character also, makes the study of its inheritance rather difficult. Almost the only possible way to solve the problem of inheritance in the potato, is to analyse the segregating families arising from heterozygous individuals by self-fertilisation or crossing. Moreover, for those varieties which do not produce viable pollen, only hybrid progenies will be available.

In many families segregation for immunity is so complex that very much material is required for a definite determination of the genetic basis of the reaction to wart disease. Besides, random variation often tends to change more or less the real proportion of immunes and susceptibles, thus making it still more difficult to reach a conclusion as to the genotype of a variety. This has been the case in some of the families

we have investigated. For these families more material will be tested later.

The investigations will be continued and the present report may be considered as preliminary. But since data on the inheritance of reaction to wart in the potato are rather scanty, we have determined to publish our results without further delay.

Results of previous investigations on the inheritance of immunity to wart disease in the potato.

The most systematic investigations on the inheritance of immunity to wart disease hitherto published are those of Salaman and Lesley (3, 4). Their immunity tests were made on wart-infected soil, chiefly at the Ormskirk trial grounds, Lancashire, England.

The results may be summarised as follows:

Immunity is dependent upon segregating factors, immunity being dominant to susceptibility. This dominance may be inhibited by other factors.

Immunes may be of at least four types: (*a*) pure (homozygous) immunes, immunes which on selfing give (*b*) 15 immunes : 1 susceptible, (*c*) 3 immunes : 1 susceptible or (*d*) 9 immunes : 7 susceptibles. Susceptibles also may be of various sorts due either to the absence of the immunity factors, or to a complementary factor, or to the presence of one (or more) inhibiting factor (or factors).

The immunity factors are designated **X** and **Y** and the complementary factor **Z**. Both **X** and **Y** may give immunity in the presence of **Z** and they may also induce immunity when both are present even in the absence of **Z**. The inhibiting factor found in some families is designated **B** and a possible second inhibitor **A**.

The late Dr John Snell made investigations at Ormskirk upon the inheritance of immunity to wart disease in some groups of seedling plants raised from selfed immune potato varieties. Some of his results were published by Cuthbertson (1). Various proportions of immunes and susceptibles were found in the different families. No attempt is made in the paper to determine the genetic base for the inheritance of immunity to wart in the varieties tested.

Köhler (2) has published some results on the reaction to wart disease in two families of seed plants. The method used for infection was that of Spieckermann and Kotthoff (Krebskompost). Richters Weisse Riesen × Hindenburg segregated in the ratio 3 immunes : 1 susceptible, and

the cross Richters Weisse Riesen × Preussen in the ratio 1 immune : 1 non-immune.

THE INFECTION METHOD USED IN OUR INVESTIGATIONS.

The infection method used has been to place the potato tubers with the rose end down in glass bowls filled with moist sphagnum moss mixed with pulverised dried potato warts. The bowls were placed in a room usually kept in complete darkness, and heated during winter with the help of a radiator to a temperature of mostly 18–21° C. The test started most years at the end of November and was concluded in the summer (June, July or August), during which time 4–5 series of tubers were tested, each series taking $1\frac{1}{2}$–2 months.

During the two first years the sphagnum was kept continuously wet, but later it was allowed to dry more or less completely between each watering, a thorough drenching then being applied each time.

Of each plant 2–3 tubers were tested, and if found free from wart as a rule one tuber at least was laid out again for further testing (this was practically always done when only two tubers per plant were used). In those cases where the result of the first testings proved uncertain (*e.g.* by rotting or poor sprouting of the tubers, appearance of very small warts, or different reaction to wart of tubers belonging to presumably one and the same plant), the plants were tested over again with the help of new tubers until a reliable result was obtained.

RESULTS OF OUR INVESTIGATIONS ON WART IMMUNITY INHERITANCE.

The results of our investigations are given in Tables I–VI. From Table I is seen that the non-immune variety Centifolia gives only non-immunes in its offspring by self-fertilisation.

Likewise from the crosses between Centifolia and the three susceptible varieties Sagerud, Marius and Louis Botha no immune plant segregated out.

In the progeny from the cross Early Puritan × Centifolia, 18 plants out of a total of 58 did not develop wart in the first year's test. Of these 18 plants, 7 were tested over again the next autumn and were all attacked by the disease; the remaining 11 plants were unfortunately discarded without further test. Later on 28 plants from the same cross were tested and were all attacked by wart. It is thus beyond doubt that the plants of this cross which did not get warted had escaped infection the first

year, and that even in this cross between two susceptible varieties no real immune plants occurred[1].

This is the only case where the results are not reliable with regard to the non-warted plants obtained.

All the progenies after self-fertilisation of immune varieties or plants that we have tested (Tables II, III and VI), are segregating in a 3 immune : 1 susceptible ratio.

This is the case with the progenies from Jubel, Hindenburg, Pepo, Parnassia, Seydlitz, Flourball, Tannenberg, and four immune plants derived from the crosses Hindenburg × Centifolia and Louis Botha × Jubel. All these varieties and plants, with the exception of Flourball and Tannenberg, are derived directly or indirectly from Jubel.

For all of them the self-fertilisation results show immunity to be dominant to susceptibility, and to be dependent on a single factor present in a heterozygous condition.

This immunity factor is designated **X** and its recessive **x**. It is regarded as identical with the **X** of Salaman and Lesley. However, we are presuming it to be independent of any other factor in producing immunity.

It might not necessarily be the same factor that is present in all the varieties segregating in the 3 : 1 ratio. It might very well be different factors present in the different varieties, though the effect is identical.

Our material, however, does not make it possible to state this with certainty, and we have therefore found it most convenient to suppose immunity to be due to the same factor **X** in all varieties segregating by self-fertilisation in the 3 : 1 ratio. The reason for this supposition is the fact that nearly all the self-fertilised varieties and plants in our material are related to Jubel.

Some of our results, however, suggest that two different **X** factors, similar or identical in effect, really are present in certain varieties.

The hybrid progenies from crosses between Centifolia and various immune varieties (cf. Table I) are probably all segregating in a 1 : 1 ratio for immunity *v.* susceptibility.

This is clearly the case in the crosses Hindenburg × Centifolia and King George V × Centifolia, and very likely also in the crosses Dukker × Centifolia, and Jubel × Centifolia. The last family, however, comprises

[1] The plants from the cross Early Puritan × Centifolia were tested late in the season the first year and the sphagnum from the previous serial was used over again without new infection material being added. Probably the sporangia of the disease organism were too scanty.

rather few individuals. In all these cases the genetic formula for immunity may be written **Xx . xx**. This result is in accordance with the above-mentioned result for Jubel and Hindenburg, selfed. Dukker and King George V are thus probably also heterozygous for a single immunity factor, probably identical with **X**. Both these varieties should also segregate by self-fertilisation in a 3 : 1 ratio for immunity, if they were self-fertile.

In some of the crosses between Jubel and non-immune varieties many more immune plants occur than would be expected on the 1 : 1 basis. This is especially the case in the cross Sagerud × Jubel. The deviation from the 1 : 1 ratio in this cross is 6·33 times the probable error and can consequently hardly be due to random variation. The result from this

TABLE I.

Results on wort immunity inheritance in progenies derived from the variety Centifolia.

	Obtained numbers		Calculated numbers		Ratio			
	Warted	Non-warted	Warted	Non-warted	Warted : Non-warted	Deviation	Prob. error	Dev./Prob. error
Centifolia*†	12	0	12	0	—	—	—	—
Sagerud† × Centifolia	14	0	14	0	—	—	—	—
Marius† × Centifolia	38	0	38	0	—	—	—	—
Louis Botha† × Centifolia	82	0	82	0	—	—	—	—
Early Puritan† × Centifolia	75	(11)	86	0	—	—	—	—
Hindenburg‡ × Centifolia	149	152	150·5	150·5	1 : 1	1·5	5·85	0·26
King George V‡ × Centifolia	136	124	130	130	1 : 1	6·0	5·44	1·11
Golden Lass‡ × Centifolia	132	100	116	116	1 : 1	16·0	5·14	3·11
			145	87	5 : 3	13·0	4·97	2·62
Dukker‡ × Centifolia	87	74	80·5	80·5	1 : 1	6·5	4·28	1·52
Jubel‡ × Centifolia	17	13	15	15	1 : 1	2·0	1·85	1·08

* Self-fertilised. † Susceptible. ‡ Immune.

cross, however, fits almost completely a 5 : 3 ratio for immunes and non-immunes, respectively, as seen in Table II. This ratio can only occur when both varieties are carrying one of a pair of complementary factors, together inducing immunity to wart independent of the immunity factor **X** of Jubel. These complementary factors might be designated **Y** and **Z**. Jubel is then presumably of the genotype **XxyyZz** and Sagerud **xxYyzz**. Also the cross Early Puritan × Jubel is probably segregating in a 5 : 3 ratio for immunes and susceptibles, Early Puritan being presumably of the same genotype as Sagerud.

The cross Louis Botha × Jubel probably represents a 5 immune : 3 non-immune ratio, but the result is here more doubtful, since it fits almost equally well a 1 : 1 or a 5 : 3 ratio.

Some of our other results can only be explained by the existence of complementary factors, together inducing immunity. Their existence has

also been fairly well proved by Salaman and Lesley (3, 4). The interrelation between these factors and **X** is not the same in our results, however, as that supposed by Salaman and Lesley for the factors identically named. We must presume that no interrelation exists between **X** on the one side and **Y** and **Z** on the other. **X** is supposed to produce immunity independently of **Y** and **Z**, and these together to produce immunity whether **X** is present or not.

Crosses between Jubel and various immune varieties have given very different results, as seen from Table II.

TABLE II.

Results on wart immunity inheritance in progenies derived from the variety Jubel.

	Obtained numbers		Calculated numbers		Ratio Warted : Non-warted	Deviation	Prob. error	Dev./Prob. error
	Warted	Non-warted	Warted	Non-warted				
Jubel*‡	37	111	37	111	1 : 3	0·0	3·55	0·0
Hindenburg*‡	24	64	22	66	1 : 3	2·0	2·74	0·73
Pepo*‡	25	89	28·5	85·5	1 : 3	3·5	3·12	1·12
Parnassia*‡	18	53	17·8	53·2	1 : 3	0·2	2·46	0·08
Louis Botha × Jubel, plant 283*‡	10	27	9·3	27·7	1 : 3	0·7	1·78	0·39
Jubel‡ × Centifolia†	17	13	15	15	1 : 1	2·0	1·85	1·08
(Early Puritan × Hindenburg), plant 27† × Jubel	5	5	5	5	1 : 1	0·0	1·07	0·0
Sagerud† × Jubel	106	178	106·5	177·5	3 : 5	0·5	5·50	0·09
Louis Botha† × Jubel	106	139	122·5	122·5	1 : 1	16·5	5·28	3·13
			91·9	153·1	3 : 5	14·1	5·11	2·76
Early Puritan† × Jubel	31	45	28·5	47·5	3 : 5	2·5	2·85	0·88
Abundance‡ × Jubel	27	100	31·5	95·3	1 : 3	4·7	3·29	1·44
Hjelvik‡ × Jubel	60	194	63·5	190·5	1 : 3	3·5	4·67	0·75
Edzell Blue‡ × Jubel	29	157	23·3	162·8	1 : 7	5·7	3·04	1·88
			34·9	151·1	3 : 13	5·9	3·59	1·64
Dukker‡ × Jubel	22	162	23	161	1 : 7	1·0	3·03	0·33
Kerr's Pink‡ × Jubel	14	249	16·4	246·6	1 : 15	2·4	2·65	0·91
Irish Cobbler‡ × Jubel	0	19	0	19	—	—	—	—

* Self-fertilised. † Susceptible. ‡ Immune.

The two crosses Abundance × Jubel and Hjelvik × Jubel have given identical results. This was also expected beforehand, since Hjelvik is undoubtedly synonymous with Abundance. Both these crosses are segregating for immunity in an approximate 3 immune : 1 non-immune ratio. The agreement between obtained and calculated numbers is rather good in both crosses. This ratio will occur if Abundance (and Hjelvik) is heterozygous for **X** (or a factor identical in effect) and lacks the complementary factor **Y**. It may or may not carry **Z**.

Its genotype might therefore be **Xxyy**(**ZZ**, **Zz** or **zz**).

The cross Edzell Blue × Jubel gives a proportion of immunes : non-immunes of 5·4 : 1. This is probably either a 7 : 1 or a 13 : 3 ratio of

immunes and non-immunes, respectively. The 7 : 1 ratio will occur if Edzell Blue is of the genotype **XxYYzz** and the 13 : 3 ratio if Edzell Blue is **XxYyzz**.

Salaman and Lesley (3, 4) have presented results on progenies derived from Edzell Blue by self-fertilisation and crossing, showing this variety to be heterozygous for a single immunity factor.

Since Jubel is heterozygous for one immunity factor, we would expect the cross Edzell Blue × Jubel to segregate in a 3 immune : 1 non-immune ratio. The deviation from the 3 : 1 ratio in this cross is nearly 4·5 times the probable error, and a deviation as large as that can hardly be due to random variation. Consequently it must be complementary factors present which are combined through the cross. The result for the first half of the progeny of this cross was in very good accordance with the 7 immune : 1 non-immune ratio. Of 84 plants tested the first year 74 were immune and 10 non-immune. In the second year 102 plants were tested of which 83 were immune and 19 non-immune, or a ratio of 4·37 immunes : 1 non-immune.

The cross Dukker × Jubel gives a result that fits almost exactly the 7 immune : 1 non-immune ratio and the genotype of Dukker is therefore supposed to be **XxYYzz**.

It is not possible from our present results to prove definitely that the immunity factor of Abundance, Edzell Blue and Dukker **X** is really identical with the **X** of Jubel. However, whether they are, or are not identical is without consequence to the results obtained, if they, as supposed, are identical in effect and are segregating independently of each other and of the factors **Y** and **Z**.

Kerr's Pink × Jubel gives another proportion of immunes and susceptibles in the offspring. The ratio found is very nearly 15 immunes : 1 non-immune. This result shows that the cross Kerr's Pink × Jubel must represent a very complicated genetic composition. The result might be explained by supposing Kerr's Pink to carry two immunity factors, **X′** and **X″**, both able to produce immunity independently of each other and of **Y** and **Z**. One of these factors, presumably **X′**, might be identical with the **X** of Jubel. Besides these two factors Kerr's Pink must also carry **Y** in a homozygous state. The genotype of Kerr's Pink might then be **X′x′X″x″YYzz** and that of Jubel **X′x′x″x″yyZz**.

Also Salaman and Lesley (3, 4) have presented results which show that Kerr's Pink is probably carrying two factors independently inducing immunity.

Irish Cobbler seems to be homozygous immune, judging from the

result of the cross Irish Cobbler × Jubel. This is not an unexpected result, for it is probably only accidental that homozygous immune varieties are not more often encountered. However, the number of plants derived from Irish Cobbler is rather small, and further material is necessary before it can be definitely regarded as homozygous. Where many factors are involved, as in the cross Kerr's Pink × Jubel, it might very well happen that no susceptible plant would come out in a progeny of only 19 plants.

The crosses between Hindenburg and non-immune varieties all seem to segregate in a 1 : 1 ratio for immunity as seen from Table III. The cross Louis Botha × Hindenburg shows a rather large deviation from this ratio, suggesting that Louis Botha may also carry an inhibiting factor for immunity. However, the deviation (2·9 times the probable error) might be due to random sampling only. The same deviation may occur once in every 20 trials, by random variation. In any case a possible inhibiting factor in Louis Botha could be only partially dominant.

The cross, Early Puritan × Hindenburg, is of special interest, since the result shows that Hindenburg probably is not carrying the **Z** factor of Jubel.

The investigations of Köhler have shown that Richters Weisse Riesen × Hindenburg (susceptible × immune) segregated in a ratio of 3 immunes : 1 non-immune. This result does not seem to agree with our results on immunity inheritance in Hindenburg. However, possibly Hindenburg and Weisse Riesen are carrying complementary factors which together produce immunity independent of the **X** factor of Hindenburg.

The cross between Dukker and the susceptible variety Geheimrat Haas (Table IV) segregated in an approximate 1 : 1 ratio as did also the cross Dukker × Centifolia. It may therefore be supposed that the genotype of Geheimrat Haas is **xx**(**YY**, **Yy** or **yy**)**zz**. It may or may not carry the **Y** factor.

The results from the variety Golden Lass (Table V) are rather doubtful. The number of warted and non-warted plants from the cross Golden Lass × Centifolia fit somewhat better a ratio of 3 immunes : 5 non-immunes than the 1 : 1 ratio. In the first part of the test of this progeny it seemed rather obvious that the segregation was in the 3 : 5 ratio. But the last plants tested changed considerably the proportion of immunes and non-immunes, making the final result rather problematic. If it is really a 3 : 5 ratio for immunes and non-immunes, then the immune variety, Golden Lass, must be supposed to segregate for two complementary factors for immunity and Centifolia to carry one of these, or a factor similar in effect, in a heterozygous condition.

TABLE III.

Results on wart immunity inheritance in progenies derived from the variety Hindenburg.

	Obtained numbers		Calculated numbers		Ratio			
	Warted	Non-warted	Warted	Non-warted	Warted : Non-warted	Deviation	Prob. error	Dev./Prob. error
Hindenburg*‡	24	64	22	66	1 : 3	2·0	2·74	0·73
Seydlitz*‡	13	42	13·7	41·3	1 : 3	0·7	2·17	0·32
Hindenburg × Centifolia†	149	152	150·5	150·5	1 : 1	1·5	5·85	0·26
Marius† × Hindenburg	88	73	80·5	80·5	1 : 1	7·5	4·28	1·75
Early Puritan† × Hindenburg	45	40	42·5	42·5	1 : 1	2·5	3·11	0·80
Louis Botha† × Hindenburg	116	88	102	102	1 : 1	14·0	4·82	2·90
Hindenburg × Centifolia, plant 53*‡	19	54	18·3	54·7	1 : 3	0·7	2·50	0·28
Hindenburg × Centifolia, plant 315*‡	15	38	13·3	39·7	1 : 3	1·7	2·13	0·80
Hindenburg × Centifolia, plant 323*‡	5	13	4·5	13·5	1 : 3	0·5	1·24	0·40

* Self-fertilised. † Susceptible. ‡ Immune.

TABLE IV.

Results on wart immunity inheritance in progenies derived from the variety Dukker.

	Obtained numbers		Calculated numbers		Ratio			
	Warted	Non-warted	Warted	Non-warted	Warted : Non-warted	Deviation	Prob. error	Dev./Prob. error
Dukker† × Centifolia*	87	74	80·5	80·5	1 : 1	6·5	4·28	1·52
Dukker × Geheimrath Haas*	16	14	15	15	1 : 1	1·0	1·85	0·54
Dukker × Jubel†	22	162	23	161	1 : 7	1·0	3·03	0·33

* Susceptible. † Immune.

TABLE V.

Results on wart immunity inheritance in progenies derived from the variety Golden Lass.

	Obtained numbers		Calculated numbers		Ratio			
	Warted	Non-warted	Warted	Non-warted	Warted : Non-warted	Deviation	Prob. error	Dev./Prob. error
Golden Lass† × Centifolia*	132	100	116	116	1 : 1	16	5·14	3·11
			145	87	5 : 3	13	4·97	2·62
Golden Lass × Flourball†	37	73	41·2	68·8	3 : 5	7·2	3·43	1·22
Louis Botha* × Golden Lass × Centifolia, plant 103†	62	48	55	55	1 : 1	7	3·54	1·97
Marius* × Golden Lass × Centifolia, plant 103	39	33	36	36	1 : 1	3	2·86	1·05

* Susceptible. † Immune.

TABLE VI.

Results on wart immunity inheritance in progenies derived from the variety Flourball.

	Obtained numbers		Calculated numbers		Ratio			
	Warted	Non-warted	Warted	Non-warted	Warted : Non-warted	Deviation	Prob. error	Dev./Prob. error
Flourball*†	13	30	10·8	32·2	1 : 3	2·2	1·92	1·15
Golden Lass† × Flourball†	37	73	41·2	68·8	3 : 5	4·2	3·43	1·22
			27·5	82·5	1 : 3	9·5	3·06	3·11

* Self-fertilised. † Immune.

However, when the results from the crosses Jubel × Centifolia, Sagerud × Centifolia and Sagerud × Jubel, and the supposed factorial compositions for these crosses are compared, it is seen that Centifolia cannot carry either the **Y** or the **Z** factor. If Centifolia really carried the **Y** factor it should give an excess of immune plants in the cross with Jubel, but this is not the case. It might therefore be supposed that the cross Golden Lass × Centifolia really segregates in the 1 : 1 ratio for immunity.

Also the cross Golden Lass × Flourball is rather problematic. Flourball, selfed, segregates in a 3 : 1 ratio for immunity, as seen from Table VI.

If Golden Lass also is segregating for a single immunity factor we should expect the cross Golden Lass × Centifolia to segregate in a 3 : 1 ratio for immunity *v.* susceptibility. The deviation from the 3 : 1 ratio is more than 3 times the probable error. The result fits much better a ratio of 5 immunes : 3 non-immunes. This result suggests that Golden Lass is really segregating for more than one immunity factor. However, before more material has been tested is it not safe to draw a definite conclusion as to the genetic composition of Golden Lass, with regard to its immunity factors.

Summary.

The results of our investigations on wart immunity inheritance in the potato may be summarised thus:

1. The susceptible varieties from which seedling families have been derived by self-fertilisation or by crossing with another susceptible variety, have given only susceptibles in their offspring.

2. All immune varieties or plants investigated segregate by self-fertilisation in an approximate 3 : 1 ratio for immunity *v.* susceptibility.

3. Crossing of immune and susceptible varieties has given various results:

In some crosses segregation occurs in an approximate 1 immune : 1 non-immune ratio;

Some crosses in which Jubel enters as the immune parent, segregate in an approximate 5 immune : 3 non-immune ratio.

4. Crossing of immune varieties has also given different results:

Some crosses segregate in an approximate 3 immune : 1 non-immune ratio, viz. Abundance × Jubel and Hjelvik × Jubel;

One cross, Golden Lass × Flourball, segregates in an approximate 3 immune : 5 non-immune ratio. However, this might only be a deviation from the 3 : 1 ratio;

One or two crosses, viz. Dukker × Jubel and Edzell Blue × Jubel, segregate in an approximate 7 immune : 1 non-immune ratio and one cross, Kerr's Pink × Jubel, is segregating in an approximate 15 immune: 1 non-immune ratio;

One cross of immune × immune, Irish Cobbler × Jubel, has given only immunes in its offspring.

5. The following factors and interrelations between these factors are used to explain our results on the inheritance of immunity to wart in the potato:

X′, a dominant factor inducing immunity independent of any other immunity factor;

X″, another dominant immunity factor, similar to or identical in its effect with **X′**;

Y and **Z**, two complementary factors, which are able to produce immunity when both are present, even in a heterozygous condition. These factors are supposed to be independent of **X′** and **X″** in their effect. All these factors are also supposed to be inherited independently of each other.

6. The effect of the immunity factors and their interrelations as assumed by us, is not in full accordance with the presumptions of Salaman and Lesley (3, 4), for the factors identically named (**X**, **Y** and **Z**).

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