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STUDIES IN THE INHERITANCE OF DISEASE-RESISTANCE.

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IN a previous paper dealing with the inheritance of certain characteristics of wheat, evidence was brought forward to show that it was probable that liability and immunity to the attacks of yellow rust (*Puccinia glumarum*), were a pair of characters in the Mendelian sense of the word[1]. The evidence was as follows: Rivet wheat, a variety which is only slightly attacked by this parasite, was crossed with an extremely susceptible variety Red King. The latter is a hybrid descended from Michigan Bronze, which in turn is extremely susceptible to yellow rust. The resulting hybrids were as susceptible to the attacks of yellow rust as the parent Red King, whilst the generation raised from them consisted of individuals which were either slightly or excessively susceptible to the disease. There was a general agreement between the extent of the disease in these two classes and in the two parents, and further the proportions of badly to slightly attacked were in the ratio of 3 : 1. In the following generation the relatively immune individuals bred true to this character, though not necessarily to other characters as well, but the susceptible types taken as a class produced either all susceptible offspring or a mixture of susceptible and relatively immune—the result expected if these characters are Mendelian. Unfortunately the statistics for this last generation were not altogether satisfactory, partly owing to unfavourable conditions at the sowing time and partly owing to the excessive mortality of the diseased individuals in the preceding generation which limited the amount of grain harvested for this trial.

While the experiments were in progress a further series was commenced in order to obtain data on a more extensive scale and

[1] Biffen, *Journ. Agric. Sci.* Vol. I. p. 40.

also to determine whether immunity to the attacks of other fungi could be traced in a similar fashion.

A survey of the commoner plant diseases seemed to indicate that the Uredineae were the most suitable for this purpose and that the yellow rust offered unusual advantages, owing to the fact that one could count with no small degree of certainty on there being sufficient rust each season to thoroughly expose all plants to the chance of infection without having recourse to artificial inoculation. In this district a year never passes without there being a more or less severe epidemic of yellow rust, so that under ordinary circumstances there appeared to be no likelihood of failure through lack of suitable external conditions.

The black rust (*Puccinia graminis*) was also included in these experiments, though it was not expected to be so satisfactory for an investigation of this kind, owing to the fact that its appearance on the plots at the University Farm is generally late in the season. It rarely occurs before the middle of June and by that time the foliage of the wheat is often partly killed by the attacks of yellow rust. In some seasons no signs of it are to be met with. On the other hand the importance of the disease from an economic point of view had to be considered, and as a plentiful supply of infecting material could generally be obtained from its alternate host plant, the barberry, growing in a neighbouring hedgerow it was resolved to make the attempt and resort to artificial infection should the natural fail.

The investigation of the inheritance of liability to the attacks of a totally different group of fungi seemed essential, and as it was desired to work as far as possible with cereals the mildew *Erysiphe graminis* was chosen. Experiments with the biologic forms on both wheat and barley were planned but in the end only that on barley was carried to its conclusion.

The chief points of the life history of these parasites as far as they are concerned in this investigation may be briefly stated here[1].

The presence of *Puccinia glumarum* is indicated by the formation of numerous shortly elliptical pustules which break through the epidermis of the host plant—in this case wheat—and shed masses of spores known as uredospores. In the mass these have a characteristic deep cadmium yellow colour. These spores if applied to the surface of a variety of wheat susceptible of infection germinate and push hyphae

[1] For a complete account and figures, reference may be made to Eriksson, *Die Getreideroste*, p. 141.

through the stomata, the mycelium then penetrates the intercellular spaces and drives haustoria through the walls of adjacent cells in order to obtain nutriment. If the conditions are favourable for development the mycelium will produce a fresh crop of uredospores in about ten days. Under these circumstances the spread of the disease is often exceedingly rapid and it is no unusual occurrence to see a field which is apparently rust free coloured yellow with the rust a week later. The period at which the uredospores are first noticed here is very variable, ranging from the beginning of March until the middle of May. Their formation continues until the foliage begins to die, generally about the middle or end of July, and then the mycelium produces a second spore form, the teleutospore, in small, flat sori. Whether a third spore form, the aecidiospore, is produced, as is the case with so many other Uredineae, is open to question, and the view is gaining ground that the fungus is homoecious.

The black rust (*Puccinia graminis*) forms darker masses of uredospores in longer sori and the teleutospores are produced in characteristic linear pustules surrounded by the torn edges of the epidermis of the host. As is well known an aecidial stage occurs on the barberry. The infection of wheat is readily brought about by uredospores or by aecidiospores, either of which produce crops of uredospores. The details of infection are very similar to those of the yellow rust.

The biologic form of *Erysiphe graminis* on barley forms a web or felt-like coating on the stems and foliage which at the period of spore formation becomes pulverulent. The fungus is distributed throughout the summer by conidia which on germination give rise to an epiphytic mycelium attached to the plant by haustoria driven into the epidermal cells. No deep-seated mycelium similar to that of the rusts is produced.

A considerable collection of both wheats and barleys was obtained and in order to select the most suitable varieties for this investigation the incidence of these three parasites was observed in detail during the year 1902. A similar series of observations had previously been made in Sweden by Eriksson[1], but in view of the fact that it is often stated that susceptibility to disease varies with climatic conditions it was thought necessary to cultivate and test the varieties under the conditions which would obtain during the experiments. In Eriksson's trials the varieties are grouped into five classes ranging from 0 with no disease to 4, very badly diseased. The attempt was made to classify

[1] Eriksson, *ibid.* pp. 333 and 342.

the series in a similar way. In all cases where Eriksson placed a variety in either of the extreme classes the results were the same on my plots, but there was often a difficulty to decide between classes 2 and 3 and 3 and 4. Where no actual standards for comparison were available this was only to be expected and the general impression which remained was that Eriksson's classification agreed well with the one made under the conditions obtaining on the Cambridge plots.

From amongst the series representatives of each class were selected and these have been kept under cultivation since, the remainder, except a few required for other experiments, being discarded. Since 1902 the rust epidemic has varied considerably in its intensity, but the varieties have still retained their relative positions on the arbitrary rust scale with one possible exception. This was a variety known as New Era which originally was placed in class 1, *i.e.* slightly susceptible. In 1906, a year in which there was comparatively little rust, it remained practically rust free until the foliage was beginning to die, when pustules appeared.

The immune varieties chosen were Einkorn, Hungarian Red and "American Club." Each of these has been kept under continuous observation, and in order that there should be no question of their not being exposed to infection they have been grown in company with the susceptible forms whose rust-coated leaves have continually overlapped them. In addition, once or twice each season they have been watered overhead with a fine spray containing quantities of uredospores in suspension.

Einkorn (*Triticum monococcum vulgare*, Kcke). This variety tillers to an enormous extent, forming a thick turf of foliage. It is notoriously rust-resistant though this dense mass of foliage would seem to provide excellent opportunities for infection. In Eriksson's trials it was the only variety immune to the three common wheat rusts. Reports from various parts of the world show that this characteristic is retained under various climatic conditions. On the Cambridge University Farm the variety has been entirely rust free each season with the exception of 1906 when on some fifty plants two leaves were found late in the season on which a few scattered pustules occurred. The majority of these were unbroken and shed no spores before the death of the leaves.

Hungarian Red. The grain of this variety was obtained under the name of "Ungarischer roter" from Haage and Schmidt of Erfurt. It is probably identical with the variety examined by Eriksson. In his

trials it proved immune to *P. glumarum*, but not to *P. dispersa*, except in the rust year 1892 when it was slightly attacked. In the trials at Cambridge it has been perfectly free from the yellow rust but no statements can be made as to its susceptibility to the attacks of other species, for their appearance during the last four seasons has been too spasmodic to ensure fair tests. It has proved a feebly growing variety and its development is often crippled by attacks of *Erysiphe graminis*.

"American Club." This is a variety of *Triticum compactum* which so far I have been unable to identify with certainty. Its morphological characters agree with those of Bearded Herisson or Hedgehog wheat, but whereas this is susceptible to yellow rust the American Club is immune. It was obtained from Mr A. E. Humphries, who found it growing in a plot raised from a commercial sample of Northern Duluth wheat. This, as usual, was graded wheat and among numerous other varieties contained a small proportion of the variety in question. By chance my culture was sown between plots of Michigan Bronze and Hungarian White, another highly susceptible wheat. Throughout the late spring and summer of 1904 its plot was a vivid green colour contrasting markedly with the bright orange yellow of its neighbours which were so badly infected that the soil below them was tinged with the masses of uredospores produced. Late in the season the plants were covered with aphis and the coating of honeydew provided a substratum for the growth of *Cladosporium herbarum*. Yet though the plants were continually exposed to infection and in the latter part of their development under peculiarly unfavourable conditions for healthy growth they remained entirely free from yellow rust.

Since then some three hundred plants have been grown and kept under close observation and only two immature pustules have been found. These occurred in August 1906 on leaves again covered by aphis. The pustules did not break through the epidermis and it is impossible to be certain, though on the whole it is probable, that they were yellow rust. In colour they were slightly darker than normal yellow rust, but their almost circular shape would distinguish them from the more linear pustules of black rust.

It is probable that this variety is susceptible to both black and brown rusts but so far the evidence to hand is not complete[1].

[1] Since writing the above, reports from the Transvaal and from Canada, where small sowings of this variety have been made, show that it is very susceptible to the black rust. It is possible that this is the wheat known as Kidd in Canada, which is similar morphologically and known to be susceptible to this rust.

In describing these varieties as immune it is essential that attention should be called to the fact that they are immune under the ordinary conditions of cultivation of wheat. Absolute immunity under all conditions is not to be expected in any wheat where the rusts are in question. In fact it is practically impossible to say that any plant is immune to the attacks of wheat-rusts if the preliminary stages of infection are to be taken as evidence of susceptibility, for the uredospores germinate on the majority of phanerogamous plants and push hyphae through the stomata into the intercellular spaces[1]. Under such circumstances no further development occurs and the mycelium perishes.

Further emphasis has to be laid on the importance of natural conditions for the development of the host plant, since Salmon[2] has shown that barley foliage may be infected with the biologic form of *Erysiphe graminis* found on wheat if only it is exposed to sufficiently drastic conditions. To secure infection the leaves have to be chloroformed, scorched, bruised, etc. and when their vitality is sufficiently lowered the mildew from the wheat succeeds in getting a hold and developing sufficiently to produce a feeble crop of conidia. Yet under normal conditions infection is impossible. As a matter of fact in the three varieties selected for these experiments the early stages of infection are readily observable in preparations made from foliage growing in the open, but the growth of the mycelium is quickly inhibited and it dies without causing any noteworthy injury to the host. As will be shown later there is also the possibility that infection may occur on foliage which is passing over to a moribund condition. Details of the histology of infection are published by Miss Marryat in this number of the Journal.

Of the slightly susceptible varieties which have been crossed with immune types the more important are Street's Imperial (Class 2) and New Era (Class 1). These grown under the same conditions as the immune varieties have each season produced numbers of sparsely scattered pustules on all of their leaves. In 1906, a poor rust year, the infection was less marked than usual and only occurred late in the season. Of the two, Street's Imperial is the more susceptible and it may be taken to represent roughly the extent to which the majority of our English varieties are susceptible. The varieties characterised by

[1] De Bary, *Comp. Morph. and Biology of the Fungi*, p. 361. Gibson, *New Phytologist*, Vol. III. p. 184.

[2] Salmon, *Anns. Bot.* Vol. XIX. p. 125.

excessive liability to infection which have been used as parents are "American 1," "American 2," Preston, Hungarian White, "Tasmanian" and Michigan Bronze. These are placed as far as possible in the order of their susceptibility.

"American 1 and 2" are varieties grown from graded Northern Duluth and Manitoba wheat. Both are varieties of *Triticum vulgare* but their local names are unknown to me. The following short description may aid in their recognition in Canada and the United States where they are probably commonly cultivated. Number 1 has lax, beardless ears with a yellow chaff: number 2 a similarly shaped ear with white chaff.

Preston is a Canadian wheat of hybrid origin.

Hungarian White, a variety from Haage and Schmidt. This Eriksson puts into classes 4 and 3, stating that it is very susceptible to yellow rust in Sweden. Each of these four varieties throughout the seasons 1903—6 inclusive has been badly attacked and it would have been difficult to count the pustules on any of the diseased leaves. In each case though the plants set a fair quantity of grain.

"Tasmanian" (a variety sent from Tasmania: proper name unknown to me) is very similar to Rough Chaff as far as external appearances go but distinguished from it by extreme liability to the attacks of yellow rust. There is little to choose between this and the succeeding variety in this respect.

Michigan Bronze has earned the reputation of being one of the most susceptible varieties in existence, and on this account it has been largely used by Eriksson in his researches[1]. The pustules generally appear on this wheat earlier than on other varieties and they quickly become so numerous that the whole of the foliage appears to be coated with rust. Every part of the plant is attacked and whereas the upper leaves, chaff and awns of moderately susceptible varieties rarely carry many pustules, in the case of Michigan Bronze these structures are as badly infected as the lower leaves. So severe is the attack that the plants set little or no grain on my plots. In 1906 for instance a plot of forty plants did not produce a single grain. Owing to this difficulty of obtaining seed the stock has to be renewed from year to year and in consequence the plants used for comparison with the hybrids are not, as one would prefer, the direct descendants of the one used as pollen plant. The stock of "Tasmanian" has died out altogether.

[1] Eriksson, *Ann. d. Sc. Nat.* T. XIV. p. 107, 1901.

Some eight hundred plants of these two varieties have been grown since 1902 and not one has escaped infection. So certain is the incidence of the disease that a practice has been made of planting rows of Michigan Bronze among the hybrids in order to ensure the presence of numerous centres of infection. During this last season this precaution was abandoned as unnecessary.

In making the crosses between immune and excessively susceptible varieties the immune parent was in each case the mother plant. Reciprocal crosses were not attempted, since previous experience had shown that there was little likelihood of their succeeding. Where moderately susceptible varieties were under experiment such crosses were successfully attempted.

The following crosses were made between excessively susceptible and immune types:

1. American Club × American 1.
2. „ „ × American 2.
3. „ „ × Preston.
4. „ „ × Tasmanian.
5. „ „ × Michigan Bronze.
6. Hungarian Red × Hungarian White.

The hybridising was carried out in 1904 and the resulting plants were kept under observation throughout the period of their growth in 1904—5. Yellow rust was first observed in the neighbourhood on March 3rd. By May 11th the attack seemed fairly general and wheat in the same field as the hybrids was showing signs of a bad rust season approaching. At this date the hybrids were standing about six inches high. The condition of the plants then was:

1. One plant only: the three lowest leaves badly attacked, the upper leaf still free from rust. This plant was killed shortly after by wireworm.

2. Three plants: a few broken pustules on the lowest leaves, foliage becoming brown and showing numerous dead areas (probably not due to rust).

3. Rust pustules numerous on all the leaves, plant very vigorous.

4. Three plants: all very badly infected with fewer pustules on the highest leaves.

5. Nine plants: the extent of infection differed on individual plants:

(*a*) leaves as far as the fourth one badly infected.
(*b*) leaves as far as the second one badly infected.
(*c*) leaves as far as the fourth one badly infected.
(*d*) leaves as far as the fourth one badly infected.
(*e*) rust on first and second leaves only.
(*f*) on the three lower leaves, upper quite free.
(*g*) infected badly as far as the fourth leaf.
(*h*) almost rust free: only a few scattered pustules on the lower leaves.
(*j*) three lower leaves infected, upper free.

All of these plants were particularly vigorous. Those most badly infected appeared to be diseased to the same extent as Michigan Bronze.

6. Six plants: five of these were uniformly infected up to the fourth leaf, one was entirely rust free. This last plant proved to be a pure Hungarian Red in the next generation, the result of accidental self-fertilization. During June the rust spread rapidly, causing an epidemic of over-average severity. By June 22nd the condition of the plants was as follows:

2. Every leaf dead and covered with the remains of pustules. Death was probably due to other causes besides the rust.
3. Foliage still living and densely coated with pustules.
4. Lower leaves dead, the upper with innumerable pustules.
5. All parts of the plants thickly coated with rust.
6. Very badly infected.

The ears were pushed through the sheaths a week later and the flowering stage was passed. In each of the five series including number 2 the glumes and paleae were becoming infected and pustules had already broken on the awns of the hybrid American Club and Michigan Bronze. At this stage the general appearance of the plants with regard to the amount of rust upon them was very similar to that of the susceptible parents and it was problematical whether enough grain would be secured to carry the experiment on to the next generation. At harvest, however, 4, 5 and 6 yielded a fair crop, far more in fact than the susceptible parents. This may point to the fact that the hybrids were not as badly attacked as the latter and that they were intermediate in this respect, or a possible explanation is that the vigorous growth so characteristic of the F. 1 had enabled the plants to withstand the attack better than the susceptible parents.

Most of the grain harvested was, as was only to be expected, badly

shrivelled but its germinating capacity was fairly satisfactory. It was sown early in the autumn of 1905 under normal conditions of cultivation, part on land which had previously carried a wheat crop, part on soil which was in better condition as it had just previously carried a clover crop. The varying soil conditions made no difference in the final results. The grain from each ear of each plant was sown separately in the case of numbers 5 and 6.

No yellow rust was found on the plots until May 16th, an unusually late date for this district. It occurred on some plots not included in this experiment, but the following day unmistakable signs of rust were found on the series with Michigan Bronze as the parent. By the 29th of this month infection appeared to be fairly general on all the plots. At this date the plants were standing about two feet high and they were in a thoroughly vigorous condition. By June 11th it was judged that any plants susceptible to the disease would have had sufficient opportunity for infection as the plots were fast assuming a bright orange colour and an examination of each individual was commenced.

American Club × Michigan Bronze. Every leaf on the plants, the dead and dying basal leaves included, was carefully inspected and wherever the slightest signs of infection could be detected the plant was entered up in the note-book as susceptible. All diseased plants were cut back to within one foot of the ground whilst the immune plants were left standing to give them further opportunities for infection. The detailed figures for the descendants of plant 5 *a* may be quoted to show the incidence of the disease at this date:

Ear	Rust free	Susceptible
1	9	21
2	9	24
3	9	26
4	8	13
5	17	41
6	7	19
	59	144

Plants 5 *b*, *c*, *d*, and *e* were examined in the same way between the 11th and the 18th of June, the susceptible plants being again cut back. The statistics were as follows:

b	57	141
c	61	128
d	43	147
e	51	157
Total, including 5 *a*	271	717

The plants left standing on these plots were examined at intervals between July 6th and the 16th and a small number of rust susceptible plants were found:

		Revised totals	
	Rusted	Free	Rusted
in 5 *a*	3	56	147
5 *b*	12	45	153
5 *c*	14	47	142
5 *d*	7	36	154
5 *e*	7	44	164
Total		228	760

In the meanwhile the foliage of the remaining plots of this series was turning yellow and dying off and teleutospores were being formed. As there appeared to be no possibility of susceptible plants having escaped infection at this date the plants were pulled up by the roots in order to make the examination more rapidly, some fifty infected ones being left for seed. Plants 5 *f*, *g*, *h* and *j* gave a total offspring of 1244, 295 of which were free from yellow rust and 949 badly infected. The whole series thus yielded 523 immune and 1609 susceptible individuals.

The immune plants which had been left standing remained green longer than the diseased ones, and their foliage did not commence to turn colour until July 24th. The leaves remained flat and polished and the straw was either a vivid red or yellow colour very unlike that of the neighbouring plots, which, as is the case with most wheats, turned a dull brown owing to the attacks of *Cladosporium herbarum* following the rust. The immune plants could readily have been sorted by the brilliancy of their colour alone.

Whilst the foliage was dying during the last week of July the immune plants were again examined in detail. They were now surrounded by strongly growing branches thrown up by the plants previously cut back and these were carrying an unusually heavy crop of uredospores. The plants were thus exposed to infection at a time when as a rule no uredospores are being formed on wheat. In addition to yellow rust these new branches were infected with both black and brown rust. Symptoms of infection were found on at least twenty of the immune plants; the symptoms being either discoloured areas on the bright yellow ground or in some cases distinct pustules. In all cases these pustules were small and unbroken and they had shed no uredospores when the leaf shrivelled. It is impossible to say whether

these immature pustules were those of *P. glumarum* or one of the other cereal rusts. On the whole I am inclined to think that they belong to the former species, and that when the chlorophyll contents were broken down, foodstuffs translocated for the finishing grain and the vitality of the leaf exhausted it became a prey to the fungus[1]. Assuming these immature pustules were those of the yellow rust this is not an unreasonable explanation though it is a little strange that no pustules could be found on the dying basal leaves earlier in the season. These twenty plants have not been included in the total of rust-susceptible plants.

In addition to the series described, about a hundred plants of the same parentage have been used for infection experiments and for pot cultures for demonstration at the Derby Show of the Royal Agricultural Society and at the Conference of Plant Breeders at the Royal Horticultural Society. No statistics of the number of immune and susceptible plants have been kept in these cases.

Concurrently with this segregation into immune and susceptible forms there was of course the usual segregation of other Mendelian characters. The two parents do not show many pairs of differentiating characteristics, the most important pair being lax and dense ears. There are slight foliage differences but these are not marked enough to discriminate with any certainty. The hybrid plant had dense ears which at first sight were very similar to those of the American Club, but which on measurement were found to be intermediate between lax and dense. The whole habit of the plant, excluding its susceptibility to yellow rust, was very similar to that of the mother parent. In the following generation lax, intermediate and dense eared individuals, occurred in, as a small trial count showed, the usual ratio of $1 : 2 : 1$[2]. The immunity and susceptibility were distributed impartially over each of these groups. The plants with lax ears were similar to Michigan Bronze, and those with dense ears to American Club, so that immune types of Michigan Bronze and susceptible types of American Club have been bred. In other words the factors which determine immunity or the reverse are transmitted as Mendelian characters.

Whether this is due to the presence of toxins and antitoxins, as seems probable, further research will have to decide.

[1] It is a well known fact that fungi can readily attack withering or even resting plant tissues which in a normal or an active state are immune. Hartig for example has shown that the mycelium of *Peziza Wilkomii* can only work its way through the tissues of the larch when in a resting condition.

[2] Spillman, see *Journ. Hort. Soc.* Vol. xxvii. p. 876.

From the statistics already quoted it is clear that if all plants which have become infected are grouped as susceptible, and those which have not as immune, then immunity is recessive to susceptibility, for they occur in the ratio of 1 : 3·07, a sufficiently near approximation to the ratio of 1 : 3. If this is the case, then, in the succeeding generation all the immune types will breed true to this character, while the susceptible types will breed true in the proportion of one in three. This part of the subject has still to be tested in this particular series, but in this connexion it may be noted that in a previous experiment the extracted (practically) immunes bred true to this character whilst the dominants split in some cases and bred true in others[1].

During the sorting of the plants into the two groups, however, another possibility presented itself. The extent of infection was obviously very different on different individuals. Whilst some were as badly diseased as Michigan Bronze others were, though by no means free from disease, relatively slightly infected. These latter plants produced considerably more grain than the very susceptible forms.

Thus fifty ears of the lax type taken at random produced 0·8 grms. where the plants were excessively susceptible, 64 grms. when moderately susceptible, and 145 grms. when immune.

These facts seem to point to the existence of intermediate liability in the heterozygote, for without question the less susceptible types were in the majority. The method adopted of cutting out each plant showing infection was not satisfactory for obtaining statistics of this sort, since intermediates would be grouped with extremely susceptible plants. If these indications are correct, and next season's tests will settle the matter, then instead of dealing with ordinary dominance the existence of intermediates will have to be recognised in the probable proportion of one immune and two intermediates to each extremely susceptible type.

Hungarian Red × Hungarian White (6)[2]. The F. 2 again consisted of extremely susceptible and immune individuals. A detailed examination of the series was not made until the third week in July, when the foliage was beginning to show symptoms of dying off. Twenty-four plants were entirely free from yellow rust and the remaining 109 were attacked to about the same extent as the susceptible parent.

American Club × American 1 (1). The grain from the F. 1 plants

[1] Biffen, *Journ. Agric. Sci.* Vol. I. p. 43.

[2] The statistics for this series were obtained by Mr S. V. Shevade of the Pusa Research Station, India.

did not in this case germinate satisfactorily, a sowing of about 250 only giving 83 plants. The majority of these were excessively rusted and many succumbed to the attacks of the parasite. Counted in the third week of July, 15 were completely rust free, 4 bore incipient rust flecks, and 64 were as badly attacked as the parent American 1.

American Club × Tasmanian (4)[1]. In the F. 2 series there was from the first a considerable difference between the extent of infection on the different susceptible plants and the attempt was made to grade them into immune, moderately susceptible and excessively susceptible forms. The first examination was made on June 19th. The number of diseased and disease free plants was then approximately equal, there being 39 of the former, and 37 of the latter. Of the 39 rusty individuals, 21 were moderately and 18 extremely susceptible. In the former group the pustules only occurred on the lower leaves whilst in the latter all the leaves were attacked. A second examination made on July 10th, showed no readily recognisable difference between the moderately and extremely susceptible individuals, though it is possible that if the count had been made before the heavy rains of the preceding week, which had washed the pustules clean, the two classes could have been distinguished. The final count gave a total of 56 rusty and 18 completely immune plants (two plants missed).

In the above cases one of the parents has been chosen for its excessive susceptibility to the attacks of yellow rust, whilst in those to follow slightly and moderately susceptible parents have been used in conjunction with an immune one. These less susceptible varieties were New Era and Street's Imperial. The former would, I think, be placed in Eriksson's class 1, the latter in class 2. In 1906, New Era was almost entirely free from rust until the end of the season, whilst Street's Imperial was only slightly attacked. Both varieties were crossed with American Club, and the F. 1's raised in 1905 matched the susceptible parent in the extent to which they became attacked.

The first generation from the hybrids of American Club and New Era remained almost rust free, and no attempts were made to obtain any statistics as to the incidence of the disease on the plots until the middle of July. A trial count then showed that the infected plants were roughly equal in number to the immune ones, and the further examination was delayed until the end of the month when the foliage

[1] S. V. S.

was showing symptoms of dying. The infected plants at this date showed few pustules on their foliage and none on the glumes and awns. Many had unbroken pustules and pale yellow flecks which possibly indicated abortive attempts at infection. All plants showing pustules were counted as diseased, with the result that 135 were placed in this class and 100 in the completely immune class. The plot contained about six hundred plants, but it was not thought worth while to examine the whole series. A comparison with the New Era at this period showed that the infection was unusually slight, and several of the plants only showed yellow flecks and no pustules. For some reason, probably connected with climatic conditions, the intensity of the attack was far less than it had been in previous years. This tendency to remain free from infection appears to have been retained in the F. 2 generation.

In the case of the hybrids with Street's Imperial and American Club, infection occurred early in the season, and there was from the first an obvious difference between the immune and susceptible individuals. When examined in detail on July 18th, 62 diseased plants and 22 immune plants were found on the plot.

One cross between two varieties, both susceptible to infection but differing in the intensity of the attack, has been kept under observation. The parents in this case were Rivet wheat and Emmer or *Triticum dicoccum*. The Rivet parent has for the last five years been slightly susceptible, and the rust has always been late in appearing on it. The Emmer is classed by Eriksson in group 2 in two seasons and group 3 in a third. No details with regard to its rustiness have been kept as the cross was originally intended for a study of the grain characters only. From the general agreement between my observations and Eriksson's with regard to the extent of the disease, it may be assumed that the rustiness of this variety would be the same in Cambridge as in Sweden. The F. 1 grown in 1905 was moderately susceptible to disease, and part of the F. 2 generation on June 20th consisted of 58 immune plants and 68 susceptible. On July 7th the whole plot was examined with the result that 204 plants were classed as rusty, 48 with traces of rust, and 23 immune. Tags were affixed to the immune plants in order to harvest them separately, as it was considered at this date that as they had resisted infection so long, they were probably really immune. The plants retained the green of their foliage longer than most of the hybrids (a characteristic of both parents) and during the first week in August it was found that those previously

marked as immune had become infected and bore pustules which had broken the epidermis. The totals thus became 204 moderately, and 71 slightly infected. The Rivet wheat was then examined and pustules were found on each of the 20 plants grown as a control, though the plants were free at the time at which the second examination of the hybrid plot had been made. Here as in the case of New Era and American Club the period at which infection occurs appears to be inherited as well as the susceptibility itself.

In addition to the series of F. 2 experiments already described, further generations of other crosses showing differences in the susceptibility of their parents have been kept under observation. In one case only was the cross made for this particular purpose, namely that between Red King and Rivet wheat already referred to. The extracted recessives only have been grown, and in the F. 4 they have retained their characteristic rust-resisting capacity unimpaired. The plots could be matched against the parent Rivet satisfactorily in this respect.

In a second case an extensive trial of a number of fixed types resulting from crosses between a susceptible Manitoban wheat and the far less susceptible varieties Rough Chaff and Lammas was being made for other purposes. Each of the plots of some forty of these fixed types contained some thousands of individual plants. Early in June symptoms of the coming rust epidemic were observable, and by the end of the month many of the plots were badly attacked, whilst their neighbours of the same descent, growing under identical conditions, were relatively free from disease. Two typical plots were examined in detail: in the first case every plant was found to be badly attacked, and the extent of the disease corresponded accurately with that of the Manitoban parent growing in a plot near, whilst in the other all the plants were slightly infected only. The extent of the disease probably corresponded with that of the relatively immune parent, though this could not be satisfactorily observed as no plot of this was grown under the same conditions. These plots represented all the possible combinations of the morphological characteristics of the parent varieties, and they afforded a striking field demonstration of the fact that there is no correlation between such characters and liability to the attacks of the yellow rust.

This was further illustrated in the case of a cross between Polish and Rivet wheat. The former has proved slightly more susceptible to the attacks of yellow rust than the latter, though the difference is by

no means as pronounced as in the case last described. A number of fixed types in the F. 3 generation were being tested for other purposes in 1905, and examples were repeatedly met with in which types as far as could be determined, absolutely identical with one another morphologically, differed markedly in rust resistance. Trial sowings in the following season showed that this peculiarity was retained.

Without doubt numerous other similar cases could have been found if all the hybrids then being cultivated could have been examined for these characters. Unfortunately in many cases no notes had been made as to the susceptibility of the parents, and the F. 1 and F. 2 generations had not been kept under special observation.

The attempt to determine whether the inheritance of immunity to the attacks of *Erysiphe graminis* was similar to that of yellow rust was made with both wheat and barley. The case of barley only will be considered here as the F. 2 generation of the wheat hybrid failed to become infected. The parent barleys were *Hordeum spontaneum* (Koch) and *Hordeum hexasticofurcatum* (K. H.). The former is as a rule completely free from mildew, whilst the latter is the most susceptible variety which could be found in a collection containing some 140 varieties. The crosses were, as in the case of most of the wheats, made on the immune parent. The resulting hybrid was attacked by the mildew, to, as far as one can judge such matters, the same extent as the susceptible parent. Its grains were sown in the spring of 1905 and gave a plot containing 79 plants. The Erysiphe did not appear until late in the season, though it was fairly abundant on field plots in the neighbourhood at an early date. The late infection may possibly have been due to the fact that the plants were unusually vigorous owing to their having been planted in garden soil at wide intervals. Fearing failure through lack of opportunity for continuous exposure to infection, artificial inoculation was resorted to. Leaves covered with mildew from a number of varieties were shaken up in water and the whole plot sprayed with it and then shaded for two days. This had the desired result, and a week later the whole plot was thick with mildew. On July 12th a detailed examination of the plot was made. The majority of the plants were very badly attacked, some bore traces of mildew, and a few were altogether immune. Those with traces of mildew and the immune individuals were kept under observation until the plants were beginning to show signs of the foliage drying preliminary to ripening, and at this stage the three types were sorted

out and counted. Fifty-six were badly attacked, 16 bore traces of mildew, and seven were altogether free from it.

At this time the parent *Hordeum spontaneum* was very slightly attacked, though no signs of disease had been seen in the two previous seasons, the severity of the attack corresponding with the traces of mildew found on some of the hybrids. The second parent *H. hexasticofurcatum* was badly diseased and matched the majority of the hybrids in this respect. No further generation of this cross has yet been grown.

The experiments with *Puccinia graminis* have not been altogether successful. The first attempts were made with Rivet wheat and Einkorn, the latter being used as the male parent in order to simplify the operation of crossing. Three strong F. 1 plants were raised in 1904, and as no black rust had appeared on these at the end of June, the plants were inoculated with aecidiospores from the barberry. Ten days after each plant was showing pustules which increased enormously in numbers, and by the time of harvest the straw was blackened with the gaping teleutospore sori. A few shrivelled grains were produced but these all failed to germinate, and in consequence no F. 2 generation was raised. The extreme susceptibility of the hybrid is rather unexpected, for Rivet wheat has not up to the present proved itself unusually so. A second F. 1 generation of this same cross has been raised, and this has entirely escaped infection with black rust, though slightly attacked with the yellow rust.

From analogy with the cases already described and from the susceptibility of the F. 1, it would appear that the susceptibility to black rust is also a dominant character.

From the foregoing series of experiments it is evident that the inheritance of immunity and susceptibility to the attacks of certain parasitic fungi can be traced as readily as that of morphological characters, and that immunity is recessive to susceptibility. Whether this is generally true or applies only to these special cases still has to be determined, but, for the time being, the fact that disease-resistance is recessive may be employed in attempts to cope with the losses due to the attacks of rust in cereals. Wherever these crops are cultivated the rusts take their toll, causing in the aggregate enormous losses. Thus in the rust year, 1891, Prussia alone is stated to have lost some £20,600,000, or approximately two-thirds of the value of the entire cereal crop[1], and according to M'Alpine[2], "at a

[1] *Zeits. für Pflanzenkrankheiten*, 1893, p. 185.

[2] M'Alpine, *Victorian Naturalist*, Vol. XXIII. p. 45.

low estimate it is considered that £100,000,000 does not cover the annual loss (due to rusts) to cultivated cereals alone."

The outcome of the numerous attempts made to minimize these losses is that prophylactic measures are useless, and the one hope left is to grow in each country varieties which prove rust-resistant. It has been known from comparatively early times that some varieties are more resistant than others. Thus Jethro Tull points out that "white cone or bearded wheat...is less subject to blight than Lammas wheat, which ripens a week later." In some countries a careful search has already been made for rust-resistant varieties, but on the whole, with comparatively little success from the economic point of view. This partial failure has not been due so much to the difficulty of finding relatively immune varieties, as to the difficulty of finding immunity in combination with other features essential for the profitable cultivation of the crop. Knight[1] appears to have been one of the first to realise the necessity of the "formation or selection" of resistant varieties, and from time to time the attempt has been made. The researches of the late William Farrer may be quoted as an example[2]. The problem has proved an exceptionally difficult one, and even Farrer's patient work has not met with the success one hoped it would. Now, however, that we are in the possession of the broad outlines of the inheritance of the more important characteristics of wheat, the attempt to combine in one variety such features as quality, proper time of ripening, cropping power and so on, together with immunity to the commoner rusts, may profitably be made. Such attempts will have to be made in each country where wheat is cultivated; for wheats suitable for English conditions will certainly find no favour in Canada or Australia for instance. Under such circumstances it would be useless for a breeder, knowing one set of conditions only, and that one not particularly suitable for experiments of this kind, to attempt to do more than indicate the mode of attack which appears to be most suitable. In the first place, the varieties most suitable for the locality will have to be selected for crossing with any which are found to be more or less rust-resistant. From Eriksson's researches it is clear that some varieties are resistant to one rust but not to others, and where this particular rust happens to be the serious one locally, such a variety may be used for breeding experiments. There is, however, one wheat which is characterised by exceptionally complete immunity to the attacks of the

[1] Knight, *The Pamphleteer*, Vol. VI. p. 402, 1815.

[2] Farrer, *Agric. Gaz. of New South Wales*, Vol. IX. p. 131, 1889.

three common rusts—the yellow, black, and brown, namely, *Triticum monococcum* or Einkorn. This primitive type will in all probability prove in the long run the most valuable source of immunity. There is, however, one drawback to its employment for this purpose, that being its complete lack of all the characteristics which go to the building up of a typical bread wheat. Consequently the breeder has to face a somewhat complex problem, but knowing the characters of each of the varieties used as parents, he can calculate the chances of obtaining the combinations required, and by growing sufficiently large cultures of the generation bred from the hybrid, make certain of their occurrence. From the experiments already described it may be inferred that the immunity is transmitted in all its entirety so that any bread wheat with Einkorn as one parent might then be handed on to the other workers to simplify the problem of raising varieties suitable for other districts.

Summary.

On crossing immune and susceptible varieties the resulting offspring is susceptible.

On self-fertilization these susceptible individuals produce immune and susceptible descendants in the proportion of one of the former to three of the latter. The degree of susceptibility is variable.

Where the degree of susceptibility differs in the two parents the hybrid resembles the more susceptible parent in that respect. Among the descendants of such hybrids the two degrees of susceptibility appear in the usual Mendelian ratio of one slightly to three very susceptible individuals.

The relatively immune forms breed true to this characteristic in the succeeding generations.

Immunity is independent of any discernible morphological character, and it is practicable to breed varieties morphologically similar to one another, but immune or susceptible to the attacks of certain parasitic fungi.