

GENETIC AND CYTOLOGICAL STUDIES IN WHEAT. IV.

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(With One Plate.)

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INTRODUCTION.

THIS paper continues directly a previous one (7) dealing with some genetic aspects of crosses between *T. turgidum* with 14 chromosomes (haploid) and *T. vulgare* with 21. In the latter is given a summary of the more important cytological results found already (5, 6) and a brief account of genetic expectation.

Crosses between species that differ in chromosome number give very complicated results. Disturbing features are introduced by sterility, bad grain germination, and premature death of plants; while generally an F_2 gives no certain ratios and may be impossible to classify for many characters. It is therefore not surprising that studies of such crosses often lack certainty; and that usually the results have to be explained by invoking the action of disturbing features which, however probable they may be on *a priori* grounds, have little direct evidence in their favour. The particular cross we are considering has many valuable features, such as complete fertility of F_1 egg-cells with parental pollen but partially sterile F_1 pollen, and by taking advantage of this we are able to proceed to an exact analysis by making back-crosses. Moreover, not only does back-crossing remove, in many cases, the difficulties of classification that confront us when we examine an F_2 , but it also shows why this difficulty exists and makes clear the relation between types

when this was previously obscure. The main objects of this paper, in conjunction with previous ones, are to illustrate these points and to give a provisional genetical explanation of the principal features. There are still many possibilities not yet properly explored, and features that are not fully understood, but the main outlines are becoming clear. It will be shown, for example, that normal pairing and segregation occurs between homologous *turgidum* and *vulgare* chromosomes, and that a 1 : 1 ratio is therefore found for F_1 egg-cells. The numbers upon which this conclusion is based are small, and further evidence is being obtained; but such behaviour is evidently usual as far as the character studies are concerned, if not universal. The paper further shows the reason for the appearance of some of the new forms that are found in F_2 ; and why these new forms are, perhaps always, associated with either a high or a low chromosome number. Finally a provisional scheme is put forward to explain the effect on these characters of the extra *vulgare* chromosomes, which remain unpaired in the reduction divisions of the F_1 . Some of the results are suggestive in connection with the problem of the evolution of the wheat species, but this question will not be discussed until the genetics of the cross has been studied more critically.

MODES OF INHERITANCE.

As indicated, the method used in studying inheritance in the cross is back-crossing the F_1 to the parents. It was concluded in an earlier paper (6) that all the F_1 egg-cells were fertile with pollen of either parent, and experience gained since then confirms this. Crosses made between pure lines may be slightly more successful, but this is still not proved, and certainly F_1 egg-cell fertility cannot be less than 95 per cent. Occasionally, an F_1 egg-cell crossed with parental pollen gives only a shrivelled grain, but this again does not seem to occur more often than in crosses between pure lines. Finally, we have seen (7) that in the cross $F_1 \text{♀} \times \textit{turgidum} \text{♂}$, grain germination was about 90 per cent.—certainly almost, but perhaps not quite, as high as occurs with grains from fertile pure line crosses. It is therefore certain that in this cross sterility cannot disturb the results to any appreciable extent. On the other hand germination of the grains from $F_1 \text{♀} \times \textit{vulgare} \text{♂}$ was only about 60 per cent., so a comparison between the two crosses should eventually show whether bad germination has a selective action on any of the characters studied.

Of the grains that germinated a few have not given mature plants: in 1925 because three or four plants only had one ear and this was

fixed for a chromosome count; in 1926 owing to injury by wheat bulb fly, *Hylemyia coarctata*.

On account of the disturbance that might be introduced by pollen sterility, the crosses between the parents and the F_1 pollen will not be considered unless to confirm conclusions already reached from the crosses between F_1 ♀ and the parents.

Difficulties may arise if there is no sharp distinction between the heterozygous and the type form. Generally, this difficulty is removed in the next generation; but it must not be forgotten that since this next generation has been raised by self-fertilisation, and under these circumstances the plants are nearly all partially sterile, we introduce here the possibility of disturbance by sterility, and the object of the investigation has been to eliminate as far as possible any uncertainty due to this cause.

In what follows, unless the contrary is stated, F_1 means *vulgare* × *turgidum* F_1 , and the following abbreviations have been adopted:

$$\begin{aligned} T \text{ ♀} \times F_1 \text{ ♂} &= \textit{turgidum} \text{ ♀} \times F_1 \text{ ♂} \\ F_1 \text{ ♀} \times T \text{ ♂} &= F_1 \text{ ♀} \times \textit{turgidum} \text{ ♂} \\ V \text{ ♀} \times F_1 \text{ ♂} &= \textit{vulgare} \text{ ♀} \times F_1 \text{ ♂} \\ F_1 \text{ ♀} \times V \text{ ♂} &= F_1 \text{ ♀} \times \textit{vulgare} \text{ ♂}. \end{aligned}$$

The above crosses will give second generation plants, though obtained by back-crossing the F_1 instead of by self-fertilisation. I have therefore called the following generation F_3 , thus

$$F_3 (T \text{ ♀} \times F_1 \text{ ♂}) = \text{progeny of } T \text{ ♀} \times F_1 \text{ ♂}$$

obtained by self-fertilisation, similarly $F_3 (F_1 \text{ ♀} \times T \text{ ♂})$, etc. All these F_3 families were obtained by bagging the parent plant, so that there was no danger of out-crossing.

Two series of plants were available. The first came from crosses made in 1924, the F_1 plants having been harvested in 1925 and their progeny in 1926. The second came from crosses made in 1925; these plants were harvested in 1926 and their progeny are not yet available; so this series has not yet been of use in all cases owing to the complete or partial dominance of some of the characters studied. For this reason there may appear at first sight to be some discrepancy in the numbers that follow: thus 58 plants have been harvested from the cross $F_1 \text{ ♀} \times T \text{ ♂}$, but some of these were sterile and others have not yet been grown on.

As before, the parents used were *T. turgidum* var. Rivet, *T. vulgare* var. Swedish Iron, and *T. vulgare* var. Yeoman; they have been already described (7). In most cases the two varieties of *vulgare* gave similar

results, and they will here be considered together unless distinction is necessary.

(a) *Keeled and rounded glumes, and the type speltoid.*

In *turgidum* the glume has a strong keel running right down to the base; in *vulgare* there is a slight keel at the top of the glume, but this is absent or only just traceable in the lower half. These differences can be seen to some extent in Plate II and in Plate XXIV of a former paper (7); they will be illustrated in detail elsewhere. Speltoid is a well-marked type (Plate II) that occurs only as a rare mutant from *T. vulgare* (8), where the literature is given) or as a segregate from *turgidum* × *vulgare* and certain other crosses between species of the second (28-chromosome) and third (42-chromosome) wheat groups; it differs from *vulgare* by its tough glumes, which invest the grains closely and make rubbing out a difficult matter, by the well-developed keel to the glume, very lax ear, and some other features that will be mentioned later. It will be shown that these differences are due to a single factor **K**, which gives the keel to *turgidum*; *turgidum* is **KK** and *vulgare* **kk**; **k** transferred to *turgidum* produces a round glumed *turgidum*, as would be expected, but **K** transferred to *vulgare* produces the new type speltoid. At first sight this appears to mean that the effect of **K** in the two species is different: Plate II is sufficient to show, I think, that the relation could not have been predicted by examining the four types—the difference between the first two (28-chromosome-**kk** and 28-chromosome-**KK**) does not appear to be the same as the difference between the last two (42-chromosome-**kk** and 42-chromosome-**KK**). The crosses on which this conclusion is based will be dealt with separately.

$F_1 \text{♀} \times \textit{turgidum} \text{♂}$. Fifty-eight plants from this cross were easily separated into 32 keeled and 26 intermediate. The intermediate plants show some fluctuation, but approach the round glumed type more closely than the keeled type. Of 24 families raised from 27 of these plants, 12 bred true to keeled, and 12 intermediates split up into round, intermediate, and keeled. Confirmation was given by a 28-chromosome plant, fully fertile and with regular chromosome behaviour, raised from the cross $T \text{♀} \times F_1 \text{♂}$, and classed as intermediate for keel; its progeny gave a ratio 45 round and intermediate : 16 keeled. We may definitely conclude that keeled and round differ by a single factor and that segregation in the F_1 is quite normal. *Turgidum* is **KK** and *vulgare* **kk**.

Vulgare × speltoid. The speltoid parent was a true breeding strain extracted from the cross Swedish Iron × Rivet. The F_1 was intermediate,

and F_2 gave 136 *vulgare* : 272 intermediate : 139 speltoid. The heterozygotes showed a wide range of fluctuation, from almost like speltoid to almost like *vulgare*; those that approach speltoid can be distinguished from it by the fact that their glumes can be pulled away from the grains more easily; those that approach *vulgare* can be recognised most easily by the partial development of the collar at the base of the glume, of the keel, and of the secondary nerves. F_3 families raised from 147 F_2 plants showed that in every case the classification had been correctly made.

Vulgare and speltoid therefore differ by a single factor.

Turgidum \times speltoid. A complete F_3 (if we except a few sterile F_2 plants) of 103 families was raised.

All the F_2 and all but two of the F_3 plants were keeled: that is, either keeled *turgidums*, speltoids, or intermediate between speltoid and *turgidum*; there were no round glumed *turgidums* or *vulgare* forms. The two exceptions were heterozygous speltoids—plants that would split into *vulgare*, intermediate and speltoid. The F_2 plants had not been bagged so, as I have shown (6), there is little doubt that these two plants had originated as natural crosses. In the case of one of them this was verified as it was the only beardless plant in a bearded family, and beardless is a dominant character; the other had only one sister plant so natural crossing could not be verified, but I have no doubt that this is the explanation of its origin. It was found impossible to classify this cross for the character speltoid as an apparently continuous series could be traced between this type and the ordinary keeled *turgidum*, as might be expected.

Clearly speltoid is **KK**; but *vulgare* we have seen is **kk** and furthermore differs by only a single factor from speltoid, so evidently it is **K** alone that has changed *vulgare* to speltoid.

$F_1 \text{ } \text{♀} \times \textit{vulgare} \text{ } \text{♂}$. A critical examination of this cross gave rise to difficulties, though the theory I have put forward was actually first suggested to me by a comparison of F_3 ($F_1 \text{ } \text{♀} \times V \text{ } \text{♂}$) with F_3 ($F_1 \text{ } \text{♀} \times T \text{ } \text{♂}$). The simplest expectation is equal numbers of *vulgare* with round glumes, breeding true, and heterozygous speltoids—the latter splitting into *vulgare*, intermediate, and speltoid. It was found that F_2 ($F_1 \text{ } \text{♀} \times V \text{ } \text{♂}$) could not be classified with precision, though heterozygous speltoids can readily be separated from *vulgare* after a little practice. One reason for this difficulty is not far to seek. Although a 42-chromosome-**Kk** plant is a heterozygous speltoid, a 35-chromosome-**Kk** plant is not: it is best described perhaps as intermediate between a heterozygous

speltoid and a heterozygous round glumed *turgidum* (28-chromosome-**Kk**). Similarly **Kk** plants from the cross $F_1 \text{♀} \times V \text{♂}$ will some of them be nearer to the 35-chromosome-**Kk** type than to heterozygous speltoid. And they will sometimes be difficult to classify, partly because they may not show any clear speltoid influence, partly because the glumes of some plants are rather abnormal in type, and partly because they will, like 28- and 35-chromosome-**Kk** plants, approach the round glumed (**kk**) type more nearly than the keeled (**KK**) type. From 19 of these plants 18 families were raised; but these again gave difficulty and must be considered in detail. Nine of the families were splitting up into the expected types—*vulgare*, speltoid, and intermediate. These evidently came from **Kk** plants. Three families were breeding true to round, and so must have come from **kk** plants. The remaining six families consisted of round and slightly keeled plants; only in a few cases did those that were slightly keeled show signs of the character speltoid, and classification was still uncertain. Now it must be realised that both *vulgare* and **kk** *turgidum* have a very slight keel to the glume, and some of these six families might be interpreted as true rounds showing a little more keel than usual; but I doubt if this can be correct, as I could draw no sharp line between families to which this interpretation might justly be applied, and those to which it certainly could not. I am inclined to regard all these six families as descended from **Kk** plants, and shall leave for further investigation why the keel of the glume, and the speltoid characters, were clearly present in so few plants. We then have, if this reasoning is correct, a ratio of 15 **K** : 3 **k** for F_1 egg cells instead of equality; but since only 19 grains germinated, out of 35 sown, a disturbance of the expected ratio is not altogether surprising. There is other evidence that under some circumstances **kk** grains may germinate badly; but this, and the other difficulties given above, are best left for further study. It may be remarked that none of these difficulties occur in the cross $V \text{♀} \times F_1 \text{♂}$, where the plants fall into two classes, viz. those like the F_1 and those like *vulgare*. Most of the latter show high fertility, and out of 14 families raised from them 8 bred true to round and 6 split into round, intermediate and speltoid, classification giving no difficulty. This confirms the impression that in the former cross the difficulties are in some way due either to sterility, or to the fact that the plants to be classified were most of them transition forms between *turgidum* and *vulgare*, not true *vulgares*, but it would be unwise to conclude this definitely, and the whole question is being thoroughly examined.

This section will be concluded by a comparison between the types

under discussion. This is not given in detailed form, as the matter will be dealt with elsewhere in discussing all the principal types of glume and rachis found in the 28- and 42-chromosome wheat species.

When we examine the four types—round glumed *turgidum* (28-chromosome-**kk**), keeled *turgidum* (28-**KK**), *vulgare* (42-**kk**), and speltoid (42-**KK**)—it certainly seems at first that the factor **K** has produced a very different effect in the two species; and I think we can be certain that a simple examination of the types would never suggest that the last two differed by the same factor as the first two. That this should be the case would not be entirely unexpected, but if we examine the four forms critically we find that morphologically a fairly similar change has been effected. The end results—speltoid and **KK** *turgidum*—appear unrelated chiefly because of the morphological differences between the original **kk** forms, and partly perhaps because the effect of **K** in the two species may differ in intensity though not in nature. In both species it gives a laxer ear, and affects the glumes in the following respects: it gives a keel, a collar at the base, greater thickness, a flatter face, increases the development of the secondary nerves, and makes the top or shoulder flatter and more parallel to the base. These changes will be illustrated fully elsewhere, but some of them can be seen in Plate II, and in Plate XXIV, figs. 1 and 5 of an earlier paper (7). Speltoid ears are strikingly lax; but, though density of ear is affected by many different factors, **kk** *turgidums* can generally be picked out with certainty by their greater density, and they are always denser than **KK** *turgidums* in any family that contains both types. In *turgidum*, **K** produces a collar to the base of the glume; in *vulgare* it does the same, but the collar in the speltoid plant is accentuated. The change in the thickness of the glume is particularly interesting. Although the tough glume of speltoid is an entirely new character, the glume of **kk** *turgidum* is remarkably thin and papery—much thinner than that of *vulgare*—so that **K** has brought about the same relative change in each case.

Indeed a close examination of the four types makes the relation between them clear, and makes it possible that **K** has had the same effect in the two species; probably however it produces a relatively greater thickness of glume in *vulgare*, and a more decided laxity of ear.

So far I have found it impossible to classify the *turgidum* × *vulgare* F_2 accurately for the character keeled or rounded glume. In the light of what is now known this is easy to understand and the reasons will be given, since they enable us to see why it is difficult to classify the F_2 for many other characters. The types found in F_2 are as follows:

- (1) round glumed *turgidum*, 28-chromosome-**kk**;
- (2) *vulgare*, 42-chromosome-**kk**;
- (3) plants with an intermediate chromosome number, intermediate in type between 1 and 2;
- (4) heterozygous round glumed *turgidum*, 28-chromosome-**Kk**;
- (5) heterozygous speltoid, 42-chromosome-**Kk**;
- (6) various grades of intermediates between types 4 and 5, with intermediate chromosome number;
- (7) *turgidum*, 28-chromosome-**KK**;
- (8) speltoid, 42-chromosome-**KK**;
- (9) various intermediates between types 7 and 8, with intermediate chromosome number.

We cannot classify the F_2 into the three types **kk**, **Kk**, and **KK**, because of the difficulty that arises in distinguishing type 5, and some plants of type 6, from some of the plants of type 9; and because of a similar difficulty that arises with some of the other types. But if we back-cross the F_1 the situation is immediately simplified. Thus $F_1 \times \textit{turgidum}$ gives almost entirely types 4 and 7, and the few low grade intermediates of types 6 and 9 that also occur do not in practice give any difficulty; on the other hand, in $F_1 \times \textit{vulgare}$, which gives types 2, 3, 5 and 6, some of the intermediate types are not easy to classify.

(b) *Rough and smooth chaff.*

Rivet has rough chaff; Swedish Iron and Yeoman, smooth.

It has often been shown that, in wheat, rough and smooth differ by a single factor, with rough dominant and the expected 3 : 1 ratio in F_2 . It must be mentioned, however, that the Howards(2) have reported the existence of two types of hair on the chaff of some wheats; and have found, in agreement with this, two separate factors for rough chaff. Biffen(1), working with crosses between Rivet and several different varieties of *T. vulgare*, found in F_2 a total ratio of 233 rough : 116 smooth, a rather wide deviation from the expected 3 : 1; but F_3 families all gave close approximations to 3 : 1, the total being 214 : 75. In crosses I have examined I have usually found a segregation close to 3 : 1 (e.g. 607 rough : 197 smooth), but sometimes there has been a suggestion of some irregularity (e.g. 104 rough : 26 smooth). I had expected that we were dealing with a single pair of factors segregating in the usual fashion, and carried by a homologous pair of *turgidum* and *vulgare* chromosomes, but in the course of the work some unexpected facts have come to light. The crosses between $F_1 \text{ } \varphi$ and the parents have shown clearly that half

the egg cells carry **R** (rough) and half **r** (actual numbers 23 : 28), and the same must be true of the F_1 pollen or a 3 : 1 ratio would not occur in F_2 . Yet, when F_1 pollen is used on the *vulgare* parent, although the ratio of **R** : **r** is still 1 : 1 (actually 15 **R** : 18 **r**), it is found that most of the 14-chromosome gametes carry **R** and the 17-21-chromosome gametes carry chiefly **r**. The numbers given below, though not large, show this quite clearly.

	35 and 36-chromosome plants		38-42-chromosome plants	
	Rough	Smooth	Rough	Smooth
No. of plants	5	1*	3	9

* This was the only plant with 36-chromosomes.

Confirmation is obtained from the fact that the plants from the cross, $V \varphi \times F_1 \sigma$, fall into two classes: the first resembling the F_1 , and including all 35-chromosome plants; the second resembling *vulgare* and including all plants with from 38-42-chromosomes(7). Here the numbers available are larger and show that nearly all the plants in the first class have rough chaff while those in the second have smooth.

	Plants like F_1		Plants like <i>vulgare</i>	
	Rough	Smooth	Rough	Smooth
No. of plants	8	1*	7	17

* This was the 36-chromosome plant, which should probably be classed as intermediate between F_1 and *vulgare*.

It would be interesting to know whether a similar association exists when using F_1 pollen on the *turgidum* parent, but the number of plants available from this cross is not yet sufficient.

The striking feature of this case is that in spite of this association between chromosome number and the factor **R**, the existence of a 3 : 1 ratio, and other similar evidence, seems to show that a single pair of factors, carried by homologous *turgidum* and *vulgare* chromosomes, is alone involved. It is not proposed to discuss the question fully until more evidence has been obtained; but it is noteworthy that in species crosses we apparently cannot accept the evidence of a 3 : 1 ratio alone as sufficient to show that a character is being inherited in a simple manner.

(c) *Waxy and waxless foliage, and resistance to Puccinia glumarum.*

The inheritance of these two pairs of characters are in some ways similar, and as it differs in some respects from that of the other characters discussed in this paper the results are included here although not yet fully worked out.

Both parents have the foliage covered with a waxy bloom; indeed this is true of all the cultivated wheats I have seen¹, though Vavilov (3) speaks of waxless varieties. In a Chinese variety of *vulgare* that is grown at Cambridge the wax may appear to be absent in autumn sown material, but traces of it can be observed if the plants are examined carefully; in spring sown material the wax is evident. The amount of wax present is very different in different varieties, and is subject to seasonal fluctuation². In the F_2 from *vulgare* \times *turgidum* waxless plants appear, and have attracted attention from the fact that they are always *turgidum*-like plants. It was found from the back-crosses that half the F_1 egg cells contain the waxy factor **W**, and half the waxless factor **w**. In the cross $F_1 \text{♀} \times T \text{♂}$ all the plants are waxy; 37 of these gave 24 families (some plants were sterile or nearly so) and 2 of these gave too few plants to classify, since waxless is recessive. Of the remaining 22 families 11 bred true to waxy, and 11 split up into waxy and waxless. $F_3 (T \text{♀} \times F_1 \text{♂})$ consisted of 12 families of which 6 bred true to waxy and 6 split into waxy and waxless; and one of these families, which came from a fertile 28-chromosome plant with regular chromosome behaviour, gave a ratio of 48 waxy : 16 waxless. Waxy and waxless therefore differ by a single factor, *turgidum* being **WW** and *vulgare* **ww**. In the cross $F_1 \text{♀} \times V \text{♂}$ all plants are waxy; 21 of these gave 19 families breeding true to waxy. *Vulgare* therefore is waxy because of a factor, or factors, that cannot be separated from the species by crossing. A simple hypothesis to explain the results would be that *vulgare* carried the factor **W** in one of the 7 chromosomes that remain unpaired when this species is crossed with *turgidum*; it will readily be seen that if this were the case all the results given above would follow. The hypothesis is being tested by further breeding.

The inheritance of susceptibility to *Puccinia glumarum* is in some respects similar, and has a special interest from the fact that Vavilov (4) has concluded that resistance to this, and some other fungi, may be taken as a definite indication of the proper genetic relation between the various wheat forms. He concludes that susceptibility to *Puccinia graminis* and to *P. triticea* characterises what are now known as the 42-chromosome wheats (*vulgare*, *compactum*, *Spelta*), except that a few varieties of *T. vulgare* were found to be relatively immune; while the

¹ Since writing the above I have grown at Cambridge a 28-chromosome wheat that appears so far (shortly before flowering) to be quite without wax.

² In view of this fluctuation it should be mentioned that most of the observations recorded here were made in a single season, 1926.

28-chromosome wheats (*dicoccum*, *durum*, *Polonicum*, *turgidum*) were immune, except for some races of *T. dicoccum*. Similarly he found that *T. turgidum* and *durum* were immune to *P. glumarum*. I think it must be granted that this generalisation expresses a good deal of truth, but it may sometimes have led to the belief that the two groups of species are more sharply separated in their reaction to fungi than they really are. At Cambridge it is usually only possible to make observations on resistance to *P. glumarum*; and it is found that excessive susceptibility as well as immunity may occur in varieties of either group.

The extent to which a variety is attacked depends a good deal upon external conditions. In 1926, when the rust epidemic was exceptionally severe at Cambridge, some plots of Rivet, the 28-chromosome parent in the crosses I am describing, were quite badly attacked; while American Club, a variety of the 42-chromosome species *T. compactum*, was free from the disease. Resistance to disease, depending as it does upon the mutual relationship between two distinct organisms, must be expected to be far less easy to define accurately than a character such as chaff colour which depends for its development solely upon the relation of a single organism to the environment in which it develops. My own impression, which may however be based on a too limited experience, is that excessive susceptibility is common among 42-chromosome varieties and rare among 28-chromosome varieties; and that complete, or almost complete, resistance is frequent in the latter group but not in the former. Under normal conditions, varieties of *T. vulgare* fall into a graded series with regard to their power of resistance, ranging from completely resistant to very susceptible. Swedish Iron, though more susceptible than some *vulgare* varieties, has generally been regarded as resistant and may be granted a fairly high place in the series. Rivet, like most other varieties of *turgidum*, is usually considered resistant, though, as we have seen, some plots of it were quite badly attacked in 1926: the small plot grown next to the crosses described in this paper escaped. Both varieties will be called resistant here.

All investigations of the inheritance of resistance to *Puccinia glumarum* have shown simple unifactorial inheritance, with susceptibility dominant. Nevertheless, in the F_2 from Iron \times Rivet, both resistant, we find plants that are very susceptible. Although the severity of the epidemic in 1926 made accurate classification impossible, and no really definite conclusion can be reached, in the back-cross cultures certain features were strikingly displayed. All the cultures from the crosses $F_1 \text{ } \varphi \times T \text{ } \delta$ and $T \text{ } \varphi \times F_1 \text{ } \delta$ appeared to be resistant, and a plant by

plant examination discovered only a few plants that were slightly attacked. The families descended from the cross $F_1 \text{♀} \times V \text{♂}$ were some of them resistant and some splitting for resistance and susceptibility; as far as I could judge 9 were resistant and 10 splitting. A much greater proportion of the families from $V \text{♀} \times F_1 \text{♂}$ appeared to be splitting, the numbers, so far as I could determine, being 19 splitting and 4 resistant; so that the character susceptibility seems to be carried by a greater proportion of pollen grains than of egg-cells: an effect, presumably of pollen sterility, and peculiarly interesting in view of the fact that susceptibility is a characteristic of the species *vulgare*. It is hoped that results obtained in a more favourable season will confirm this conclusion. It will not be possible to explain finally the mechanism of inheritance of this character until conditions of the epidemic allow an accurate classification by single plants instead of an approximate one by cultures, but the results resemble those obtained for waxy and waxless; apparently half the egg-cells carry one factor, and the other half its allelomorph, but the segregation is only made visible when the F_1 is crossed back to *vulgare*, instead of to *turgidum* as in the waxy and waxless case. A somewhat similar explanation might be suggested, and it is hoped to test this by further observations.

In both the cases given here it is interesting to see that we have to deal with a factor which only expresses itself in one of the two species; in one case in *vulgare*, in the other in *turgidum*.

CONCLUSION.

From what has been said it will be appreciated that in crosses like the one under discussion back-crossing readily reveals features of inheritance that would otherwise be hard to discover, and still harder to prove. The method is not an easy one to use in cereals, and only realises its full value if we are able to ensure at least 80 per cent. success, and preferably 90 per cent., in crossing: a condition that leaves us largely at the mercy of the climate. But since it gives greater certainty to our conclusions, and enables us quickly to grasp the reasons for facts that would otherwise remain obscure, it should be adopted wherever possible. An F_2 from *vulgare* \times *turgidum* is practically impossible to classify for the characters keeled, round, and speltoid, and it is doubtful whether the relation between these characters could ever be discovered by such a method of breeding.

We saw that *vulgare* and *turgidum* owe their principal difference in glume shape to a single factor **K**, *turgidum* being **KK** and *vulgare* **kk**.

We now have to consider in what way the extra *vulgare* chromosomes bring about the difference in glume shape between *turgidum* and speltoid, and between round glumed *turgidum* and *vulgare*. In the last paper (7) it was pointed out that the change here produced by the extra chromosomes was similar to that produced by the factor **K** itself; or more definitely, that the change from round glumed *turgidum* to *vulgare* is similar to the change from *vulgare* to speltoid. Elsewhere I shall discuss fully the possibility that this is because the extra chromosomes actually carry a factor **K'**, similar to or identical with **K**. If we accept this the formula for *vulgare* becomes (**kk**) **K'K'** and for *turgidum* (**KK**), where factors enclosed in brackets are carried by homologous *turgidum* and *vulgare* chromosomes and those not enclosed are carried by the extra *vulgare* chromosomes, which remain unpaired. If we now turn to the characters waxy and waxless we find that *turgidum* is (**WW**), and *vulgare* (**ww**); but that all plants with more than 35 chromosomes—obtained from crosses between F_1 and *vulgare* and by subsequent self fertilisation—are waxy. The simplest explanation of this is that the extra chromosomes carry a factor **W'** producing waxy, and which may or may not be identical with **W**. We therefore have for *turgidum* the formula (**WW**), and for *vulgare* (**ww**) **W'W'**. This perhaps explains why the *turgidum* parent, Rivet, was more waxy than the *vulgare* parent Iron.

A similar scheme can be put forward for the inheritance of resistance to *Puccinia glumarum*; though here, for the reasons indicated, we are on less certain ground. Since we find that susceptible forms only occurred in plants derived from crosses between F_1 and *vulgare*, and their progeny, it seems that the extra chromosomes carry a factor **P'** that gives rise to susceptibility. Since the parent *vulgare* was moderately resistant, and differed apparently by a single factor from the moderately resistant Rivet, we may write the latter (**PP**) and the former (**pp**) **P'P'**. It must be assumed that both are slightly susceptible because they have only two factors for susceptibility, and that very susceptible forms only occur among the high chromosome forms with four doses—(**PP**) **P'P'** forms. This view appears to fit the facts without undue straining, but is not entirely satisfactory perhaps, and further tests are being carried out. If we accept it for the present we arrive at the following formulae:

$$\begin{array}{l} \textit{turgidum} = \mathbf{KK} \qquad \mathbf{WW} \qquad \mathbf{PP} \\ \text{and} \quad \textit{vulgare} = (\mathbf{kk}) \mathbf{K'K'} \quad (\mathbf{ww}) \mathbf{W'W'} \quad (\mathbf{pp}) \mathbf{P'P'}, \end{array}$$

where **K** and **K'**, **W** and **W'**, **P** and **P'**, are similar or identical.

These formulae, though provisional only, are suggestive. It is hoped to confirm them, and to extend them to other characters. It will be noticed that the third series of factors from which we must suppose *T. vulgare* to have been built up, since it is a hexaploid species, has not yet been revealed. All we can say is that the corresponding series belonging to *turgidum* is probably closely similar(7).

It has been concluded from the observations recorded in this paper that, in general, random segregation between homologous *turgidum* and *vulgare* chromosomes is the rule; but this statement needs some qualification. If we consider the segregation between **K** and **k** we know that random segregation occurs as far as these factors are concerned; but if **K'**, the factor carried by the extra *vulgare* chromosomes, is actually identical with **K**, we do not know whether segregation in the F_1 occurs between **k** from *vulgare* and **K** from *vulgare*, or between **k** from *vulgare* and **K** from *turgidum*. The question which of these two possibilities actually occurs seems to be of no practical importance: clearly if *turgidum* and *vulgare* introduce to the F_1 almost identical chromosomes, each carrying **K**, it matters little which pairs with the *vulgare* chromosome carrying **k**. It may be stated here, as bearing on the question, that keeled plants (**KK**) extracted from crosses between F_1 and *turgidum* are like the parent *turgidum* apart from differences caused by extra chromosomes, when these are present, or by the usual recombination of factors (such as rough and smooth) not associated with **K**. The observations show, in fact, that very probably pairing occurs between homologous *turgidum* and *vulgare* chromosomes, not between chromosomes derived from the same species; secondly, that if *vulgare* and *turgidum* chromosomes sometimes pair with one another, then the two species must contain two series of chromosomes that are almost identical.

SUMMARY.

The paper continues an investigation into the genetics of a cross between *T. vulgare* with 21 chromosomes (haploid) and *T. turgidum* with 14. By back-crossing the F_1 a complete analysis is made possible since all F_1 egg-cells are fertile, and all grains from the cross $F_1 \text{♀} \times \textit{turgidum} \text{♂}$ germinate.

Except for certain reservations given in the text, the characters studied show that usually, perhaps always, normal pairing and segregation occurs between homologous *turgidum* and *vulgare* chromosomes.

One of the most important specific characters in the genus is the keel of the glume. The difference between the keeled glume of *turgidum* and the round glume of *vulgare* is due to a single factor, **K**, showing normal segregation; *turgidum* being **KK** and *vulgare* **kk**. *Turgidum* forms with a round glume (28-chromosome-**kk**) extracted from the cross have a very dense ear and thin papery glumes. Keeled *vulgare* forms extracted from the cross (42-chromosome-**KK**) have a very lax ear and tough glumes; they are the new type speltoid. This relation between the types *turgidum*, *vulgare*, and speltoid, could not have been predicted by examining the types; it may provide the key to the relation between all the glume types found in the genus, of which a full discussion will be given elsewhere.

Rough (**RR**) and smooth (**rr**) chaff appear to differ by a single factor. Half the F_1 egg-cells carry **R** and half **r**, and approximations to 3 : 1 ratios have been found in F_2 . Apparently **R** is carried by one of the *turgidum* chromosomes that pairs with a *vulgare* chromosome carrying **r**. Yet 14 chromosome pollen usually, or always, carries **R**, and 17-21 chromosome pollen chiefly **r**. This is being further investigated.

Waxy and waxless differ by a single factor showing normal segregation in the F_1 . Waxless appears only in plants with less than 35 chromosomes—*turgidum*-like plants.

Both parents are fairly resistant to *Puccinia glumarum*, but susceptible forms are found in F_2 . This is probably due to a single factor, derived from *turgidum* and showing normal segregation in F_1 ; but the factor only expresses itself in plants with more than 35 chromosomes—*vulgare*-like plants, all plants with less than 35 chromosomes probably being resistant.

Consideration of the effect of the extra *vulgare* chromosomes on the characters keeled and round, waxy and waxless, resistance and susceptibility to *Puccinia glumarum*, has given rise to the following provisional factorial scheme to express the composition of the parent species:

$$\begin{array}{lll} \textit{turgidum} & = & (\mathbf{KK}) \quad (\mathbf{WW}) \quad (\mathbf{PP}) \\ \textit{vulgare} & = & (\mathbf{kk}) \mathbf{K}'\mathbf{K}' \quad (\mathbf{ww}) \mathbf{W}'\mathbf{W}' \quad (\mathbf{pp}) \mathbf{P}'\mathbf{P}' \end{array}$$

where factors enclosed in brackets are carried by homologous *turgidum* and *vulgare* chromosomes, and those not enclosed are carried by the extra *vulgare* chromosomes; and the factors **K** and **K'**, **W** and **W'**, **P** and **P'** are similar if not identical.

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EXPLANATION OF PLATE II.

- Ears of: *a*, Round glumed *turgidum* = 28-chromosome-**kk**. Extracted type.
b, Keeled *turgidum*, parent variety = 28-chromosome-**KK**.
c, Round *vulgare*, parent variety = 42-chromosome-**kk**.
d, Keeled *vulgare*, the type speltoid = 42-chromosome-**KK**. Extracted type.
- All $\times \frac{5}{6}$.

